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COSMOCHILUS CARDINALIS, A NEW CYPRINID FISH FROM
THE LANCANG-JIANG OR MEKONG RIVER IN
YUNNAN PROVINCE, CHINA

By

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ABSTRACT: *Cosmochilus cardinalis* is a large, deep-bodied cyprinid fish recently discovered in southern Yunnan Province in the mainstream of the Lancang-jiang or Mekong River. It is distinguished from all other cyprinids in China and Southeast Asia in having all of its fins bright red; it is further distinguished from the two previously known species of *Cosmochilus* by having longer barbels, reduced labial papillae, a concave nape, more numerous scales (also more numerous vertebrae?) and nine instead of eight branched dorsal fin rays.

INTRODUCTION

In the present paper we describe a distinctive new species of large cyprinid fish from the Mekong River or Lancang-jiang of China. The type-specimens were collected during an ongoing, long-term ichthyological survey of Yunnan Province undertaken by the Kunming Institute of Zoology of Academia Sinica.

The Lancang-jiang or Mekong is the largest river in Southeast Asia and probably has the richest ichthyofauna of any river in Asia. It is some 4300 km long and arises at an elevation of 5090 m below an enormous glacier on the northern slopes of the Dza-Nag-Lung-Mung or Tanglha Range of the Tibetan highlands of China's Tsinghai Province. In Tibet it is known as the Lan-

cang-jiang or Dza Chu. It leaves Tibet and enters Yunnan Province at an elevation of about 2800 m, assuming a generally southerly course of nearly 900 km through mountainous and hilly country of Yunnan. In its upper reaches in Tibet and Yunnan it flows through canyonlike gorges between and parallel to the Salween and Yangtze. In lower Yunnan, where the new species of cyprinid was collected, the elevation is only about 500 m. Here the river has a relatively gentle gradient and moderate current and is about 150 m wide during the dry season. The bottom is rocky in places but predominantly muddy. The local fishermen know the new species as bia liang or hong chi ("red-finned fish"). We have identified it as an undescribed *Cosmochilus*.

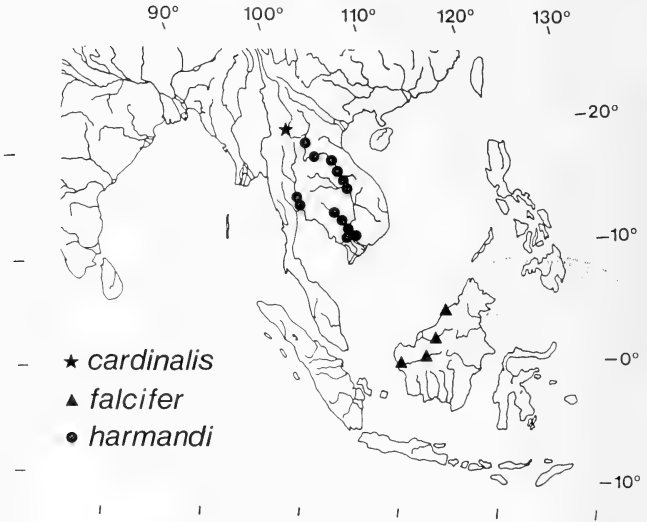


FIGURE 1. Geographical distribution of the species of *Cosmochilus*

***Cosmochilus* Sauvage, 1878**

Cosmochilus SAUVAGE, 1878:240 (type-species *Cosmochilus harmandi* SAUVAGE, by monotypy).

DIAGNOSIS.—Large, deep-bodied and laterally compressed labeoine cyprinids; dorsal fin large and falcate, with 4 simple and 8–9 branched rays; last simple dorsal fin ray greatly enlarged, its posterior border more or less strongly serrated for its entire length; anal fin relatively small, with 3 simple and 5–6 branched rays; head relatively small, compressed; snout truncate, without enlarged tubercles or pores; mouth small and inferior, its opening transverse; rostral and maxillary barbels large and relatively elongate; lips moderately thick, entirely covered with large, contiguous papillae; horny jaw sheaths transverse, moderately thick but with relatively weak cutting edge; gill rakers fleshy, relatively unспе-

cialized, 15–18 on first gill arch; pharyngeal teeth triserial, morphologically generalized for Cyprinidae, usually 1,3,5/5,3,1 or 2,3,5/5,3,2; lateral line almost perfectly straight; each lateral line tubule with a short ventroposterior branch terminating in a small pore on exposed portion of posterior shield; scales in lateral line series 35–48; circumpeduncular scales 16–18; scales oblong, with relatively huge posterior shields; radii of posterior shield strongly convergent; radii of anterior shield frequently conjoined or bifurcate; vertebrae 35–43.

In addition to *C. harmandi* from the Chao Phrya and Mekong rivers, the genus includes *C. falcifer* Regan, 1906 from the Baram and Rejang rivers in Sarawak and Kapuas in Kalimantan Barat (western Borneo). The distribution of the species is shown in Figure 1. *Cosmochilus harmandi* is known to undertake lengthy spawning

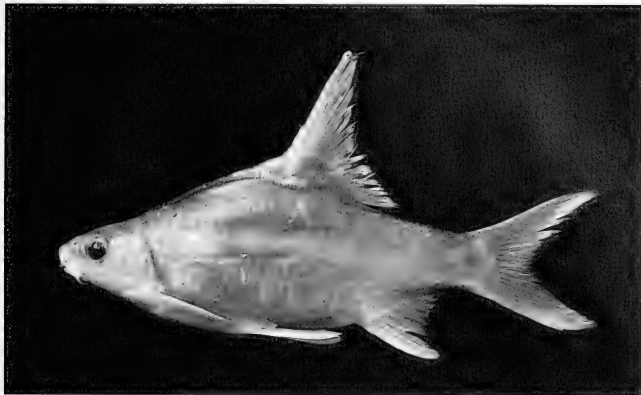


FIGURE 2. *Cosmochilus cardinalis*, holotype (KIZ 735113, 177 mm).

migrations. This is suspected in *C. falcifer*, and thus may also be characteristic of *C. cardinalis*. Mekong localities for *C. harmandi* are from Rainboth et al. 1976.

Cosmochilus cardinalis new species

(Figures 2–5)

HOLOTYPE.—KIZ (Kunming Institute of Zoology) 735113, 177 mm (standard length), mainstream of Lancang-jiang near Jinghong, southern Yunnan Province, lat. 21°50'N, long. 100°55'E, gill net, May 1973.

PARATYPES.—KIZ 734079–80, 734082, 735107, 735109–112, 735025, 735030, 735075, 735160, 12: 165–326 mm, same locality and collecting method as holotype, April–May 1973.¹

DIAGNOSIS.—A large, deep-bodied, and laterally compressed *Cosmochilus*, attaining at least 400 mm standard length. Rostral and maxillary barbels relatively long and thick, dorsal fin high with a falcate margin and elevated base; dorsal fin rays iv9–1/2, last simple ray an elongate stiff spine strongly serrate posteriorly; anal fin rays iii6–1/2. It differs from all or almost all other cyprinids in China and Southeast Asia in having all of the fins including the pectoral and pelvic

and both caudal lobes entirely bright cardinal red in life. Body dusky dorsally, silvery or whitish on sides and abdomen. Opercle golden. Scales in lateral series 46–48, between dorsal fin and lateral line 9–10, between lateral line and pelvic fin origin 5, circumpeduncular 16–18. Vertebrae 24 + 19 = 43 (holotype).

Head relatively small and laterally compressed, its length 4.0–4.5; dorsal profile of head to nape moderately sloped, then abruptly steeper at nape until dorsal fin origin. Snout 2.7–3.2 in head, eye 4.1–5.3 in head, interorbital width 2.4–2.7 in head. Eye with a narrow gelatinous rim or hyaline eyelid. Barbels thick and relatively long; anterior or rostral barbel extending posteriorly almost to below posterior border of eye, its length 1.8–2.2 in head; posterior or maxillary barbel somewhat longer, extending posteriorly almost to pectoral fin, its length 1.4–1.7 in head. Mouth subinferior and moderately wide, extending posteriorly to directly below anterior margin of eye or slightly farther. Rostral cap well developed with deeply incised rostral groove complete between rostral barbels of either side. Sublacrimar groove also well developed and deeply incised, extending from rostral barbel to posterior end of jaws. Lips moderately well developed; upper lip

¹ KIZ 735111, 251 mm, has been transferred to the Ichthyology Department collection of the California Academy of Sciences and is now CAS 55592.

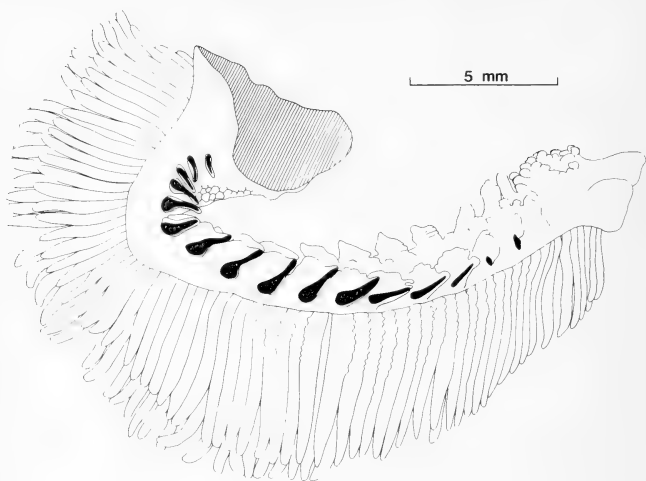


FIGURE 3. *Cosmochilus cardinalis*, holotype. First gill arch (lateral view; bony supports of gill rakers in black).

well defined, entirely separate from rostral cap and upper horny jaw sheath; lower lip with oral margin separated from horny jaw sheath only by a shallow groove, and with posterior margin well defined laterally but entirely interrupted for transverse portion of lower jaw; upper and lower horny jaw sheaths well developed, with a broadly rounded surface and very weakly developed transverse grooves or sulci. Anterior margin of lower jaw truncate.

Rostral cap and horny jaw sheaths relatively smooth; lips and oral epithelium (including gular flap) covered with large, close-set or contiguous but low-lying papillae (probably unculiferous) comparable in distribution and basic morphology to the greatly enlarged and elevated contiguous papillae characteristic of the other two species of *Cosmochilus*.

Gill openings relatively broad, isthmus narrow; upper portion of gill cover with posterior margin very slightly concave. First gill arch (Fig. 3) with $5 + 11$ or $12 = 16$ or 17 gill rakers on

anterolateral margin and $0 + 11$ gill rakers on posterodorsal margin in holotype; paratypes with $17-19$ anterolateral gill rakers on first gill arch. Gill rakers all relatively short and fleshy, those on lower limb of gill arches more or less triangular in shape with broad bases; posterior gill rakers similar in shape to anterior rakers but relatively somewhat larger. Pharyngeal bones (Fig. 4) strongly arched; dorsal edentulous limb and dorsal half of toothbearing portion thick and evenly curved; external ala moderately broad; edentulous lower limb and ventral half of toothbearing portion below external ala with concave lateral margin. Entire medial surface of lower limbs of either pharyngeal bone forming a broad symphysis. Pharyngeal teeth basically uncinata, $2,3,5/4,3,2$ in holotype, those of principal row compressed.

Scales (Fig. 5) large, slightly longer than high, and relatively numerous. Anterior margin relatively straight but with a well defined convex median projection; posterior margin broadly



FIGURE 4. *Cosmochilus cardinalis*, holotype. Pharyngeal jaws (dorsal view).

rounded; radii most numerous and longest on posterior field, least numerous and shortest on lateral fields; radii near central portion of posterior field strongly convergent. Lateral line complete and nearly straight. Scales of lateral line with straight primary tubules and a single small pore arising from a short ventroposteriorly directed secondary tubule originating from anterior half of primary tubule. Scales in lateral line series 46–48, 9–10 above and 5 below lateral line; predorsal scales 24–26, circumpeduncular 16–18. Two or three scale rows extend on caudal fin base posterior to last pored scale of lateral line series. Scales between vent and anal fin origin 2. Circumferential scales 35–37 (18–20 dorsal + 2 lateral line + 15 ventral).

Dorsal fin origin near middle of body, somewhat closer to snout tip than to caudal fin base. Anal fin origin distinctly posterior to vertical through base of last dorsal fin ray. Pelvic fin or-

igin well in advance of vertical through dorsal fin origin. Base of dorsal fin with well developed, strongly convex scale sheath comprising three somewhat irregular rows of large scales (of which the middle row is somewhat smaller); anal fin scale sheath only slightly convex, with one or two rows of scales. Pelvic fin with two moderately elongate axillary scales. Dorsal fin spine length 3.0–3.7, with 20 serrae in holotype. Anal fin much smaller than dorsal fin, with last simple and first two branched rays slightly prolonged to form a lobe. Pectoral and pelvic fins almost equal in shape and size, pectoral fin extending posteriorly almost to pelvic fin origin and pelvic fin reaching or almost reaching vent; pectoral fin length 3.8–4.3, pelvic 4.0–4.3. Pectoral fin rays usually 15, pelvic 9. Caudal fin deeply forked, upper and lower lobes nearly equal in length and shape, with slightly pointed tips.

Abdomen anterior to and between pelvic fins



FIGURE 5. *Cosmochilus cardinalis*, holotype. Scales. Below, 30th scale in lateral line scale series. Above, scale two scale rows about 30th scale in lateral line scale series. Dashed lines indicate areas of overlap by scales neighboring exposed portion of posterior shield.

somewhat flattened from side to side; abdomen posterior to pelvic fins rounded or very slightly (almost imperceptibly) carinate. Body depth 2.4. Caudal peduncle laterally compressed and moderately deep, its length 6.1–7.9 and depth 6.4–

7.2. Dorsal surface of head and lateral surface of lacrimal region more or less uniformly covered with fine, widely spaced granular tubercles; stronger tuberculation or tubercles on fins not observed in specimens of either sex. Swim bladder with two chambers. Intestine about three times as long as body.

COMPARISON WITH OTHER SPECIES OF *COSMOCHILUS*.—The basically similar morphology of the scales, scaly fin sheaths, fleshy gill rakers, pharyngeal teeth, and papillose lips of *C. cardinalis*, *C. harmandi*, and, so far as known, *C. falcifer*, leads us to conclude that the three are correctly placed together within *Cosmochilus*.

Our new species differs from *C. harmandi* and *C. falcifer* in having more numerous scales (44–48 vs. 36–39 in lateral series), three instead of two scale rows in scaly sheath on dorsal fin base, 9 instead of 8 branched dorsal fin rays, dorsal profile strongly concave at nape (vs. relatively evenly sloped), more elongate barbels, labial papillae much reduced in size, and all fins bright red. It additionally differs from *C. harmandi* in having 6 instead of 5 branched anal fin rays, a less pointed snout viewed from above or from the side, and 43 instead of only 35 vertebrae (number of vertebrae unknown in *C. falcifer*). *Cosmochilus cardinalis* also differs from *C. falcifer* in having the fourth simple dorsal fin ray relatively less elongate, very straight, and with large, strong serrae on its posterior margin. In *C. falcifer* this ray is exceptionally elongate (sometimes extending posteriorly to caudal fin base when adpressed), very strongly curved, and with very weak serrae on its posterior margin.

Life color of *C. harmandi* is recorded as back rich pale blue, dorsal and caudal fins black-edged; in some specimens anal fin with black tip (Smith 1945:132). We note that the dorsal fin may also be black-tipped. Life color of *C. falcifer* has not been reported previously. A fresh 316-mm specimen caught in the Kapuas and photographed in the market at Sintang by the junior author had overall color white or milk white, especially ventrolaterally and ventrally; dorsolaterally and dorsally distinctly brownish or violaceous brown; posterior margins of scales, especially on upper parts of body, with broad dark margins; dorsal surface of head faintly yellowish and entire gill cover distinctly yellow; iris and ventral portion of head milk white; entire dorsal fin rosy pink or faintly orangish except black at tip; pectoral fin

white, pelvic white or pinkish; anal and caudal fins dusky, caudal very dark, its posterior margin almost black.

In conclusion, *C. harmandi* and *C. falcifer* seem to be much more similar to each other than either of them is to *C. cardinalis*.

RELATIONSHIPS OF *COSMOCHILUS*

Sauvage (1878:240) stated that *Cosmochilus* is related to *Labeo* but did not discuss this assessment. The pattern of strongly convergent radii on the posterior shield and conjoined or bifurcating radii on the anterior shield of the scales of *Cosmochilus* is seen in relatively few Chinese cyprinids (Chu 1935). Those in which this pattern is most clearly present are species of *Osteochilus*, *Sinilabeo*, and *Garra* (Chu 1935, pls. 15–16). These genera are referable to the cyprinid subfamily Labeoinae. We have observed scales with a similar pattern of radii in various non-Chinese Labeoinae including *Morulus chrysophekadion* and various African and Asian species currently assigned to *Labeo*, but not in genera belonging to other subfamilies. This suggests that *Cosmochilus* might indeed belong in Labeoinae. On the other hand, the general morphology of *Cosmochilus*, including the relatively simple mouth parts; deep, laterally compressed body;

and elongate, serrate dorsal fin spine suggest relationship to a group of Southeast Asian barbels including *Cyclocheilichthys*. A serrate dorsal fin spine is unknown in the Labeoinae.

ACKNOWLEDGMENTS

We wish to express our gratitude to Walter J. Rainboth, who first noted the similarity of the new species to *Cosmochilus*, Susan Middleton for photographing the holotype, George Zorzi and David Catania for preparation of radiographs, and Reeve M. Bailey and Douglas W. Nelson for loaning specimens of *C. harmandi*. The manuscript was typed by Francis Bertetta.

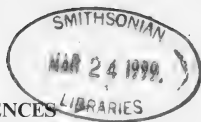
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TWO NEW GENERA AND TWO NEW SPECIES OF DEEPWATER
WESTERN ATLANTIC WORM EELS
(PISCES: OPHICHTHIDAE)

By

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ABSTRACT: Two new genera and two new species of Atlantic worm eels, family Ophichthidae, subfamily Myrophinae, tribe Myrophini, are described and illustrated. *Mixomyrophis pusillipinna*, gen. nov., sp. nov., trawled from deepwater off the Lesser Antilles, is an elongate species with uniserial conical teeth, a labial posterior nostril, a minute pectoral fin, and 178 vertebrae. *Asarcenchelys longimanus*, gen. nov., sp. nov., collected off Belém Brazil, is an elongate species with biserial conical teeth, a labial posterior nostril, well-developed pectoral fins, and 149 vertebrae. Osteological characteristics of the new genera are described from radiographs and compared with those of related myrophines.

INTRODUCTION

The ophichthid worm eels of the subfamily Myrophinae (sensu McCosker 1977) occupy a variety of sand and mud habitats as well as the midwater environment, ranging from the shallow intertidal to depths of 400 fathoms or more. The shallow-water species of the genera *Myrophis*, *Muraenichthys*, and *Ahlia* are common in collections and are probably abundant within their milieu. The deeper water species are rare, being difficult to trawl or dredge, and are often known from but a single specimen.

While preparing the ophichthid eel section of The Fishes of the Western North Atlantic (FWNA), the late James E. Böhlke discovered a single specimen of a new species of myrophine collected by trawl off Anguilla, Lesser Antilles. In taking over the completion of the FWNA project, I discovered another new species of deep-water myrophine, from Brazil, which is also generically distinct. I intend to make these

taxonomic names available for the FWNA volume and to describe the significant osteological characters that are visible by radiographic examination. It is my hope that subsequent specimens will be discovered, which will allow a more thorough osteological examination and comparison with other myrophine genera.

MATERIALS AND METHODS

Measurements are straight-line, made either with a 300-mm ruler with 0.5-mm gradations (for total length, trunk length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length was measured from the snout tip to the posterodorsal margin of the gill opening; trunk length was taken from the end of the head to mid-anus; maximum body depth did not include the median fins. Vertebral counts (which included the hypural) were

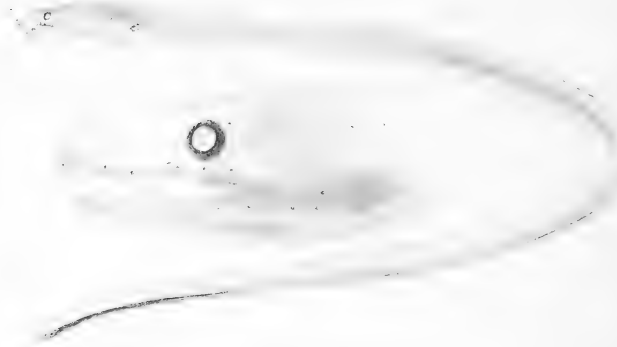


FIGURE 1. Holotype of *Mixomyrophis pusillipinna* McCosker, sp. nov., ANSP 152305, 407 mm TL. Inset: Head of holotype of *Mixomyrophis pusillipinna* McCosker, sp. nov.

taken from radiographs. Stained and cleared gill arches were prepared using the Taylor (1967) trypsin technique. Institutional abbreviations of material examined are explained in the acknowledgments section of this paper.

Mixomyrophis McCosker, gen. nov.

TYPE SPECIES.—*Mixomyrophis pusillipinna* McCosker, sp. nov.

DIAGNOSIS.—An elongate myrophine, tribe Myrophini, with tail longer than head and trunk, laterally compressed, particularly posteriorly; snout subconical, broad from above, not grooved ventrally; anterior nostril tubular, posterior nostril on outer edge of lip and covered by a flap; dorsal fin origin in mid-trunk; pectoral fin a minute flap in posterodorsal corner of upper gill opening; eye large, behind middle of jaw; third preopercular pore present; head and lips smooth, without cirri or lappets; teeth of jaws and vomer small, conical, uniserial, and close set, with slightly retrorse tips; gill arches well developed for a myrophine, first basibranchial ossified, upper pharyngeal toothplates fused; neurocranium stout, slightly sloping posteriorly; suspensorium anteriorly inclined; pterygoid stout, not bracing maxilla; maxillae elongate, tapering posteriorly; opercular series apparently moderately developed; pectoral girdle reduced to a slender clei-

thrum and supracleithrum; epipleural ribs on all precaudal vertebrae; caudal transverse processes apparently absent; caudal vertebrae more numerous than precaudal. Other characteristics those of single species.

ETYMOLOGY.—From the Greek *μῆξις*, *mixis*, a mixing, and *Myrophis* (masculine), a genus of ophichthid eel. Named in reference to the combination of myrophine characters that this eel possesses.

Mixomyrophis pusillipinna McCosker, sp. nov. (Figures 1, 2, 6b)

HOLOTYPE.—ANSP 152305 (originally UMM 30290), 407 mm, a female with ripening ovaries, captured off Anguilla, Lesser Antilles (18°26.4'N, 63°12.6'W to 18°28'N, 63°11.1'W), by 10-m otter trawl, between 393–451 m depth, by the RV Pillsbury, sta. 984, on 22 July 1969.

COUNTS AND MEASUREMENTS (IN MM).—Total length 407; head length 36.5; trunk length 115.5; tail length 255; body depth at gill openings 9.0; body width at gill openings 7.1; body depth at anus 8.8; body width at anus 6.0; gill opening 1.5; snout tip to origin of dorsal fin 94; left pectoral fin length 1.0; snout length 7.9; upper jaw length 12.1; eye diameter 2.9; fleshy interorbital distance 4.2 Total vertebrae 178; predorsal vertebrae 33; preanal vertebrae 57.

DESCRIPTION.—Body elongate, its depth 45 in total length (TL), laterally compressed in tail region. Head and trunk 2.7 and head 11.2 in TL.

Snout subconical, broad as seen from above; lower jaw included, its tip reaches the anterior

nostril bases. Anterior nostrils tubular, directed ventrally, their anterior edge looped upward; posterior nostril at outer edge of lip, covered by a flap.

Eye large, its anterior edge behind midpoint of upper jaw.

Gill opening mid-lateral, a constricted opening.

Median fins low, lying partially within a groove, but elevated above last 20 vertebrae, meeting each other and extending beyond caudal tip. Dorsal fin arises above posterior trunk region. Pectoral fin minute.

Head pores developed. Single temporal and interorbital pores. Six pores along left mandible; 5 along right. Two pores between anterior and posterior nostrils. Four supraorbital pores. Three preopercular pores. Left lateral line pores ca. 149; 9 above branchial basket; 57 before anus.

Teeth small, conical, nearly uniform in size. An intermaxillary chevron of 8 teeth, followed by 2 on each side, closely adjoining ca. 20 uniserial vomerine teeth and 25 maxillary teeth. Approximately 30 uniserial mandibular teeth, with a secondary pair at symphysis.

Gill arches removed, stained and cleared. Basibranchial 1 ossified, basibranchials 2–4 absent. Hypobranchials 1 and 2 ossified; hypobranchial 3 cartilaginous. Ceratobranchials 1–4 ossified; ceratobranchial 5 absent. Infrapharyngobranchials 2 and 3 ossified.

Lower tooth plate small, with 2 rows of conical teeth, medial row largest. Upper pharyngeal tooth plate fused, subrectangular, with 4–5 rows of conical teeth, medial row largest.

Body color in isopropyl alcohol yellow on head, chin, tail, and dorsal surface of trunk. Throat and belly whitish. Finely peppered throughout body and tail with small brown specks. Peritoneum black.

ETYMOLOGY.—From the Latin *pusillus*, puny or insignificant, and *pinna*, fin, to be treated as a noun in apposition.

REMARKS.—*Mixomyrophis* is separable from all other myrophines by the combination of its minute pectoral fin, elongate body, and posterior nostril located within the outer lip. *Mixomyrophis* appears most similar to the elongate species of *Pseudomyrophis*, which differ by having the posterior nostril before the eye, more extreme body elongation, a reduced and rounded neurocranium (cf. Fig. 6b and 6d), and reduced gill

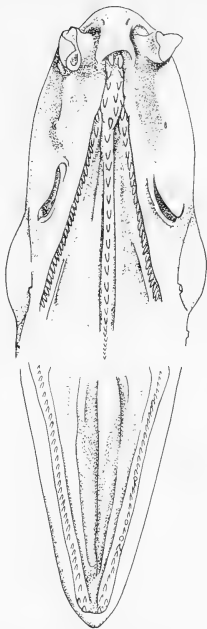


FIGURE 2. Dentition of holotype of *Mixomyrophis pusillipinna* McCosker, sp. nov., ANSP 152305.

arch components (Böhlke 1960; McCosker 1977). The nostril condition of *Pseudomyrophis* appears to be a slight posterodorsal translocation of the opening from its location along the lip (although it is difficult to interpret which state might be the primitive condition), and the other characters seem to be advanced specializations. The nearly bulbous snout, large eye, and body elongation of *Mixomyrophis* are conditions shared by other deepwater myrophines such as the species of *Pseudomyrophis*, *Neenchelys*, *Asarcenchelys longimanus*, and *Muraenichthys puhioilo* McCosker (1979).



FIGURE 3. Reconstructed appearance of holotype of *Asarcenchelys longimanus* McCosker, sp. nov., MNHN 1968-215, 277 mm TL. The actual specimen is intact, but badly torn in the anterior trunk region.

Asarcenchelys McCosker, gen. nov.

TYPE SPECIES.—*Asarcenchelys longimanus* McCosker, sp. nov.

DIAGNOSIS.—A very elongate myrophine, tribe Myrophini, with tail longer than head and trunk, laterally compressed throughout trunk and tail; snout subconical, tumid, not grooved ventrally; anterior nostril tubular; posterior nostril on outer edge of lip and covered by a flap that is incised posteriorly; dorsal fin origin in anterior trunk region; anal fin elevated; pectoral fin lanceolate, well developed, slightly longer than snout; eye large, behind middle of jaw; third preopercular pore present; head and lips smooth, without cirri or lappets; teeth of jaws and vomer large, not close set, conical and slightly recurved; teeth biserial anteriorly in jaws and vomer, outer row smaller; gill arches appear to be well developed for a myrophin; neurocranium stout, truncate posteriorly; supraoccipital crest developed; suspensorium posteriorly inclined; maxillae taper posteriorly; pectoral girdle reduced to stout

cleithrum and thin supracleithrum; epipleural ribs present only on anterior trunk vertebrae; caudal temporal processes apparently absent; caudal vertebrae more numerous than precaudal. Other characteristics those of single species.

ETYMOLOGY.—From the Greek *ασαρκος*, *asarkos*, lean, and *ενχελος*, *enchelys*, eel (treated as feminine according to Opinion 915 of the Bulletin of Zoological Nomenclature, 1970), in reference to its emaciated appearance.

Asarcenchelys longimanus McCosker, sp. nov.

(Figures 3–5, 6c)

HOLOTYPE.—MNHN 1968-215, 277 mm, sex undetermined, captured near Belém, Brazil, at 55 m depth by P. Fourmanoir, September 1966.

PARATYPE.—MNHN B. 2994, 147 mm, sex undetermined, collected with the holotype.

COUNTS AND MEASUREMENTS (IN MM).—Data for the paratype parenthetically follow those of the holotype. Total length 277 (147); head length 27 (18); trunk length 78 (46); tail length 172 (83); body depth behind gill openings 3.8 (~2); body width behind gill openings 3.6 (1.4); body depth at anus ~1.5 (~2);

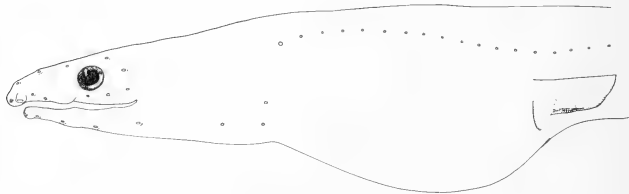


FIGURE 4. Head of holotype of *Asarcenchelys longimanus* McCosker, sp. nov., MNHN 1968-215.

body width at anus 1.5 (1.2); gill opening 1.4 (0.9); snout tip to dorsal fin origin 55 (34); left pectoral fin length 4.0 (3.3); snout length 3.8 (3.7); upper jaw length 6.6 (5.8); eye diameter 1.4 (1.3); fleshy interorbital distance 1.6 (1.3). Total vertebrae 148 (131, tail incomplete); predorsal vertebrae 27 (27); preanal vertebrae 53 (55).

DESCRIPTION.—Body very elongate, its depth 72.9–73.5 in TL, laterally compressed behind head. Head and trunk 2.3–2.6, and head 8.2–10.3 in TL.

Snout subconical, bulbous; lower jaw included, its tip reaches to front of anterior nostril bases, leaving several intermaxillary teeth exposed. Anterior nostrils tubular, directed ventrally; posterior nostril at outer edge of lip, covered by a flap whose posterior edge is incised.

Eye large, anterior edge of orbit above middle of upper jaw.

Gill openings mid-lateral, not as constricted as those of most myrophines, about equal in length to isthmus.

Dorsal fin low, arising in anterior trunk region. Anal fin elevated. Median fins expanded in posterior tail region, extended beyond caudal tip. Pectoral fin lanceolate, broad based, well developed for a myrophine.

Head pores developed, much more apparent than those of lateral line. Single temporal and interorbital pores. Five pores along mandible, widely spaced posteriorly. Two pores between anterior and posterior nostrils. Four supraorbital pores. Three preopercular pores. Lateral line pores difficult to discern; 14 above branchial basket.

Teeth conical, fairly large for a myrophine, not close set, nearly uniform in size, recurved. An intermaxillary chevron of 6 teeth, visible when mouth is closed, followed by closely abutting vomerine dentition consisting of 3–4 pairs of teeth and a uniserial row of 13 teeth. Maxillary teeth biserial anteriorly, with an inner row of 6 teeth and an outer row of 22–24 smaller teeth. Lower jaw biserial anteriorly, with an inner row of 5 teeth and an outer row of 23–25 smaller teeth.

Gill arches, as viewed from radiograph, appear to be myrophin-like and not reduced. First basibranchial is ossified, others appear to be cartilaginous or absent. Hypobranchials 1 and 2 ossified; hypobranchial 3 appears cartilaginous or absent. Ceratobranchials 1–4 ossified; ceratobranchial 5 not apparent.

Upper and lower tooth plates appear to have 2–3 rows of conical teeth; upper plate appears to be fused.

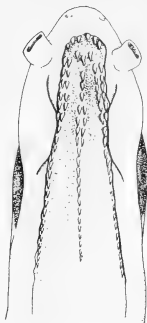


FIGURE 5. Dentition of holotype of *Asarcenchelys longimanus* McCosker, sp. nov., MNHN 1968-215.

Body coloration in isopropyl alcohol cream to white, numerous fine, chocolate-brown spots overlying snout, dorsal surface, and area behind eye. All fins transparent. Peritoneum light colored.

ETYMOLOGY.—From the Latin *longus*, long, and *manus*, hand, to be treated as a noun in apposition. Named with reference to the elongate pectoral fins.

REMARKS.—This new myrophine is separable from all related ophichthids by a combination of internal and external morphological charac-

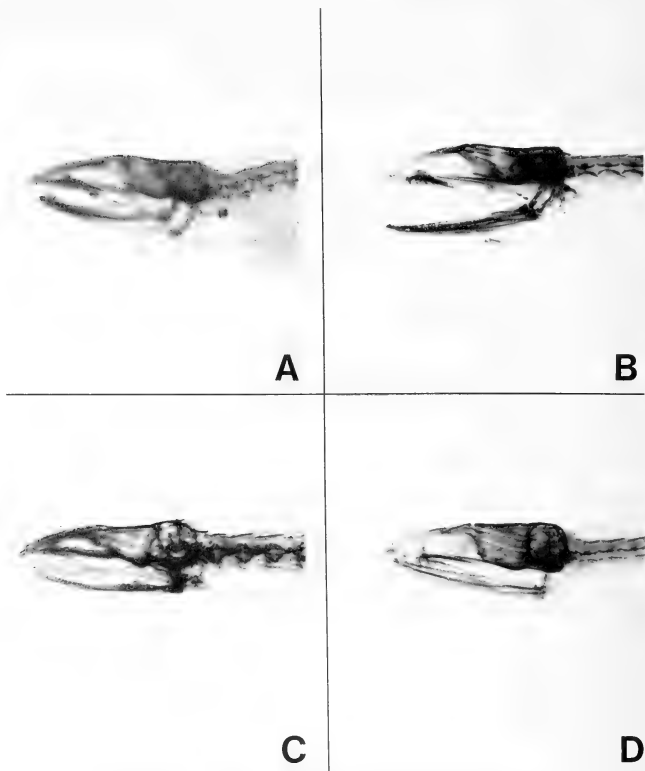


FIGURE 6. Enlarged radiographs of neurocrania of selected myrophins: A) *Myrophis vafer*, CAS 17823, 220 mm TL. B) *Mixomyrophis pusillipinna*, ANSP 152305, 407 mm TL. Gill arches have been removed. C) *Asarcenchelys longimanus*, MNHN 1968-215, 277 mm TL. D) *Pseudomyrophis micropinna*, CAS 50978, 109 mm TL.

ters. Particularly significant are its well-developed pectoral fins, posterior nostril located on the edge of the lip, elongate body and tail, and elongate dentition. The body elongation, anal fin

development, nostril location, and snout shape are not unlike those of certain species of *Neenchelys* and *Pseudomyrophis* (cf. McCosker 1982; Smith and Böhlke 1983), and are probably

adaptive for living in deepwater soft benthic habitats. Its close affinities, however, lie with the species of *Myrophis*, which share with it the derived character state of having lost epipleural ribs beyond the fifteenth vertebra, a condition shared as well with *Ahlia egmontis*. *Asarcenchelys longimanus* also shares with the species of *Myrophis* the primitive states of neurocranial shape (Fig. 6a, 6c), gill arch condition, and pectoral fin development. Species of *Pseudomyrophis* and *Neenchelys* are further specialized and separable from the "*Myrophis* group" in having a much-reduced neurocranium, and posterior nostrils before the eye and lacking a flap (McCosker 1977, 1982).

It should be noted that both specimens of *A. longimanus* are damaged and thereby the total length measurement of each specimen may be in error by a few percent. The paratype is intact, but the radiograph indicates that the tail has probably been severed and regrown. The specimen has 17 fewer vertebrae than the holotype. During capture the holotype was broken behind vertebra 15 and is twisted in preservative. The head remains attached by the skin to the trunk region and is sufficiently intact to allow precise measurements to be taken and characters to be analyzed.

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A REVIEW OF THE FISHES OF THE AGONID
GENUS *XENERETMUS* GILBERT

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ABSTRACT: The agonid genus *Xeneretmus* is reviewed and found to be composed of two subgenera: *Xenopyxis*, containing *X. latifrons*, *X. leiops*, and *X. ritteri*; and *Xeneretmus*, containing only *X. triacanthus*. The osteology of the type species of the genus, *X. triacanthus*, is described, illustrated, and compared with the other members of the genus, as well as to members of the agonid genera *Agonus*, *Hypsagonus*, and *Podothecus*. On the basis of a comparison with 15 other agonid taxa, the subgenera *Xeneretmus* and *Xenopyxis* are demonstrated to be monophyletic. A key is provided, along with synonymies, diagnoses, and descriptions for the genus, the subgenera, and species. Lectotypes are designated for *X. triacanthus* and *X. latifrons*.

INTRODUCTION

The family Agonidae is composed of typically small, benthic, scorpaeniform fishes that are almost totally encased in rows of overlapping dermal plates; the centers of these plates often bear spines or protuberances. The majority of the species are found in the North Pacific Ocean and Bering Sea; only 3 of the approximately 50 recognized species (distributed among some 20 currently recognized genera) are restricted to other regions: two in the North Atlantic Ocean (*Aspidophoroides monopterygius* and *Agonus cataphractus*), and one off southern South America (*Agonopsis chilensis*).

Only two major reviews of the family have been written. The first is that of Jordan and Evermann (1898). While this work was primarily concerned with American species, all known agonids were considered; little osteology was discussed, and only a very few specimens of each species were examined. The second review of the family is that of Freeman (1951), a widely known, but unpublished doctoral dissertation written at

Stanford University. Once again, little osteology was examined, and few specimens were used. Only two notable osteological investigations of agonids have been published: Rendahl's (1934) work on *Hypsagonus quadricornis* and Ilina's (1978) work on the genera *Podothecus* and *Agonus*. Both were limited to aspects of cranial osteology.

The taxonomic history of the genus *Xeneretmus* began with Gilbert's (1890) erection of *Xenochirus*, established to contain three species: *X. triacanthus*, *X. pentacanthus*, and *X. latifrons*. Five years later, Gilbert (1895) described a fourth species, *Xenochirus alascanus*. In 1903 Gilbert (in Jordan 1903) became aware of the prior use of the name *Xenochirus* by Gloger (1842) for a genus of marsupial mammals, and therefore offered *Xeneretmus* as a replacement name. In the following year, a fifth member of the genus, *X. infraspinatus*, was described by Gilbert (1904). In his final paper on this genus, Gilbert (1915) described two additional species, *X. ritteri* and *X. leiops*, moved *X. alascanus*, *X. infraspinatus*,

and *X. pentacanthus* into a new genus, *Asterotheca*, and created two subgenera within *Xeneretmus*: *Xenopyxis* containing *X. latifrons*, *X. leiops*, and *X. ritteri*; and *Xeneretmus* containing only *X. triacanthus*. Jordan et al. (1930), without explanation, raised the subgenus *Xenopyxis* to generic status. Although a few later workers (Barnhart 1936; Clemens and Wilby 1961) followed Jordan et al. (1930), the majority of recent workers (Freeman 1951; Peden and Gruchy 1971; Miller and Lea 1972; Hart 1973; Barraclough and Peden 1976; Robins 1980; Eschmeyer et al. 1983) retained Gilbert's (1915) classification.

Since Gilbert (1915), only minor publications on the genus have appeared. Bolin (1937), while noting that Gilbert's (1915) labels on the illustrations of *X. ritteri* and *X. leiops* were switched, extended the geographic range of *X. leiops* north from Santa Catalina Island to Monterey Bay. Peden and Gruchy (1971) expanded the range of *X. triacanthus* into British Columbian waters. Ginn and Bond (1973) extended the range of *X. leiops* north to the Columbia River. Three years later, Barraclough and Peden (1976) extended the range of *X. leiops* further north to southern British Columbia and noted, as did Bolin (1937), the switching of Gilbert's (1915) labels.

The purposes of this study are to provide a complete osteological description of the genus *Xeneretmus*, to describe variation in a number of systematically important characters, to designate type material for the species where it is in question, and to investigate the phyletic nature of the genus, subgenera, and closely related taxa.

MATERIALS AND METHODS

All measurements were taken from the right side of the fish. Standard length (SL), used throughout, was measured from the tip of the snout to the posteroventral corner of the last supralateral plate. Other measurements were made as follows:

- Anal, first dorsal, and second dorsal lengths.—from the tip of the snout to the insertion of the first ray of the respective fin
- Caudal peduncle length.—from the insertion of the posteriormost anal ray to the posteroventral corner of the last supralateral plate
- Vent length.—from the tip of the snout to the anterior margin of the anal opening
- Ventral head length.—from the tip of the snout to the posterior margin of the isthmus

Depth at first and second dorsal.—the shortest distance from the first ray of that fin to the ventral contour of the body

Head length.—from the tip of the snout to the posteriormost margin of the opercular membrane

Supraoccipital pore to snout.—from the tip of the snout to the anterior edge of the acoustico-lateralis pore located dorsal to the supraoccipital bone

Snout length.—from the tip of the snout to the anterior margin of the orbit

Upper jaw length.—from the anteriormost extent of the premaxilla to the posteriormost margin of the maxilla

Length of orbit.—greatest distance between the rims of the orbit

Interorbital width.—least distance between the lateral margins of the frontals

Length of pectoral and pelvic fins.—from the base of the longest ray to its tip

Caudal depth.—least depth of the caudal peduncle

Pectoral width.—the greatest width measured between the pectoral bases

Ural centra are included in vertebral counts obtained from radiographs.

Nomenclature for, and the method of enumeration of, dermal plates follow the system outlined by Gruchy (1969) with the following additions: the number of plates anterior or posterior to a fin is counted to or from, but not including, the plate on which the first or last ray of the fin is inserted; the ventrolateral series of plates is considered to start at the pelvic fin base.

Cladistic analysis was performed using Joseph Felsenstein's (Department of Genetics, University of Washington) Package for Inferring Phylogenies. Summary statistics were calculated using SPSS and SCSS (Nie et al. 1975, 1980). All programs were run on a Digital Electronics Corporation VAX, under the VMS operating system.

For the phylogenetic analysis, characters from the following in-group were recorded: *Aspidophoroides bartoni*, *A. olriki*, *Bathyagonus alascanus*, *B. infraspinalis*, *B. nigripinnis*, *B. pentacanthus*, *Bothragonus swani*, *Odontopyxis trispinosa*, *Xeneretmus latifrons*, *X. leiops*, *X. ritteri*, and *X. triacanthus*. A close relationship of these taxa was hypothesized by Freeman (1951); all are members of his subfamily Xeneretminae. A set of morphological characters (Table 1) was

| Species | Circum- orbital 1 spines | Circum- orbital 3 spines | Pterotic spines | Posttem- poral spines | Parietal spines | Frontal spines | Nasal spines | Exposed supra- ethmoid spines | Pre- opercu- lar spines | Free-fold of isthmus | Maxillary barbels | Exposed rostral plate | Rostral plate spines | Dermal body plate spines | Breast plates about tongue | Arrange- ment of ventral pectoral rays | Develop- ment of thick- ened fingerlike projec- tion of |
|--------------------------|--------------------------------|--------------------------------|--------------------|-----------------------------|--------------------|-------------------|-----------------|--|----------------------------------|----------------------------|----------------------|-----------------------------|----------------------------|-----------------------------------|-------------------------------------|---|---|
| <i>Aspidophoroides</i> | | | | | | | | | | | | | | | | | |
| <i>barioni</i> | absent | absent | absent | absent | absent | absent | one | absent | absent | present | one | present | none | absent | yes | tight | no |
| <i>Aspidophoroides</i> | | | | | | | | | | | | | | | | | |
| <i>obitaki</i> | absent | absent | absent | absent | absent | absent | one | absent | absent | present | one | present | none | absent | yes | loose | no |
| <i>Bathygomus</i> | present | present | absent | present | present | present | one | absent | two | absent | two | present | five | present | yes | tight | much |
| <i>alaxanus</i> | present | present | absent | present | present | present | one | absent | two | present | two | present | five | present | yes | tight | much |
| <i>Bathygomus</i> | absent | present | present | present | present | present | one | absent | two | absent | two | present | five | present | yes | loose | no |
| <i>infiraspindus</i> | present | present | present | present | present | present | one | absent | two | absent | two | present | five | present | yes | loose | much |
| <i>Bathygomus</i> | present | present | present | present | present | present | one | absent | two | absent | two | present | five | present | yes | loose | no |
| <i>penicacanthus</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | two | present | five | present | yes | loose | much |
| <i>Bathygomus</i> | present | present | present | present | present | present | one | absent | two | absent | two | present | five | present | yes | loose | much |
| <i>swani</i> | absent | absent | absent | absent | absent | absent | one | absent | absent | absent | one | present | none | absent | yes | tight | much |
| <i>Odontopyxis</i> | present | present | absent | absent | absent | present | one | absent | absent | absent | one | present | one | present | yes | tight | slight |
| <i>trispinosa</i> | absent | present | absent | absent | absent | present | one | absent | absent | absent | one | present | one | present | yes | tight | slight |
| <i>Xeneretmus</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | one | present | no | absent | much |
| <i>latifrons</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | one | present | no | absent | much |
| <i>Xeneretmus</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | one | present | no | absent | much |
| <i>leucops</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | 1-3 | present | no | absent | much |
| <i>Xeneretmus</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | one | present | no | absent | much |
| <i>ritteri</i> | absent | present | absent | absent | absent | present | one | absent | one | present | one | present | one | present | no | absent | much |
| <i>Xeneretmus</i> | absent | present | absent | absent | absent | present | one | absent | two | absent | two | present | three | present | yes | loose | much |
| <i>tracanthus</i> | absent | present | absent | absent | absent | present | one | absent | two | absent | three | present | none | present | yes | loose | much |
| <i>Agonopsis vulsa</i> | absent | present | absent | absent | absent | present | one | absent | two | absent | three | present | none | present | yes | loose | much |
| <i>Hypsigomus</i> | absent | present | absent | absent | absent | present | one | absent | two | absent | one | absent | none | present | no | absent | much |
| <i>quadricornis</i> | absent | present | absent | absent | absent | present | one | absent | two | absent | one | absent | none | present | no | absent | much |
| <i>Orella</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | two | absent | none | present | yes | absent | no |
| <i>dodecadron</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | two | absent | none | present | yes | absent | no |
| <i>Pallasiina</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | none | absent | none | absent | yes | loose | no |
| <i>barbata</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | one | absent | none | absent | no | absent | slight |
| <i>Percis japonicus</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | one | absent | none | absent | no | absent | slight |
| <i>Podathetus</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | one | absent | none | absent | yes | absent | slight |
| <i>acipenserinus</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | four | absent | none | absent | yes | absent | slight |
| <i>Sarritor frenatus</i> | absent | absent | absent | absent | absent | absent | one | absent | two | absent | four | absent | none | absent | yes | absent | slight |

TABLE 2. BINARY CODING OF THE CHARACTERS LISTED IN TABLE 1.

| | Circumorbital 1 spine | Circumorbital 3 spines | Pterotic spine | Posttemporal spine | Parietal spine | Frontal spines | Nasal spines | Exposed supra- ethmoid spine | Preopercular spine | Isthmus free-fold | Maxillary barbels | Exposed rostral plate | Spines on rostral plate | Five spines on rostral plate | Three spines on rostral plate | One spine on rostral plate | Spines on dermal body plates | Breast plates abutting | Arrangement of cheek plates | Development of fingerlike pectoral rays |
|---|--------------------------|---------------------------|----------------|--------------------|----------------|----------------|--------------|---------------------------------|--------------------|-------------------|-------------------|--------------------------|----------------------------|---------------------------------|----------------------------------|-------------------------------|---------------------------------|---------------------------|--------------------------------|---|
| <i>Aspidophoroides bartoni</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Aspidophoroides olrikii</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Bathylagonus alascanus</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>Bathylagonus infraspinalus</i> | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>Bathylagonus nigripinnus</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>Bathylagonus pentacanthus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| <i>Bohragonus swani</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| <i>Odontoptoxis trispinosa</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| <i>Xeneretmus latifrons</i> | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Xeneretmus leiops</i> | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Xeneretmus ritteri</i> | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Xeneretmus triacanthus</i> | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Agonopsis vulsa</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| <i>Hypsogonus quadricornis</i> | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Ocella dodecaedron</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pollasina barbata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Percis japonicus</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Podathicus acipenserinus</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>Sarritor frenatus</i> | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Estimated ancestral character states | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

collected and converted to binary characters (Table 2) by additive binary coding (Sokal and Sneath 1963; Kluge and Farris 1969). The ancestral state of each binary character was established by examining an out-group, that is, a group of taxa considered not to be members of the smallest monophyletic unit that contains all members of the in-group. The most frequent character state found among the species of the out-group was considered to be the primitive character state for the taxa of the in-group. The out-group was composed of *Agonopsis vulsa*, *Hypsagonus quadricornis*, *Ocella dodecadron*, *Pallasina barbata*, *Percis japonicus*, *Podothecus acipenserinus*, and *Sarritor frenatus*, seven agonid species considered to be related to but not members of the in-group (Jordan and Evermann 1898; Freeman 1951).

Several methods of estimating phylogenies from binary data have been proposed (Felsenstein 1982, and references cited therein). Of these methods, Wagner analysis (Farris 1970; Farris et al. 1970a, 1970b) has been the most widely employed (Baird and Eckhardt 1972; Simon 1979; Presch 1980; Jensen and Barbour 1981; Miyamoto 1983) and has been examined in detail (Colless 1981; Felsenstein, 1973, 1978, 1979; Mickevich 1978, 1980, Mickevich and Farris 1981; Schuh and Farris 1981; Schuh and Polhemus 1980; Sokal and Rohlf 1981). Felsenstein (1973, 1978, 1979) has shown some assumptions of the method:

1. Characters evolved independently.
2. Changes of character states through time are a priori improbable.
3. Polymorphisms of character states for a species are exceedingly unlikely.
4. Inequality of lengths of segments of the tree is not so extreme that two changes of states along a long segment is more probable than one change along a short segment.
5. Different lineages evolved independently.

While these assumptions do not exactly express how the world is believed to work, without assumptions no explicit model could be advanced; with them at least we know the assumptions upon which the hypothesis rests. All systematists make assumptions when trying to work out a phylogeny, but their assumptions are not as open to examination as are those of a model. The Wagner method searches for the cladogram that requires

the fewest number of steps for all the characters. Some hypothesized monophyletic sets may not be supported by uniquely derived characters.

Osteological material was cleared and stained with alizarin red S following the method of Taylor (1967). Osteological drawings were prepared with the aid of a Wild M5 stereomicroscope and camera lucida. Osteological terminology follows Weitzman (1974).

The following cleared and stained specimens were examined: *Xeneretmus latifrons*: UW 18216, 3 (148–171 mm); *X. leiops*: OSU 7309, 2 (186, 191 mm); *X. ritteri*: SIO 59-92, 1 (141 mm); *X. triacanthus*: UW 20948, 3 (146–167 mm).

The following abbreviations are used in the osteological illustrations:

| | | | |
|-----|------------------------------|-----|---------------------|
| ANG | angular | MSP | mesopterygoid |
| ARP | articular process | MTP | metapterygoid |
| ASP | ascending process | MVP | mid-ventral plate |
| BPT | basipterygium | N | nasal |
| BR | branchiostegal ray | NZ | neural zygapophysis |
| BSB | basibranchial | OP | opercle |
| BSO | basioccipital | PC | postcleithrum |
| CBR | ceratobranchial | PHY | parahypural |
| CHY | ceratohyal | PLT | palatine |
| CL | cleithrum | PM | premaxilla |
| CO | circumorbital | POP | preopercle |
| COR | coracoid | PPH | parapophysis |
| DH | dorsal hypohyal | PRO | prootic |
| DLP | dorsolateral plate | PRT | parietal |
| DN | dentary | PSP | parasphenoid |
| ECT | ectopterygoid | PTG | pterygiophore |
| EPB | epibranchial | PTO | pteroic |
| EPH | epiphyal | PTS | pterosphenoid |
| EPO | epiotic | PTT | posttemporal |
| EPU | epural | Q | quadrate |
| ER | epiplural rib | R | radial |
| EXO | exoccipital | RAT | retroarticular |
| F | frontal | RP | rostral plate |
| FHA | first haemal arch | SBO | subopercle |
| HPP | hypural plate | SCL | supracleithrum |
| HYB | hypobranchial | SCP | scapula |
| HYM | hyomandibular | SET | supraethmoid |
| IHY | interhyal | SLP | supralateral plate |
| ILP | infralateral plate | SOC | supraoccipital |
| INT | intercalar | SPH | sphenotic |
| IOP | interopercle | SPN | spine |
| IPB | infrapharyngo branchial | SYM | symplectic |
| LC | lacrimal | T | tabular |
| LE | lateral ethmoid | UC | ural centrum |
| LLS | lateral-line scale | URN | uroneural |
| M | maxilla | V | vomer |
| MDP | mid-dorsal plate | VH | ventral hypohyal |
| MIS | medial interopercular socket | VLP | ventrolateral plate |

Material examined is deposited at the following institutions: California Academy of Sciences,

San Francisco (CAS); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); National Museum of Canada, Ottawa (NMC); Oregon State University, Corvallis (OSU); Scripps Institution of Oceanography, La Jolla, California (SIO); Stanford University (SU), material now housed at CAS; University of Alberta, Museum of Zoology, Edmonton, Alberta (UAMZ); United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and School of Fisheries, University of Washington, Seattle (UW).

COMPARATIVE MATERIAL EXAMINED

Agonopsis vulsa: UW 4798 (27), UW 5359 (40).

Aspidophoroides bartoni: CAS 10842 (2), CAS 15508 (1), CAS 15509 (1), CAS 22355 (2), CAS 26764 (3), CAS 26773 (1), MCZ 28323 (1), MCZ 32463 (1), SU 20421 (1), SU 26136 (5), SU 31699 (3), USNM 125584 (5), USNM 149047 (7), UW 20940 (1), UW 20941 (1), UW 20942 (1), UW 20943 (1), UW 20944 (4), UW 20945 (2), UW 20946 (2), UW 20947 (3).

Aspidophoroides olrikii: NMC 77-1537 (26), USNM 177610 (1), UW 20935 (3), UW 20936 (2), UW 20937 (1), UW 20938 (2).

Bathygadus alascanus: NMC 650219 (3), NMC 65-319 (3), NMC 66-16 (1), SIO 69-138 (3), SU 3088 (13), UAMZ 1985 (5), UAMZ 2774 (4), USNM 48741 (1), USNM 53582 (1), USNM 53583 (3), USNM 53586 (2), USNM 53589 (5), USNM 53592 (1), USNM 60484 (1), USNM 208391 (2), UW 1422 (5), UW 14392 (11).

Bathygadus infraspinus: CAS 14911 (2), NMC 65-259 (1), SIO 63-203 (2), SIO 69-110 (2), SIO 72-230 (1), SIO 72-239 (1), SU 24967 (3), USNM 53593 (1), USNM 53595 (4), USNM 53596 (1), USNM 53597 (2), USNM 53598 (1), USNM 60416 (1), USNM 104676 (15), USNM 207968 (1), USNM 207990 (1), USNM 208117 (1), UW 1660 (1), UW 2886 (5), UW 5006 (1), UW 7583 (1).

Bathygadus nigripinnis: CAS 45524 (1), CAS 45525 (1), CAS 45526 (1), SIO 63-205 (8), SIO 69-140 (3), USNM 46613 (3), UW 7333 (4), UW 18147 (8), UW 20931 (1), UW 20932 (7), UW 20933 (1).

Bathygadus pentacanthus: CAS 15130 (4), NMC 65-397 (1), NMC 65-423 (6), NMC 71-693 (1), SIO 75-355 (3), SIO 80-9 (1), USNM 46612 (3), USNM 63444 (1), UW 18145 (15), UW 18472 (6), UW 19140 (3), UW 20934 (1).

Bothragonus swani: UW 14155 (2), UW 17971 (1), UW 20929 (1), UW 20930 (2).

Hypsogadus quadricornis: UW 11721 (32).

Ocella dodecaedron: UW 20999 (5).

Odontopyxis trispinosa: UW 1752 (4), UW 4375 (5).

Pallasina barbata: UW 4206 (3).

Percis japonicus: UW 21000 (1), UW 21001 (1).

Podothecus acipenserinus: UW 3977 (125), UW 7340 (12).

Sarritor frenatus: UW 20998 (5).

OSTEOLOGY OF *XENERETMUS TRIACANTHUS*

CRANIUM (Figs. 1, 9).—Rostral plate unpaired, situated anterodorsal to nasals, most anterior os-

teological element and bears a single, dorsally directed spine; on either side, a laterally directed spine.

Nasals in contact anteriorly, but separated posteromedially by anterior third of supraethmoid. Each, bordered laterally by respective lacrimal (Fig. 9), bears a strong, posterodorsally directed nasal spine.

Lateral ethmoids lie posterior to nasals. Each comes into contact with frontal medially, lacrimal laterally (Fig. 9), and parasphenoid ventrolaterally.

Frontals are in contact with each other on midline for most of their length, separated by supraethmoid anteriorly. Each frontal bordered posteriorly by sphenotic, pterotic, and parietal; posterovertrally by pterosphenoid. A sharp spine is present on the dorsal surface of each frontal, just posterodorsal to the orbit.

Parietals meet on dorsal midline. Bordered along lateral margin by pterotic, tabular, and posttemporal. Each bears two posterodorsally directed spines: anteriormost spine knoblike, posteriormost strong and sharp.

Most of the anterodorsal surface of supraoccipital, covered by parietals, comes into contact with exoccipitals along posterior margin. Pterotic meets sphenotic anteriorly, tabular posteriorly, and prootic, exoccipital, intercalar, and posttemporal ventrally.

Tabular dorsal to the epiotic; posttemporal bears a spine at posterior margin. Supracleithrum articulates with posteroventral surface of posttemporal.

Epiotic attaches at posterolateral corner of cranium, situated ventral to tabular and posttemporal. Exoccipital forms lateral and dorsal borders of foramen magnum; anteriorly, it forms posterolateral portion of otic capsule. A condyle at its posteroventral corner contacts the lateral process of the anteriormost vertebral centrum (preural centrum 41).

Basioccipital, broad anteriorly, narrowing posteriorly, forms ventral margin of foramen magnum. A single large condyle situated posteriorly, abuts against the anteriormost vertebral centrum. A posterior projection of parasphenoid overlaps anterior midline of basioccipital ventrally; its anterolateral corner forms postero-medial portion of otic capsule.

Parasphenoid runs from vomer anteriorly to basioccipital posteriorly, forms ventral margin of cranium; anteriorly receives shaft of vomer.

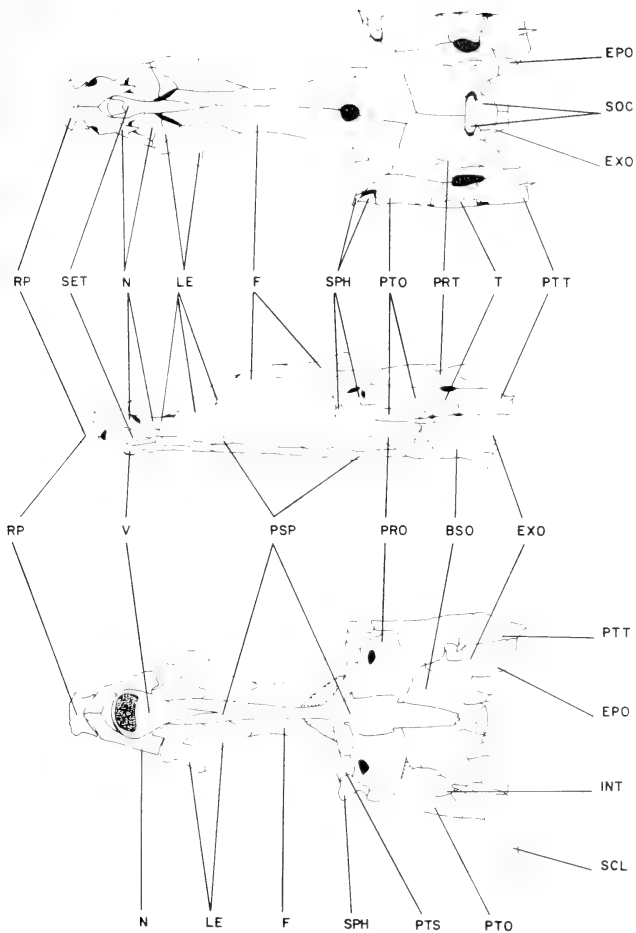


FIGURE 1. Dorsal, left lateral, and ventral views of cranium of *Xeneretmus triacanthus*, UW 20948, 158 mm SL. Dotted lines portray canals of the acoustico-lateralis system.

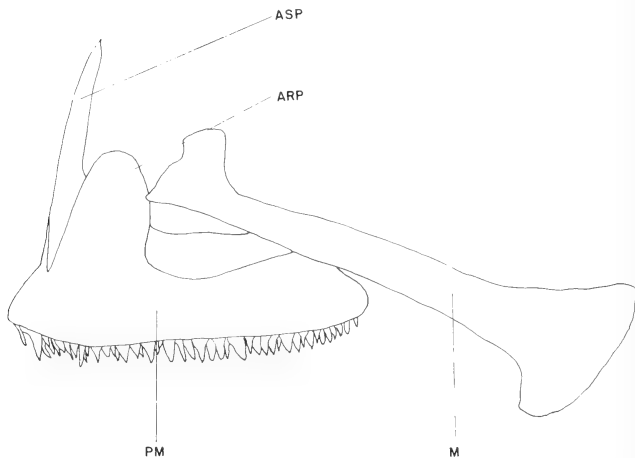


FIGURE 2. Left lateral view of upper jaw of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

Lateral ethmoids border on its anterolateral surface and its dorsolateral projections abut on pterosphenoïds dorsally and form posterior margin of orbits. Vomer is "tear"-shaped; teeth borne

along its anteroventral surface arranged in semi-circular pattern.

Prootic forms anterior portion of otic capsule; does not reach posterior margin of orbit.



FIGURE 3. Left lateral view of lower jaw of *Xeneretmus triacanthus*, UW 20948, 158 mm SL. Dotted lines portray acoustico-lateralis canals.

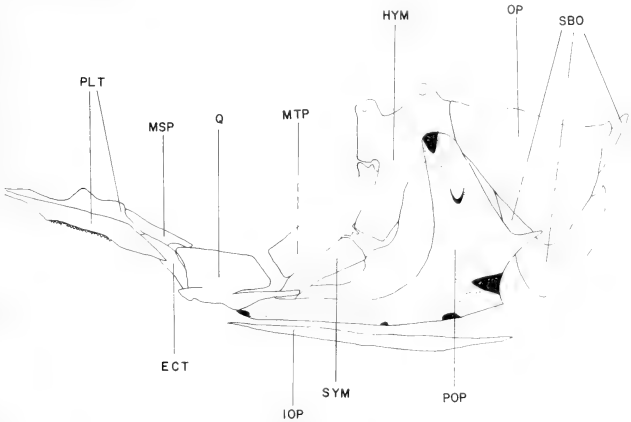


FIGURE 4. Lateral view of suspensorium and opercular apparatus of *Xeneretmus triacanthus*, UW 20948, 158 mm SL, right side reversed. Dotted lines portray acoustic-lateralis canals.

Intercalar approximately circular; dorsally bordered by exoccipital and pterotic. Antero-medially directed projection of posttemporal overlies its posteroventral face.

UPPER JAW (Fig. 2).—Premaxilla toothed along

entire ventral surface in a broad band. The maxilla forked anteriorly to receive ascending process of premaxilla and widens abruptly posteriorly.

LOWER JAW (Figs. 3, 4).—Anterodorsal three-fourths of dentary toothed. Angular bears socket

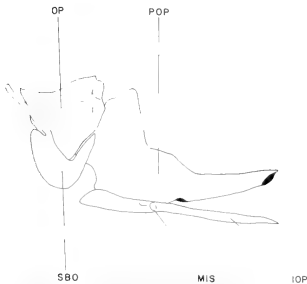


FIGURE 5. Left medial view of opercular apparatus of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

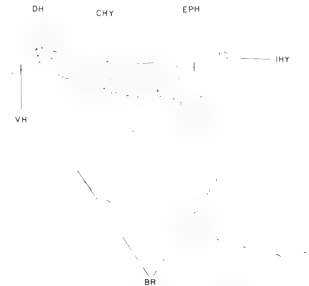


FIGURE 6. Left lateral view of hyoid apparatus of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.



FIGURE 7. Dorsal view of branchial basket of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

on posteromedial surface to receive a process of quadrate (Fig. 4). Retroarticular attaches to the posteroventral corner of angular.

SUSPENSORIUM (Figs. 1, 4-6, 9).—Palatine toothed for a third of its length, teeth centered about midpoint. It articulates posteriorly with mesopterygoid and ectopterygoid. Anterodorsal surface of palatine articulates with ventral surface of lateral ethmoid (Fig. 1). A lateral process of palatine articulates with medial surface of lacrimal.

Mesopterygoid borders ectopterygoid ventrally, quadrate posteriorly; does not contact metapterygoid. The ectopterygoid lies between palatine, mesopterygoid, and quadrate. Posteroventral surface of quadrate contacts preopercle. Metapterygoid thin and flat; borders symplectic anteroventrally and hyomandibular posteroventrally.

Hyomandibular has three dorsal articulating facets: anteriormost, articulating with sphenotic and prootic; medial articulating with pterotic; and posteriormost articulating with anterodorsal corner of the opercle (Fig. 1).

Preopercle crescent-shaped with two spines along posterior margin. It is dorsally overlain by circumorbital 3 (Fig. 9). Elongate interopercle bears medial socket that fits onto posterior cor-

ner of epihyal (Figs. 5, 6). Opercle triangular and slightly striated; a socket on anterodorsomedial face receives posterior facet of hyomandibular. Subopercle V-shaped, with crotch of the V lying dorsal to opercle (Fig. 5); posterior arm long and thin, lying on medial face of opercle for majority of its length; anterior arm short, its most dorsal point reaching only half the height of opercle.

HYOID ARCH (Figs. 5, 6).—Dorsal hypohyal anterodorsal to ceratohyal. Ventral hypohyal forms an anterior cap over ceratohyal. Ceratohyal has four branchiostegal rays connected to it: anterior two ventrally attached, posterior two ventrolaterally. Epihyal connected to the remaining two basibranchials ventrolaterally. Posterodorsally, interhyal connects epihyal to hyomandibular. Posterior corner of epihyal fits into medial socket of interopercle (Fig. 5).

BRANCHIAL ARCHES (Fig. 7).—Hypobranchials 1-3 broad and flat. Hypobranchial 2 two-thirds length of hypobranchial 1; hypobranchial 3 tear-shaped and two-thirds length of hypobranchial 2. All four ceratobranchials have anterior rows of gillrakers that bear toothlike structures; ceratobranchials 1-3 also possess posterior rows of similar, "tooth"-bearing gillrakers. Ceratobranchials 3 and 4 articulate with hypobranchial 3. Ceratobranchial 5 oval, completely toothed. Epi-



FIGURE 8. Dorsal view of urohyal of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

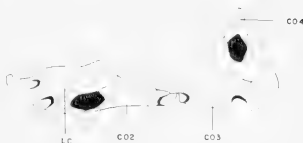


FIGURE 9. Left lateral view of circumorbital bones of *Xeneretmus triacanthus*, UW 20948, 158 mm SL. Dotted lines portray acoustico-lateralis canals.

branchials 1–4 all articulate dorsally with a single, large, well-toothed infrapharyngobranchial. Epibranchial 1 forked dorsally in some specimens.

UROHYAL (Fig. 8).—Urohyal triangular, with a dorsomedial ridge rising posteriorly.

CIRCUMORBITAL SERIES (Figs. 1, 9).—Lacrimal forms majority of dorsal surface area of snout and connects with lateral ethmoid and nasal (Fig. 1). Circumorbital 2 is tubelike. Circumorbital 3 has a single centrally located and posteriorly directed spine on lateral surface. Circumorbital 4 also tubelike, forming posterior margin of orbit.

PECTORAL GIRDLE (Fig. 10).—Three rectangular radials and two postcleithra present. Scapula crescent-shaped and attached to posterior margin of cleithrum by two arms. Coracoid L-shaped, its anterior arm in contact medially with ventrolateral face of cleithrum; the dorsal arm with ventral margin of scapula and anterior borders of two ventralmost radials. Cleithrum the largest element of pectoral girdle; dorsally attaches to supracleithrum.

PELVIC GIRDLE (Fig. 11).—Basipterygia paired and connected medially to each other along posterior tenth of their length. A ventral ridge runs anteroposteriorly. One spine and two rays present; lateralmost ray tightly bound to medial surface of spine.

VERTEBRAL COLUMN (Fig. 12).—There are 41 preural centra in all the specimens of *Xeneretmus triacanthus* dissected. The 41st preural centrum has three anterior concave facets (a large central facet and two smaller lateral ones) that articulate with posterior surface of cranium; neuropophyses not dorsally ankylosed; 41st through 31st preural centra bear epiplural ribs. Neural zygapophyses become more pronounced posteriorly. Haemal spines on 29th through first preural

centra. Haemal spines posterior to posteriormost anal fin pterygiophore lie ventral to adjacent posterior centrum (this tendency increases posteriorly).

Posterior two rays of anal and second dorsal fin articulate with last pterygiophore of ventral and dorsal series, respectively. Four pterygiophores lie between first and second dorsal fins. No ray articulates with these pterygiophores. Anterior two pterygiophores of ventral series do not articulate with any rays.

Neural spines on 40th through first preural centra; centra posterior to last dorsal pterygiophore have broad neural spines that lie between neural zygapophyses of adjacent posterior ural centrum.

One parahypural fused to ventral margin of hypural plate. One uroneural tightly bound to dorsal margin of hypural plate. Epurals absent.

DERMAL PLATES (Fig. 13).—All dermal plates of supralateral, dorsolateral, and mid-dorsal series bear posteriorly directed spines. All infralateral plates bear similar spines as well, except those medial to pectoral fin. Ventrolateral plates spineless, except for those behind pelvic fin insertion to approximately four plates anterior to insertion of first anal fin ray. Mid-ventral plates spineless.

Anterior supralateral plates overlain posteriorly by next supralateral plate for approximately half their length; those more posterior in position overlain by as little as 20% of their length. Supralateral plates overlain by dorsolateral and mid-dorsal plates dorsally, and lateral-line scales ventrally.

Anterior infralateral plates have half their length overlain by adjacent posterior infralateral plate; length covered reduced to 20% posteriorly. Infralaterals overlain by lateral-line scales dor-

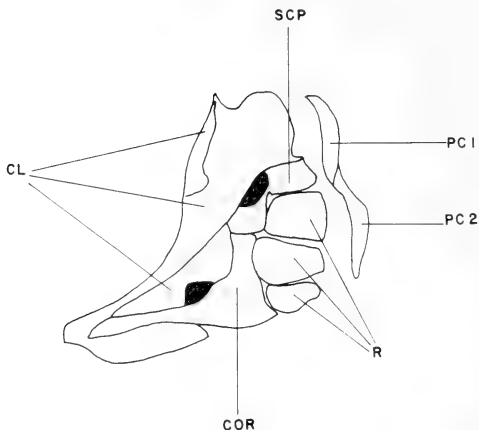


FIGURE 10. Left lateral view of pectoral girdle of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

sally and ventrolateral and mid-ventral plates ventrally.

Ventrolateral plates bordering anal fin have medial projections that meet on midline such that fin rays surrounded by plates. A third of the length of each ventrolateral plate overlain pos-

teriorly by next ventrolateral plate. Medially, ventrolateral plates slightly overlap each other on midline.

Each mid-ventral plate posteriorly overlain by immediately posterior mid-ventral plate; length covered approximately 15%.

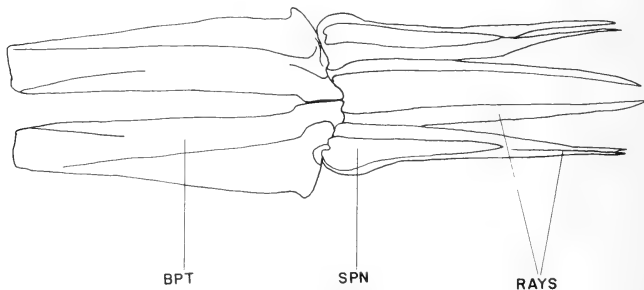


FIGURE 11. Ventral view of pelvic girdle of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

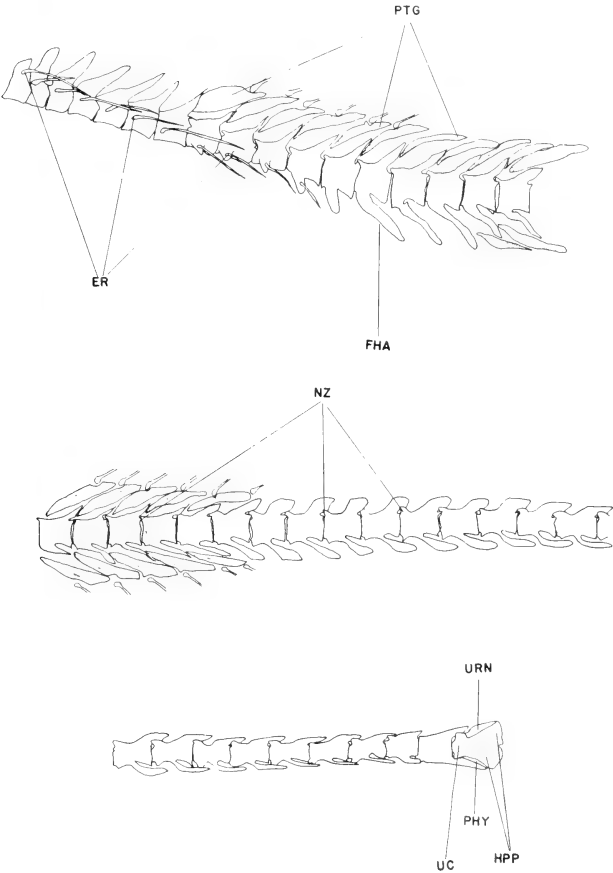


FIGURE 12. Left lateral view of vertebral centra of *Xeneretmus triacanthus*, UW 20948, 158 mm SL.

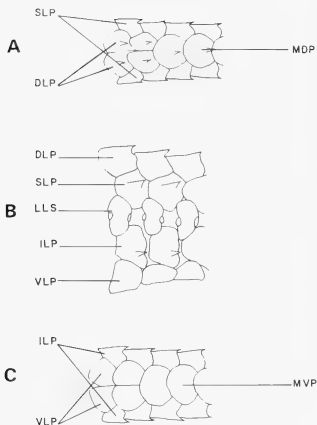


FIGURE 13. Dermal body plates of *Xeneretmus triacanthus*, UW 20948, 158 mm SL: (A) Dorsal view of plates immediately posterior to insertion of posteriormost ray of second dorsal fin. (B) Left lateral view of plates immediately posterior to pectoral fin. (C) Ventral view of plates immediately posterior to insertion of posteriormost anal fin ray.

Each dorsolateral plate overlain posteriorly by next dorsolateral plate for approximately 35% of length. Like ventrolaterals, dorsolateral plates bordering first and second dorsal fins have medial projections that meet on dorsal midline such that only a small break in plates exists where dorsal rays insert.

Each mid-dorsal plate overlain posteriorly for 20% of length by adjacent posterior mid-dorsal plate.

ACOUSTICO-LATERALIS SYSTEM (Figs. 1, 3, 4, 9).—Acoustico-lateralis system of cranium passes posteriorly through nasals. Canal enters frontals through an anterior pore and extends along medial border to a medial pore where it turns laterally, continuing to posterolateral pore of frontal where it branches (Fig. 1). Anteriorly directed branch of acoustico-lateralis system passes through entire circumorbital series (Fig. 9). Posteriorly directed branch passes through pterotic and branches again beneath tabular. Medially

directed branch passes beneath posterior spine of parietal to a medial pore dorsal to supraoccipital where it meets its counterpart from the other side. Posteriorly directed branch passes through posttemporal and supracleithrum, continues posterolaterally along entire length of fish (Fig. 1). A second acoustico-lateralis canal passes posteriorly through dentary, angular, and preopercle (Figs. 3, 4).

COMPARATIVE OSTEOLOGY

The osteology of the other species of the genus is almost identical with that of *X. triacanthus* described above; very few differences were found between species that exceeded variation within species. *Xeneretmus triacanthus* has two spines on the posterior margin of the preopercle whereas its congeners possess only one. The rostral plate of the other members of the genus do not have lateral spines (except in some individuals of *X. leiops*). *Xeneretmus ritteri* has two spines on circumorbital 3, whereas the other species of *Xeneretmus* have only one. Finally, the pterotic of *X. ritteri* bears two spines while in the other members of the genus only a ridge may be discerned.

The following comparisons can be made with Rendahl's (1934) work on the agonid species *Hypsagonus quadricornis*. The rostral plate, diagnostic for *Xeneretmus* (Fig. 1), does not occur in *Hypsagonus* (Rendahl 1934, figs. 1–3). The vomer of *Hypsagonus* is toothless (Rendahl 1934, fig. 2). The frontal spine of *Hypsagonus* is much larger than that of *Xeneretmus* (Fig. 1; Rendahl 1934, figs. 1, 3). In *Hypsagonus*, Rendahl (1934, fig. 1) depicted the supraoccipital as lying along the entire medial border of the parietal, in such a configuration that the parietals are not in contact along their medial edges; the parietals meet along their entire medial edges in *Xeneretmus* (Fig. 1). Rendahl (1934, figs. 28A, 28B) depicted the retroarticular as lying only on the medial face of the angular whereas in *Xeneretmus* the retroarticular is visible from both a medial and lateral view (Fig. 3). Rendahl (1934, fig. 24A) showed the mesopterygoid and metapterygoid of *Hypsagonus* to be in contact with each other; in *Xeneretmus* the quadrate is between these two bones such that they do not meet (Fig. 4). Finally, the posterior arm of the subopercle of *H. quadricornis* is considerably shorter than is the case for *Xeneretmus* (Figs. 4, 5; Rendahl 1934, figs. 24A, 24B).

The following comparisons can be made with the work of Ilina (1978). Neither of the genera *Podothecus* and *Agonus* possesses a rostral plate. Ilina (1978, figs. 2–4, 6) portrayed the supraoccipitals of *Podothecus acipenserinus*, *P. veternus*, *P. gilberti*, and *P. thompsoni* as lying between the parietals, such that they do not meet along their medial edges, as they do in *Xeneretmus* (Fig. 1). The posttemporal of *Podothecus acipenserinus*, *P. veternus*, and *Agonus cataphractus* apparently makes no contact with the intercalar (Ilina 1978, figs. 2, 3, 7); in *Xeneretmus* the anteriorly directed projection of the posttemporal touches the intercalar (Fig. 1).

SYSTEMATICS

Genus *Xeneretmus* Gilbert

Xenochirus GILBERT, 1890:90 (type-species *Xenochirus triacanthus* GILBERT, 1890, by original designation; preoccupied by *Xenochirus* GLOGER, 1842, a genus of marsupial mammal).

Xeneretmus GILBERT, in Jordan 1903:360 (substitute name for *Xenochirus* GILBERT, 1890 [preoccupied, therefore taking the same type-species *Xeneretmus triacanthus*]).

DIAGNOSIS.—The genus *Xeneretmus* is distinguished from all other agonid genera by the absence of a supraoccipital pit and by the presence of an exposed rostral plate bearing a single dorsally directed spine.

DESCRIPTION.—Body tapering uniformly from pectoral girdle to caudal fin; anterior cross sections octagonal, cross section through caudal peduncle hexagonal; completely encased in overlapping dermal plates. All dorsolateral, mid-dorsal, and supralateral plates bearing posteriorly directed spines; all but those plates medial to pectoral fin of infralateral series bearing posteriorly directed spines; ventrolateral plates between pelvic fin insertion and insertion of first anal fin ray bearing posteriorly directed spines; no spines present on mid-ventral plates; dorsolateral plates 22–24; mid-dorsal plates 12–19; supralateral plates 39–45; infralateral plates 35–42; ventrolateral plates 21–23; mid-ventral plates 14–20. In comparison with the other genera of Agonidae, *Xeneretmus* has long spines on slightly flexible angular dermal plates.

Cephalic spines. One nasal spine; one frontal spine dorsal to posterior edge of orbit; two parietal spines; one posttemporal spine; one or two spines on circumorbital 3; one or two spines on posterior margin of preopercle.

Fin rays. All simple; four ventralmost pectoral

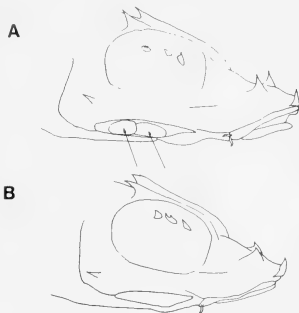


FIGURE 14. Right lateral view of head of two species of *Xeneretmus*: (A) *X. triacanthus*; (B) *X. latifrons*. Arrows indicate dermal plates of cheek region.

rays thickened (in comparison to the dorsalmost pectoral rays), and projecting fingerlike from the fin membrane; dorsal two thickened rays longest rays of pectoral fin. First dorsal, 5–8; second dorsal, 6–8; anal, 5–8; pectoral, 12–16; pelvic 1, 2; branchiostegal rays, 6.

Mouth. Both jaws of equal length, mouth terminal; teeth present on premaxilla, dentary, palatine, and vomer. Barbels present along ventral margin of dentary at edges of acoustico-lateralis pores and at posterior corner of maxilla.

Measurements. The following ranges for proportions of all species of the genus are expressed in thousandths of standard length (number of specimens measured in parentheses): anal length, 305–510 (201); vent length, 210–335 (197); caudal peduncle length, 370–479 (199); second dorsal length, 443–592 (201); depth at second dorsal, 47–72 (197); first dorsal length, 258–386 (203); depth at first dorsal, 65–132 (171); pectoral length, 123–217 (189); pelvic length, 51–105 (197); pectoral width, 92–157 (189); head length, 166–241 (203); ventral head length, 80–155 (200); length from supraoccipital pore to snout, 147–189 (203).

The following proportions, associated with characteristics of the head, are expressed in thousandths of head length (number of specimens measured in parentheses): orbit length, 249–476 (207); upper jaw length, 229–363 (141); snout

TABLE 3. RANGE, MEAN, STANDARD DEVIATION, AND SAMPLE SIZE FOR MERISTIC CHARACTERS OF SPECIES OF *Xeneretmus*.

| Character | <i>X. latifrons</i> | | <i>X. leiops</i> | | <i>X. ritteri</i> | | <i>X. triacanthus</i> | |
|--|---------------------|---|------------------|--|-------------------|---------------------------------------|-----------------------|--|
| First dorsal spines | 6-8 | $\bar{x} = 6.9$ SD = 0.50 $n = 110$ | 6-7 | $\bar{x} = 6.7$ SD = 0.45 $n = 30$ | 6-7 | $\bar{x} = 6.4$ SD = 0.54 $n = 7$ | 5-7 | $\bar{x} = 6.0$ SD = 0.28 $n = 63$ |
| Second dorsal rays | 6-8 | $\bar{x} = 7.0$ SD = 0.43 $n = 110$ | 7-8 | $\bar{x} = 7.4$ SD = 0.49 $n = 30$ | 6-7 | $\bar{x} = 6.9$ SD = 0.38 $n = 7$ | 6-7 | $\bar{x} = 6.6$ SD = 0.50 $n = 63$ |
| Anal fin rays | 6-8 | $\bar{x} = 7.2$ SD = 0.15 $n = 110$ | 6-8 | $\bar{x} = 6.9$ SD = 0.57 $n = 30$ | 6-7 | $\bar{x} = 6.9$ SD = 0.38 $n = 7$ | 5-7 | $\bar{x} = 6.1$ SD = 0.49 $n = 63$ |
| Pectoral fin rays | 13-15 | $\bar{x} = 14.1$ SD = 0.40 $n = 109$ | 13-15 | $\bar{x} = 14.0$ SD = 0.33 $n = 29$ | 16 | $\bar{x} = 16$ SD = 0.00 $n = 7$ | 12-14 | $\bar{x} = 13.0$ SD = 0.22 $n = 61$ |
| Eyeball plates | 3-6 | $\bar{x} = 4.2$ SD = 0.62 $n = 110$ | 0 | $\bar{x} = 0.0$ SD = 0.00 $n = 30$ | 3-6 | $\bar{x} = 5.0$ SD = 1.0 $n = 7$ | 2-6 | $\bar{x} = 3.9$ SD = 0.76 $n = 63$ |
| Supralateral plates | 39-42 | $\bar{x} = 40.9$ SD = 0.65 $n = 109$ | 43-45 | $\bar{x} = 43.9$ SD = 0.80 $n = 28$ | 40-41 | $\bar{x} = 40.7$ SD = 0.49 $n = 7$ | 41-43 | $\bar{x} = 42.0$ SD = 0.46 $n = 58$ |
| Infralateral plates | 35-40 | $\bar{x} = 37.6$ SD = 0.92 $n = 108$ | 39-42 | $\bar{x} = 40.3$ SD = 0.98 $n = 28$ | 36-38 | $\bar{x} = 36.9$ SD = 0.69 $n = 7$ | 38-40 | $\bar{x} = 39.0$ SD = 0.49 $n = 58$ |
| Mid-dorsal plates | 12-16 | $\bar{x} = 14.7$ SD = 0.63 $n = 108$ | 16-19 | $\bar{x} = 17.7$ SD = 0.72 $n = 29$ | 14-15 | $\bar{x} = 14.7$ SD = 0.49 $n = 7$ | 15-17 | $\bar{x} = 16.2$ SD = 0.54 $n = 58$ |
| Dorsolateral plates between first and second dorsal fins | 3-5 | $\bar{x} = 4.1$ SD = 0.53 $n = 110$ | 4-5 | $\bar{x} = 4.4$ SD = 0.50 $n = 30$ | 4-5 | $\bar{x} = 4.6$ SD = 0.54 $n = 7$ | 4-6 | $\bar{x} = 5.1$ SD = 0.33 $n = 64$ |
| Mid-ventral plates | 14-17 | $\bar{x} = 15.4$ SD = 0.66 $n = 109$ | 16-20 | $\bar{x} = 18.2$ SD = 0.83 $n = 28$ | 14-16 | $\bar{x} = 14.9$ SD = 0.69 $n = 7$ | 16-18 | $\bar{x} = 16.7$ SD = 0.50 $n = 59$ |
| Cheek plates | 0-1 | $\bar{x} = 0.0$ SD = 0.10 $n = 110$ | 0 | $\bar{x} = 0.0$ SD = 0.00 $n = 30$ | 0 | $\bar{x} = 0.0$ SD = 0.00 $n = 7$ | 1-4 | $\bar{x} = 2.75$ SD = 0.69 $n = 64$ |
| Vertebrae | 40-42 | $\bar{x} = 40.6$ SD = 0.79 $n = 7$ | 43-45 | $\bar{x} = 43.7$ SD = 0.82 $n = 6$ | 40-41 | $\bar{x} = 40.7$ SD = 0.52 $n = 6$ | 42 | $\bar{x} = 42.0$ SD = 0.00 $n = 6$ |

length, 157-330 (206); interorbital length, 58-123 (107).

KEY TO THE SPECIES OF THE GENUS *XENERETMUS*

- 1a. Cheek plates present, filling area between circumorbitals and elements of the lower jaw (Fig. 14)
Xeneretmus (Xeneretmus) triacanthus, p. 36
- 1b. Cheek plates absent, or rarely represented by a single plate that does not fill the area between the circumorbitals and elements of the lower jaw (Fig. 14)
Subgenus *Xenopyxis* 2
- 2a. Two or more dermal plates on eyeball 3
- 2b. No dermal plates on eyeball
Xeneretmus (Xenopyxis) leiops, p. 35
- 3a. Two or more barbels present at posterior corner of maxilla, 16 pectoral rays
Xeneretmus (Xenopyxis) ritteri, p. 36
- 3b. One barbel present at posterior corner of maxilla, 13-15 pectoral rays
Xeneretmus (Xenopyxis) latifrons, p. 32

Subgenus *Xenopyxis* Gilbert

Xenopyxis GILBERT, 1915:345 (type-species *Xeneretmus (Xenopyxis) latifrons* Gilbert 1890, by original designation). Jordan et al. 1930:396 (elevated to generic level).

DIAGNOSIS.—Distinguished from the subgenus *Xeneretmus* by the absence of dermal plates in the cheek region (Fig. 14B), and the failure of the breast plates to abut against each other. It further differs in having higher average counts for rays in the first and second dorsal, anal, and pectoral fins (Table 3); having larger eyes (Table 4); and in general being more robust.

Xeneretmus (Xenopyxis) latifrons (Gilbert) [Blacktip Poacher]

(Figure 15)

Xenochirus latifrons GILBERT, 1890:92 (original description, lectotype USNM 43091).

Xeneretmus latifrons GILBERT, in Jordan 1903:360 (new combination, *Xenochirus* preoccupied).

Xeneretmus (Xenopyxis) latifrons GILBERT, 1915:345 (description, key).

Xenopyxis latifrons JORDAN ET AL., 1930:396 (checklist).

MATERIAL EXAMINED.—One hundred and eighty-two specimens, 62 to 173 mm.

TABLE 4. RANGE, MEAN, AND SAMPLE SIZE FOR BODY PROPORTIONS OF SPECIES OF *Xeneretmus*.

| Character | <i>X. latifrons</i> | <i>X. leiops</i> | <i>X. ritteri</i> | <i>X. triacanthus</i> |
|---|-----------------------------|----------------------------|---------------------------|----------------------------|
| Anal length/SL | 305-486 x̄ = 462 n = 109 | 434-493 x̄ = 457 n = 28 | 484-508 x̄ = 498 n = 7 | 448-510 x̄ = 477 n = 57 |
| Vent length/SL | 220-335 x̄ = 253 n = 109 | 224-288 x̄ = 244 n = 24 | 253-280 x̄ = 265 n = 7 | 210-255 x̄ = 230 n = 57 |
| Caudal length/SL | 370-447 x̄ = 414 n = 106 | 384-479 x̄ = 434 n = 30 | 380-409 x̄ = 393 n = 7 | 384-439 x̄ = 410 n = 56 |
| Second dorsal length/SL | 443-592 x̄ = 487 n = 108 | 446-498 x̄ = 464 n = 29 | 490-516 x̄ = 501 n = 7 | 459-500 x̄ = 483 n = 57 |
| Depth at second dorsal/SL | 48-72 x̄ = 59 n = 106 | 48-64 x̄ = 57 n = 29 | 58-64 x̄ = 61 n = 7 | 47-67 x̄ = 58 n = 55 |
| First dorsal length/SL | 258-386 x̄ = 307 n = 108 | 269-319 x̄ = 291 n = 30 | 315-335 x̄ = 323 n = 7 | 287-317 x̄ = 302 n = 58 |
| Depth at first dorsal/SL | 73-132 x̄ = 91 n = 88 | 72-98 x̄ = 85 n = 22 | 86-117 x̄ = 95 n = 7 | 65-109 x̄ = 82 n = 54 |
| Pectoral length/SL | 123-217 x̄ = 167 n = 104 | 139-205 x̄ = 171 n = 29 | 163-188 x̄ = 173 n = 7 | 151-202 x̄ = 175 n = 49 |
| Pelvic length/SL | 57-105 x̄ = 84 n = 108 | 56-96 x̄ = 77 n = 25 | 72-99 x̄ = 83 n = 7 | 51-94 x̄ = 77 n = 57 |
| Pectoral width/SL | 97-157 x̄ = 113 n = 102 | 92-151 x̄ = 106 n = 23 | 107-127 x̄ = 119 n = 7 | 95-125 x̄ = 109 n = 57 |
| Head length/SL | 166-241 x̄ = 212 n = 109 | 191-227 x̄ = 204 n = 25 | 231-248 x̄ = 238 n = 7 | 190-215 x̄ = 201 n = 57 |
| Ventral head length/SL | 80-146 x̄ = 121 n = 105 | 99-155 x̄ = 113 n = 30 | 133-151 x̄ = 142 n = 7 | 110-143 x̄ = 125 n = 58 |
| Supraoccipital pore to snout length/SL | 147-186 x̄ = 166 n = 109 | 150-181 x̄ = 163 n = 28 | 167-189 x̄ = 180 n = 7 | 149-171 x̄ = 160 n = 57 |
| Orbit length/head length | 249-476 x̄ = 374 n = 109 | 335-419 x̄ = 374 n = 30 | 334-372 x̄ = 358 n = 7 | 299-358 x̄ = 326 n = 61 |
| Upper jaw length/head length | 255-363 x̄ = 293 n = 53 | 234-313 x̄ = 280 n = 28 | 278-300 x̄ = 286 n = 7 | 229-283 x̄ = 251 n = 53 |
| Snout length/head length | 157-330 x̄ = 258 n = 109 | 230-316 x̄ = 284 n = 30 | 249-271 x̄ = 258 n = 7 | 258-301 x̄ = 282 n = 60 |
| Interorbital length/head length | 58-123 x̄ = 100 n = 107 | 66-96 x̄ = 81 n = 30 | 84-125 x̄ = 95 n = 7 | 71-112 x̄ = 89 n = 60 |
| Caudal depth/caudal length | 37-68 x̄ = 47 n = 95 | 35-48 x̄ = 40 n = 28 | 49-60 x̄ = 57 n = 7 | 39-58 x̄ = 45 n = 53 |

LECTOTYPE.—USNM 43091, 131 mm, Albatross station 2935, San Diego, California, 32°45'N, 117°23'W, 227 m.
PARALECTOTYPES.—CAS 5072, 3 (108–110 mm), Albatross station 2973, Point Conception, California, 34°20'N, 119°44'W, 124 m; USNM 46602, 8 (72–136 mm), Albatross station 2935, San Diego, California, 32°45'N, 117°23'W, 227 m; USNM 46605, 2 (110–112 mm), Albatross station 3059, Lincoln City, Oregon, 44°56'N, 124°13'W, 141 m; USNM 46608, 120 mm, Albatross station 2972, Santa Barbara, California, 34°19'N, 119°41'W, 112 m; USNM 46611, 111 mm, Albatross station 2948, Santa Cruz Island, California, 33°56'N, 119°42'W; UW 1416, 2 (109–110 mm), Albatross station 2973, Santa Barbara, California, 34°20'N, 119°44'W, 124 m.

ADDITIONAL NON-TYPE MATERIAL.—CAS 12572, 141 mm, Farallones, California, 37°43'N, 123°03'W; CAS 14282, 2 (128, 131 mm), San Pedro, California, 33°45'N, 118°11'W; CAS 26404, 2 (114, 134 mm), Port Heuneme, California, 34°09'N,

119°12'W; CAS 26447, 116 mm, Gaviota, California; CAS 26554, 3 (112–113 mm), Goleta Point, California, 34°27'N, 119°50'W; CAS 26560, 4 (97–112 mm), Santa Barbara Point, California, 34°30'N, 120°00'W; CAS 26563, 4 (118–130 mm), Santa Barbara Channel, California, 34°15'N, 119°55'W; CAS 26596, 120 mm, Santa Monica, California, 33°50'N, 118°38'W; CAS 26630, 19 (62–103 mm), Point Dume, California, 34°00'N, 118°50'W; CAS 37497, 149 mm, Half Moon Bay, California, 37°10'N, 122°42'W; CAS 40310, 136 mm, Santa Cruz, California, 34°07'N, 119°42'W; CAS 47107, 4 (99–110 mm), Goleta, California, 34°27'N, 119°50'W; CAS 47110, 8 (91–128 mm), Santa Monica Bay, California, 33°58'N, 118°38'W; CAS 47111, 6 (66–108 mm), Morro Bay, California, 35°30'N, 121°15'W; CAS 47112, 156 mm, Marin County, California, NMC 65-0259, 5 (121–153 mm), Kwatna Inlet, British Columbia, 52°07'N, 127°38'W.

SU 16903, 2 (77, 95 mm), Santa Barbara Channel, Califor-



FIGURE 15. *Xeneretmus latifrons*, 142 mm SL. Courtesy of R. H. Gibbs, Jr., and the Fish Division, National Museum of Natural History.

nia, 30°26'N, 120°14'W; SU 39779, 118 mm, Santa Barbara Channel, California, 34°25'N, 120°18'W.

USNM 61176, 152 mm, Albatross station 3671, Santa Cruz, California, 37°00'N, 122°20'W; USNM 63435, 3 (70–114 mm), Point Soma, California, 32°41'N, 117°14'W; USNM 63437, 3 (82–123 mm), Point Soma, California, 32°41'N, 117°14'W.

UW 1415, 131 mm, Albatross station 3174, Bodega Bay, California, 38°16'N, 123°14'W; UW 2943, 10 (116–150 mm), Camano Island, Washington, 47°59'N, 122°13'W; UW 3151, 123 mm, Burrard Inlet, British Columbia, 49°10'N, 123°00'W; UW 3168, 4 (93–138 mm), Elliot Bay, Washington, 47°36'N, 122°22'W; UW 3907, 43 (66–142 mm), Hoodport, Washington, 47°30'N, 123°10'W; UW 4224, 12 (76–130 mm), Hood Canal, Washington, 47°17'N, 122°42'W; UW 4308, 129 mm, Hood Canal, Washington, 47°30'N, 123°10'W; UW 5780, 2 (137, 144 mm), Hoodport, Washington, 47°30'N, 123°10'W; UW 5861, 120 mm, Golden Gardens, Washington, 47°40'N, 122°24'W; UW 5872, 124 mm, Tulalip Bay, Washington; UW 5960, 132 mm, Meadow Point, Washington, 47°36'N, 122°22'W; UW 7347, 4 (104–133 mm), Puget Sound, Washington; UW 8016, 142 mm, Ballard, Washington, 47°40'N, 122°25'W; UW 18216, 5 (158–163 mm), Columbia River, 46°N, 124°W; UW 18297, 162 mm, Columbia River, 46°N, 124°W; UW 18507, 3 (162–173 mm), 46°N, 124°W; UW 20939, 146 mm, Bainbridge Island, Washington, 47°37'N, 122°33'W.

DIAGNOSIS.—Distinguished from other members of subgenus by following combination of characters: three to six spine-bearing dermal plates on each eyeball; one barbel at posterior corner of maxilla; 13–15 pectoral rays (Table 5).

DESCRIPTION.—Posterior free-fold of bran-

chiostegal membrane narrow; two barbels on ventral surface of dentary, one at each posterior margin of two anteriormost acoustico-lateralis pores; breast plates surrounded by skin, and having slightly raised centers; first dorsal fin with black distal margin; second dorsal fin membrane lightly pigmented along rays, clear between rays; counts and proportions are given in Tables 3 and 4.

DISTRIBUTIONS.—Gilbert (1890) described *X. latifrons* from specimens obtained from Albatross stations situated off the coasts of California and Oregon, ranging between approximately 33° and 45°N latitude. Material examined in this study ranged from Ensenada, California to Kwatna Inlet, British Columbia (Fig. 16). Gilbert (1890, 1915) reported *X. latifrons* occurred in depths from 35 to 399 m. All the lots examined for this study fell within that depth range.

COMMENTS.—In Gilbert's (1890) original description of the species, no type-specimen was designated. When the single specimen in a lot now registered as USNM 43091 was transferred to the United States National Museum by Gilbert and his associates, it was indicated in an accompanying letter that this specimen was soon to be described as the type of the species (Susan Jewett, USNM, personal communication, 7 June 1982). After examination of this specimen and the other members of the syntypic series available to me (CAS 5072, USNM 46602, USNM 46605, USNM 46608, USNM 46611 and UW 1416), USNM 43091 is hereby designated as the lectotype. This decision was reached for the following reasons: It appears to have been Gilbert's intention to designate this specimen as the type for the species, it is very close to the average for the species in the majority of characters, and its condition is as good as, if not better than, that of any other member of the syntypic series.

In comparison to its congeners, *X. latifrons* has

TABLE 5. CHARACTERS USED IN DISCRIMINATING AMONG THE SPECIES OF *Xeneretmus*.

| Taxa | Characters | | | |
|-------------------------------|-----------------|-------------------|--------------|---------------|
| | Eye-ball plates | Maxillary barbels | Cheek plates | Pectoral rays |
| <i>Xeneretmus latifrons</i> | 3–6 | 1 | 0 or small | 13–15 |
| <i>Xeneretmus leiops</i> | 0 | 1 | 0 | 13–15 |
| <i>Xeneretmus ritteri</i> | 3–6 | 2 | 0 | 16 |
| <i>Xeneretmus triacanthus</i> | 2–6 | 2–3 | 1–4 | 12–14 |

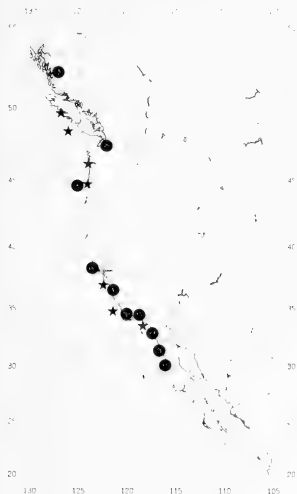


FIGURE 16. Distribution of *Xeneretmus latifrons* (circles) and *X. ritteri* (stars).

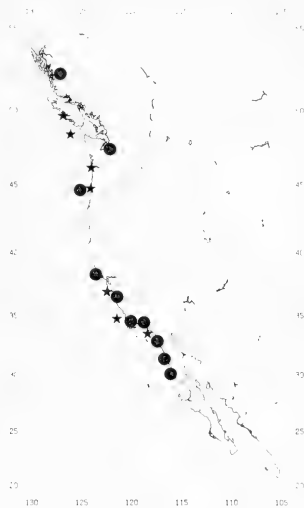


FIGURE 17. Distribution of *Xeneretmus triacanthus* (circles) and *X. leiops* (stars).

low counts for numbers of mid-ventral plates, mid-dorsal plates, infralateral plates, supralateral plates, and vertebrae; and high counts for numbers of unpaired fin rays (Table 3). Its snout is shorter, orbits longer, and interorbital distance greater than those of the other *Xeneretmus* (Table 4).

***Xeneretmus* (*Xenopyxis*) *leiops* (Gilbert)**
[Smoother Poacher]

Xeneretmus (*Xenopyxis*) *leiops* GILBERT, 1915:348 (original description, key, illustration, holotype USNM 75813).
Xenopyxis leiops JORDAN ET AL., 1930:396 (checklist).

MATERIAL EXAMINED.—Forty-four specimens, 67–211 mm.
HOLOTYPE.—USNM 75813, 163 mm, Albatross station 4410, Catalina Island, California, 323–357 m.

PARATYPE.—SU 22988, 2 (108, 136 mm) Albatross station 4410, Catalina Island, California.

ADDITIONAL NON-TYPE MATERIAL.—LACM 93744, 5 (83–160 mm), Catalina Basin, California, 32°N, 118°W.

NMC 67-0348, 2 (147, 163 mm), Rennell Sound, British Columbia, 53°21'N, 133°04'W; NMC 72-0613 (192–211 mm), Barkley Sound, British Columbia, 48°30'N, 126°10'W.

OSU 7305, 67 mm, Newport, Oregon, 44°40'N, 124°10'W; OSU 7309, 15 (134–191 mm), Columbia River, 46°10'N, 124°05'W.

SIO 72-81, 206 mm, Neah Bay, Washington, 48°22'N, 126°10'W.

SU 3623, 7 (132–172 mm), Central California Coast, 34°45'N, 121°29'W; SU 16711, 2 (153, 165 mm), Monterey Bay, California, 36°49'N, 122°30'W; SU 26420, 3 (161–182 mm), Monterey Bay, California, 36°49'N, 122°30'W.

UW 18123, 198 mm, Columbia River, 46°N, 124°W; UW 18473, 2 (171, 179 mm), Columbia River, 46°N, 124°W.

DIAGNOSIS.—Distinguished from the other members of the subgenus by the following combination of characters: absence of dermal plates on eyeball; one barbel at posterior corner of maxilla; 13–15 pectoral rays (Table 5).

DESCRIPTION.—Posterior free-fold of branchiostegal membrane wide; breast plates thin and completely surrounded by skin; one to three barbels at posterior margin of anteriormost acoustico-lateralis pore of dentary, and one or none at posterior margin of middle acoustico-lateralis

pore of dentary; first dorsal whitish at base, black at distal margin, black pigmentation nearly reaching origin of fin, retreating distally posteriorly; second dorsal black at distal margin.

DISTRIBUTION.—Gilbert (1915) described *X. leiops* from specimens captured off Santa Catalina Island, southern California (Albatross station 4410). *Xeneretmus leiops* has a geographic distribution that ranges from Santa Catalina Island north to the Queen Charlotte Islands (Fig. 17). Specimens examined during this study were captured from depths between 183 and 357 m.

COMMENTS.—Relative to its congeners, *X. leiops* has high counts for second dorsal rays, supralateral plates, infralateral plates, mid-dorsal plates, mid-ventral plates, and vertebrae (Table 3). It also has a shorter precaudal region, longer caudal peduncle and orbits, and a smaller interorbital distance than the other members of the genus (Table 4).

***Xeneretmus* (*Xenopyxis*) *ritteri* (Gilbert)
[Stripectin Poacher]**

Xeneretmus (*Xenopyxis*) *ritteri* GILBERT, 1915:350 (original description, key, illustration, holotype USNM 75814).
Xenopyxis ritteri JORDAN ET AL., 1930:396 (listed).

MATERIAL EXAMINED.—Nine specimens, 106–141 mm.

HOLOTYPE.—USNM 75814, 123 mm, Albatross station 4366, Point Loma, California, 320–331 m.

PARATYPE.—SU 22980, 106 mm, Albatross station 4322, San Diego, California, 353–415 m.

ADDITIONAL NON-TYPE MATERIAL.—LACM 88182 2 (111, 137 mm) Gulf of California, Mexico, 29°N, 112°W.

SIO 59-92, 4 (121–141 mm), Cedros Island, Mexico, 28°23'N, 115°21'W; SIO H50-245B, 126 mm, Torrey Pines, California, 32°10'N, 117°10'W.

DIAGNOSIS.—Distinguished from the other members of the subgenus by the following combination of characters: three to six spine-bearing plates on eyeball, two barbels at posterior corner of maxilla, 16 pectoral rays (Table 5).

DESCRIPTION.—Posterior free-fold of branchiostegal membrane narrow; two barbels on ventral margin of dentary, one at posterior margin of each of two anteriormost acoustico-lateral pores; breast plates with bony prickles at centers, each surrounded by skin (such that they do not contact each other at their edges); dorsal fins with black bars along base and distal margin.

DISTRIBUTION.—Gilbert (1915) described *X. ritteri* from specimens captured near San Diego (Albatross stations 4366 and 4322). Since that time *X. ritteri* has been obtained from Cedros Island, Baja California, north to Malibu, Cali-

fornia, and in the northern section of the Gulf of California (Fig. 16). Specimens examined for this study were captured at depths from 274 to 415 m.

COMMENTS.—In comparison to its congeners, *X. ritteri* has low counts for supralateral plates, infralateral plates, mid-dorsal plates, mid-ventral plates, and vertebrae (Table 3). It also has a larger head, a longer precaudal region, and a shorter caudal peduncle than other species of *Xeneretmus* (Table 4). Its spines and ridges are more strongly developed than those of its congeners.

Subgenus *Xeneretmus* Gilbert

***Xeneretmus* (Gilbert) 1915:345**

[Type species *Xeneretmus* (*Xeneretmus*) *triacanthus* Gilbert, 1890, by original designation.]

DIAGNOSIS.—Distinguished from the subgenus *Xenopyxis* by the presence of one to four dermal plates in the cheek region leaving little or no skin exposed in the cheek region (Fig. 14), and the tight arrangement of the breast plates. It further differs in having lower average counts for fin rays in the first and second dorsal, anal, and pectoral fins (Table 3); having larger eyes (Table 4); and in general being slender in comparison.

***Xeneretmus* (*Xeneretmus*) *triacanthus* (Gilbert)
[Bluespotted Poacher]**

Xenochirus triacanthus GILBERT, 1890:91 (original description, lectotype USNM 43089).

Xeneretmus triacanthus GILBERT, in Jordan, 1903:360 (New combination, *Xenochirus* preoccupied).

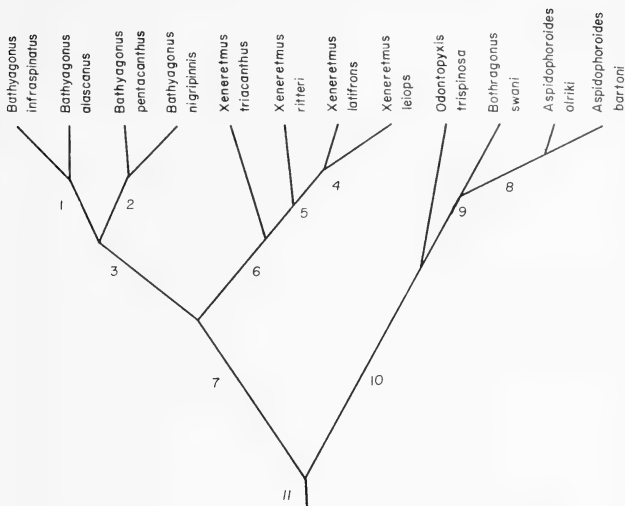
Xeneretmus (*Xeneretmus*) *triacanthus* GILBERT, 1915:345 (description, key).

MATERIAL EXAMINED.—Seventy-six specimens, 74–167 mm.
LECTOTYPE.—USNM 43089, 151 mm, Albatross station 2893, Santa Barbara Channel, California, 34°13'N, 120°33'W, 265 m.

PARALECTOTYPES.—USNM 46601, 2 (124, 154 mm), Albatross station 2893, Santa Barbara Channel, California, 34°13'N, 120°33'W, 265 m; USNM 46606, 117 mm, Albatross station 3059, Lincoln City, Oregon, 44°56'N, 124°13'W, 141 m; USNM 125577, 5 (137–152 mm), Albatross station 2973, Point Conception, California, 34°20'N, 119°44'W, 124 m.

ADDITIONAL NON-TYPE MATERIAL.—CAS 13100, 2 (78, 90 mm), San Pedro, California, 33°43'N, 118°23'W; CAS 14270, 4 (132–144 mm), Monterey Bay, California, 36°48'N, 122°07'W; CAS 26405, 134 mm, Port Hueneme, California, 34°10'N, 119°10'W; CAS 26441, 138 mm, Gaviota, California, 34°05'N, 119°02'W; CAS 47113, 2 (142, 147 mm), Point Baja, California, 30°05'N, 115°58'W.

LACM 320303, 141 mm, Bahia San Quintin, Mexico,



30°18'N, 115°53'W; LACM 322463, 5 (120–155 mm), Santa Monica Bay, California, 33°54'N, 118°25'W.

NMC 65-258, 147 mm, Kwatna Inlet, British Columbia, 52°25'N, 127°34'W.

SIO 51-255-56, 7 (88–151 mm), Channel Islands, California, 34°01'N, 119°24'W; SIO 6047156, 154 mm, Baja California Norte, Mexico, 31°18'N, 116°38'W; SIO 63104256, 8 (75–154 mm), Point Arguello, California, 34°10'N, 120°00'W.

SU 16712, 3 (141–142 mm), Monterey Bay, California, 36°44'N, 121°58'W; SU 19172, 104 mm, Santa Barbara Channel, California, 34°25'N, 120°06'W; SU 21363, 4 (127–148 mm), Point Pinos, California; 36°37'N, 121°55'W; SU 39780, 131 mm, Santa Barbara Island, California, 33°37'N, 119°05'W; SU 39781, 6 (105–134 mm), Santa Barbara Island, California, 34°25'N, 120°18'W.

USNM 59370, 74 mm, Albatross station 3171, Russian River, California, 38°21'N, 123°20'W; USNM 63422, 129 mm, Point Soma, California, 32°41'N, 117°16'W; USNM 63423, 122 mm, Point Pinos, California, 36°38'N, 121°56'W; USNM 63427, damaged, Santa Cruz, California, 36°58'N, 122°01'W; USNM 103719, 136 mm, Mukilteo, Washington, 47°57'N, 122°18'W.

UW 4175, 117 mm, Saratoga Passage, Washington, 47°50'N, 122°30'W; UW 4725, 4 (106–159 mm), Richmond Beach, Washington, 47°50'N, 122°30'W; UW 20948, 9 (129–167 mm), Ballard, Washington, 47°30'N, 122°30'W.

DESCRIPTION.—Two to six spine-bearing plates on eyeball; two, rarely three, barbels at posterior corner of maxilla; 12–14 pectoral rays (Table 5); branchiostegal membrane without a posterior free-fold; three barbels on ventral surface of dentary, one at each posterior margin of three acoustico-lateralis pores; dorsal fins unpigmented, blue spots present on head.

DISTRIBUTION.—Gilbert (1890) described *X. triacanthus* from specimens captured at Albartross stations located off the coasts of California and Oregon, between approximately 34° and 45° N latitude. Material examined in this study ranged from Point Baja, Baja California, north to Kwatna Inlet, British Columbia (Fig. 17). Gilbert (1915) reported *X. triacanthus* occurred in depths from 73 to 364 m; all lots examined for this study fell within that depth range.

COMMENTS.—As was the case for *X. latifrons*, Gilbert (1890) did not designate a type-species for *X. triacanthus*. When the single specimen of

TABLE 6. CHARACTER STATES, NUMBER OF EVOLUTIONARY STEPS, AND THE LOCATION OF THE EVOLUTIONARY STEPS FOR THE DATA OF TABLES 1 AND 2 ON THE CLADOGRAM ILLUSTRATED IN FIG. 18.

| Character states | Number of steps | Branches where the steps take place |
|---|-----------------|---|
| Spination | | |
| Circumorbital 1 spines | | |
| Present, absent | 3 | 6, 9, <i>Bathyagonus nigripinnis</i> |
| Circumorbital 3 spines | | |
| Present, absent | 1 | 10 |
| Pterotic spines | | |
| Present, absent | 2 | 2, <i>Xeneretmus ritteri</i> |
| Posttemporal spines | | |
| Present, absent | 1 | 7 |
| Parietal spines | | |
| Present, absent | 1 | 10 |
| Frontal spines | | |
| Present, absent | 1 | 9 |
| Nasal spines | | |
| One, two | 0 | — |
| Exposed mesethmoid spines | | |
| Present, absent | 0 | — |
| Preopercular spines | | |
| Present, absent | 1 | 10 |
| 2<, ≥2 | 2 | 5, 10 |
| Spines on rostral plate | | |
| Present, absent | 2 | 9, 11 |
| 5, ≠5 | 1 | 3 |
| 3, ≠3 | 1 | <i>Xeneretmus triacanthus</i> |
| 1, ≠1 | 2 | 5, <i>Odontopyxis trispinosa</i> |
| Spines on dermal body plates | | |
| Present, absent | 1 | 9 |
| Free-fold of isthmus | | |
| Present, absent | 4 | 5, 8, 11, <i>Bathyagonus infraspinnatus</i> |
| Maxillary barbels | | |
| ≤1, ≥2 | 2 | 4, 10 |
| <3, ≥3 | 0 | — |
| Exposed rostral plate | | |
| Present, absent | 1 | 11 |
| Breast plates abutting | | |
| True, false | 1 | 5 |
| Presence and arrangement of cheek plates | | |
| Present, absent | 2 | 5, 11 |
| Abutting, not abutting | 3 | 1, 10 <i>Aspidophoroides olrikii</i> |
| Development of thickened fingerlike projection of ventral pectoral fin rays | | |
| Present, absent | 2 | 9, <i>Bathyagonus nigripinnis</i> |
| Slightly developed, greatly developed | | |
| Greatly developed | 2 | 7, <i>Bathyagonus nigripinnis</i> |
| First dorsal fin | | |
| Present, absent | 1 | 8 |

a lot now registered as USNM 43089 was transferred to the United States National Museum by Gilbert and his associates, it was indicated in an accompanying letter that this specimen was soon to be described as the type of the species. That lot is hereby designated the lectotype of *X. triacanthus* for the same reasons cited above (see p. 34).

PHYLETIC RELATIONSHIPS

A Wagner analysis of the binary data set (Table 2) yields Figure 18 as the most parsimonious hypothesis for the cladistic history of the agonid taxa under consideration. This cladogram requires 37 steps for the 25 characters examined. *Xeneretmus*, *Bathyagonus*, and *Aspidophoroides* are all hypothesized to be monophyletic, as is the subgenus *Xenopyxis*. *Bathyagonus* is the sister group of *Xeneretmus*; together they form the sister group of *Odontopyxis*, *Bothragonus*, and *Aspidophoroides*. The character states, the number of steps each character takes on the tree, and where the steps take place are given in Table 6.

The least derived genus *Bathyagonus*, requires only three steps from the base of the cladogram to the node that unites its members. The most derived group consists of *Bothragonus* and *Aspidophoroides*; there are eleven steps required from the root to the node that unites this group. *Xenopyxis* is intermediate between these two groups. There are eight evolutionary steps on the lineage leading from the base of the cladogram to the node that connects its three species.

Monophyly for *Xeneretmus* is evidenced by the loss of spines on circumorbital 1. This character state, however, is not unique to *Xeneretmus*; four other species also lack spines on circumorbital 1, and this loss is hypothesized to have occurred on three separate lineages (Table 6). Wagner analysis attempts to find the cladogram that best fits the entire data set. This may result in hypothesized monophyletic sets that are not supported by unique unreversed characters, as it has for *Xeneretmus*. Their existence is hypothesized because any other arrangement of the taxa would be less parsimonious.

Monophyly for the subgenus *Xenopyxis* is supported by five synapomorphies. The arrangement of the breast plates is the one unique character that unites the subgenus. These plates are separated in all members of *Xenopyxis*, whereas

they abut in all other members of the in-group and the majority of the out-group. The other four characters are not unique to *Xenopyxis*: (1) Possession of one preopercular spine is hypothesized to be a reduction from the ancestral state of two preopercular spines; a reduction in the number of preopercular spines has also occurred on the lineage leading to *Odontopyxis*, *Bothragonus*, and *Aspidophoroides*. (2) The presence of a free-fold of the branchiostegal membrane across the isthmus is hypothesized to be a reversal back to the primitive state, and one that has occurred in two other lineages, *Aspidophoroides* and *Bathyragnus infraspinus*. (3) The possession of only one spine on the rostral plate is a derived character state shared with *Odontopyxis*. (4) The absence of cheek plates is considered to be a reversal back to the primitive condition.

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SPECIES OF THE *EMOIA SAMOENSIS* GROUP OF LIZARDS
(SCINCIDAE) IN THE FIJI ISLANDS, WITH
DESCRIPTIONS OF TWO NEW SPECIES

By

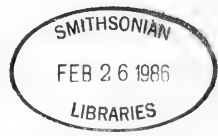
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ABSTRACT: *Emoia* lizards, generally referred to as *E. samoensis* in the Fiji, Samoa, and Tonga islands, actually represent four distinct species, two of which are newly described. *Emoia samoensis* and *Emoia murphyi* are limited to the Samoa and Tonga islands; three species, *Emoia concolor*, *E. trossula* n. sp., and *E. cambelli* n. sp. occur in the Fiji Island group. A key to the species of the *Emoia samoensis* group in the Samoan, Tonga, and Fiji islands is provided.

INTRODUCTION

The Fiji Island group in the South Pacific Basin, about midway between Vanuatu (formerly New Hebrides) to the west and the Samoa and Tonga islands to the east, is comprised of about 320 islands. Several small, limestone and coral islands surround a number of larger, ancient, volcanic islands. The principal large islands are Viti Levu, Vanua Levu, Taveuni, Kadavu, Ovalau, Koro, Gau, Rabi, and Moala.

The Fijis are the Pacific outpost for amphibians, with two endemic species of the ranid genus *Platymantis*. Other terrestrial vertebrates include a number of endemic species, and some endemic genera. Until recently, however, no species of the scincid lizard genus *Emoia* were

thought to be endemic to the Fijis. The recognized species were the apparently wide ranging ones, *E. caeruleocauda*, *E. cyanura*, *E. nigra*, *E. samoensis*, and possibly *E. cyanogaster*.

The present study is primarily concerned with those populations of the *E. samoensis* evolutionary line that occur in the Samoa, Tonga, and Fiji islands and that have generally been referred to the species *E. samoensis*. Other species of this evolutionary line that have previously been recognized as distinct from *E. samoensis* are not considered in detail, although some of them are included in Table 1 and the key at the close of this paper.

The (evolutionary) line of the genus *Emoia* includes species which range from relatively small, *E. parkeri*, to the largest in the genus, *E.*

TABLE 1. SCALE COUNTS AND OTHER PERTINENT CHARACTERS FOR SPECIES OF THE *Emoia samoensis* GROUP OF SPECIES IN THE SAMOA AND FIJI ISLANDS.*

| | Snout-vent length at maturity (mm) | Number in sample for scale counts | Midbody scale rows | Scale rows between parietals and base of tail | Fourth toe lamellae |
|---|------------------------------------|-----------------------------------|--------------------|---|---------------------|
| <i>E. campbelli</i> n. sp. (Fiji Islands) | 68.9-97.8 | 13 | 30-36 | 56-65 | 44-56 |
| <i>E. concolor</i> (Viti Levu Island) | 61.3-78.9 | 16 | 28-32 | 56-60 | 44-52 |
| <i>E. concolor</i> (other Fiji Islands) | 52.8-88.9** | 66 | 28-34 | 54-66 | 44-64 |
| <i>E. murphyi</i> (Samoa and Tonga islands) | 52.2-74.9 | 14 | 26-32 | 52-58 | 59-82 |
| <i>E. nigra</i> | 85.0-121.0 | 20 | 33-40 | 59-72 | 30-39 |
| <i>E. parkeri</i> | 44.5-53.8 | 18 | 28-32 | 52-59 | 34-43 |
| <i>E. samoensis</i> (Samoa Islands) | 78.0-118.0 | 21 | 30-34 | 58-68 | 45-54 |
| <i>E. trossula</i> n. sp. (Fiji Islands) | 66.0-103.0 | 37 | 32-38 | 62-76 | 52-54 |

* Four other species of *Emoia* occurring in these islands belong to other groups (evolutionary lines).

** This size range is based on 50 adults. One specimen measuring 100 mm from Vanisea, Kandavu Islands is referred to this species with some reservations.

nigra. The genus may be characterized as follows: habitus varies from slender to fairly stout; snout moderately tapered and slightly to moderately depressed; subdigital lamellae usually broadly rounded (moderately thinned for two species), and number 30-82 under the fourth toe; number of midbody scale rows 26-42; number of paravertebral rows between parietals and base of tail 52-84; frontoparietals fused; interparietal nearly always distinct, ranging from long and narrow to small; nasal bones separate; parietal eye present; alpha-type palate. This group of species ranges through the south Pacific Islands from Samoa in the east to Vanuatu and Bismarcks in the west.

Emoia samoensis and *E. concolor* were the first species of this group to be described (Duméril 1851). The type locality for *samoensis* was given as Samoa and that for *concolor* as Ambon, an island in the Moluccas to the west of New Guinea. The latter locality was not given in the original description, but subsequently by Jacquinet and Guichenot (1853). Peters (1877) described another species of this complex, *E. resplendens*, from the Fijis, stating that the type was in the Godeffroy Museum.

Boulenger (1887) recognized the close relationship of these three species and placed *E. concolor* and *E. resplendens* in the synonymy of *E. samoensis*. Most later authors (e.g., Werner 1899; Schmidt 1923; Burt and Burt 1932; Smith 1937; Brown 1956), followed this synonymy, assigning specimens from various islands between Samoa and Vanuatu to *E. samoensis*. Exceptions were Roux (1913) who described a race of *samoensis*

from the Loyalty Islands and *E. speiseri* and *E. nigromarginata* from Vanuatu, Burt (1930) who described *E. murphyi* from Samoa, and Schmidt and Burt (1930) who described *E. sanfordi* from the Vanuatu and Solomons. Medway (1974) described yet another species, *E. aneityumensis*, from Vanuatu. At the same time, these authors as well as Medway and Marshall (1975) continued to refer all Fiji specimens as well as examples from some populations in Vanuatu to *E. samoensis*.

Brown (1953:20) recognized that the species *E. concolor* was distinct from *E. samoensis*, but without examining the types and assuming the type locality to be Ambon, erroneously suggested that the species might belong to the *E. physicae* group.

Thus it was not until the 1970s that field work in the Fijis by several zoologists, J. C. Pernetta, D. Watling and W. Beckon among them, began to raise serious questions about the taxonomic status of the Fijian *Emoia* populations. Both Pernetta and Beckon pointed out the coexistence of uniformly colored populations and more typical dark-spotted or banded *samoensis*-like populations on various islands in the Fiji group. Several of the uniformly colored specimens were compared with the type specimens of *E. concolor* by W. C. Brown and were judged to belong to the same species. This evidence, supported by the fact that no examples of the species other than the types have ever been recorded from Ambon, was interpreted as an indication that the types of *E. concolor* were doubtless from the Fijis, and

the locality Ambon was in error. In a subsequent paper, Pernetta and Watling (1979) listed both *E. samoensis* and *E. concolor* (the latter apparently endemic) as occurring in the Fijis, and noted differences in habit as well as color pattern but not other characters for the two groups of populations represented in their samples. Beckon (personal communication) also recognized *samoensis* and *concolor*, suggesting that both could probably be divided into several island races or subspecies. Brown et al. (1980) described a second endemic Fijian species, *E. parkeri*, which is possibly related to *E. nigromarginata* from Vanuatu.

The purpose of this study is to determine the status of those populations of *Emoia* (previously referred to *E. samoensis*) in the Samoa, Tonga, and Fiji islands.

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MATERIALS AND METHODS

We have examined the types of *Emoia samoensis*, *E. concolor*, and *E. murphyi* as well as other examples from the Samoan and Tonga islands. In addition, relatively large samples of *E. sanfordi* from Vanuatu and populations on some of the Fiji Islands, as well as small samples (one to a few specimens) from other islands of the Fijis have also been studied. Data on size at maturity, size of eye, length of snout, length of limbs, variation in color patterns, and scale characters such as number of midbody scale rows, paravertebral scale rows between the parietals and the base of the tail, the number of lamellae beneath the fourth toe of the hind foot, and the pattern of the squamation of the head were determined.

RESULTS

Our analysis of populations in the Samoa, Tonga, and Fiji islands, which were generally referred to *Emoia samoensis*, have shown that these populations represent five distinct taxa. We treat them as separate species and provide detailed descriptions of *E. samoensis* and the Fijian species.

Emoia samoensis (A. Duméril)

Eumeces samoensis (part) Duméril, 1851:157 (type loc.: Samoa; type in Muséum National d'Histoire Naturelle, Paris); Jacquinot and Guichenot, 1853:10, in Hombron and Jacquinot 1853.

Emoia samoensis (part) Girard, 1858:265.

Lygosoma samoense (part) Boulenger, 1887:293; Sternfeld, 1920:407; Boettger 1893:106; Boulenger, 1897:307.

Emoia samoensis (part) Burt and Burt, 1932:531; Mertens, 1934:160; Smith, 1937:227; (part) Brown, 1956:1487; Mittleman, 1952:30; Greer, 1970:171.

Emoia samoense, Schwaner, 1980:8.

Duméril (1851:157) described *Eumeces samoensis* on the basis of two specimens in the Muséum National d'Histoire Naturelle in Paris which were said to be from Samoa. He also attributed the name to Hombron and Jacquinot based on an illustration published earlier (sometime between 1845 and 1851). This illustration

is part of Plate V in the Atlas (1845–1853) which accompanied Jacquinot and Guichenot's text (1853). However, the plate bears only the French name *Eumeces* de Samoa and therefore does not establish publication of the valid scientific name.

Scale counts and color (even in the faded condition) of the syntypes of *Emoia samoensis*, however, indicate that only one of them (MNHN 7070) is in close agreement with other examples from the populations in the Samoa Islands. And even though the head is damaged on one side, this specimen must be chosen as the lectotype. The second syntype (MNHN 7070a), the undamaged one and the one apparently used for the illustration in Hombron and Jacquinot, even in its present faded condition, exhibits some distinct white longitudinal dashes on the dorsum (prominent in the illustration), which are typical of most examples of the larger, previously undescribed species from the Fijis.

MATERIAL EXAMINED.—Samoa Is. (without definite locality): MNHN 7070 (syntype), 81; RMHN 3103; ZMC 373–374; BMNH 66.8.25.2; MCZ 3951, 8963. Upola Is.: CAS 157233; MCZ 69487; AMNH 29241, 29245; BMNH 1969.631–633; AM R1473. Tutuila Is.: CAS 50236–38; CAS-SU 13600–603, 18071; AMNH 27206, 27695, 27702, 27706. Savaii Is.: AMNH 41737–38, 41744. Tau Is.: AMNH 27668–73, 27675–76. Western Samoa: BMNH 1969.622–24, 1969.628–30.

LECTOTYPE (NEW DESIGNATION).—MNHN 7070, collected on Samoa during the voyage of the *Astrolabe* and the *Zelee*, 1837–1840.

DESCRIPTION OF LECTOTYPE.—Adult male, snout-vent length 105+ mm; head damaged but most head-shield characters recognizable; rostral broader than high, forming slightly curved suture with frontonasal; prefrontals in contact; frontal damaged but was in contact with first and second supraoculars; four large supraoculars; interparietal moderate size; anterior loreal about as long as posterior, in contact with first and second and probably third upper labials; sixth upper labial on right side enlarged and beneath eye; dorsal scales smooth, vertebral rows not distinctly enlarged; 32 midbody scale rows; 59 paravertebral rows between parietals and base of tail; 52 rounded lamellae under fourth toe; 16 under first toe.

COLOR (IN PRESERVATIVE).—Surface layer lost from most scales, but remaining undamaged scales indicate a dorsal pattern of olive green with blackish blotches.

DEFINITION (BASED ON SAMPLE OF ABOUT 20 SPECIMENS).—A relatively large *Emoia*, snout-vent length 78–118 mm for 120 mature males

and 84–114 mm for 80 mature females (data from Schwaner 1980:8); habitus moderately stout with well-developed limbs; snout moderately tapered, rounded at tip, its length 36–40% of head length and 56–68% of head breadth; head breadth 57–60% of head length and 13–16% of snout-vent length; eye moderate, its diameter 52–73% of snout length and 30–42% of head breadth; ear diameter $\frac{1}{2}$ –% of eye diameter with three or four small lobules anteriorly; rostral broader than high, forming moderate, nearly straight suture with frontonasal; prefrontals in moderate contact (occasionally narrowly separated); frontal longer than broad, about as long as or slightly longer than fused frontoparietals, broadly rounded posteriorly, in contact with first and second supraoculars; four large supraoculars; six to seven supraciliaries; interparietal moderately long and narrow to moderately wide; parietals in contact posteriorly; one pair of nuchals; anterior loreal shorter than to about as long as and higher than posterior loreal, in contact with first and second, second and third, or first, second, and third upper labials; six to eight upper labials, sixth (rarely fifth or seventh) largest and beneath eye; usually seven lower labials; scales smooth, paravertebral rows not enlarged or only slightly enlarged; 30–35 midbody scale rows (very rarely greater than 34); 58–68 paravertebral rows between parietals and base of tail; limbs well developed, length of extended hind limb 86–110% of axilla-groin distance and 46–54% of snout-vent length; 45–54 rounded lamellae beneath fourth toe; 13–16 lamellae beneath first toe; rank of adpressed toes from longest to shortest four, three, two through five, one; tail longer than body.

MEASUREMENTS (IN MM) OF LARGE FEMALE (CAS 50238).—Snout-vent length 107.0; axilla-groin distance 54.4; hind limb length 55.2; head length 25.6; head breadth 16.0; snout length 9.6; eye diameter 6.2; ear diameter 2.1.

COLOR (IN PRESERVATIVE).—Dorsal ground color is greenish-tan to tan, marked with few to numerous dark brown spots varying from less than scale-size to vague, irregular transverse bands or partial bands involving several scales in transverse rows. Occasionally these show short whitish bars as in *E. trossula*. The venter is yellowish ivory to dusky tan. The top of head is not distinctly darker than the body.

NOTE ON REPRODUCTION.—Schwaner (1980:8) states that the clutch size for 30 specimens ranges

FIGURE 1. *Emoia concolor*.

from 4–7 eggs. He gives a snout-vent length of 31 mm for one hatchling.

HABITAT NOTE.—Schwaner (1980:8) states that examples of this species were found primarily on tree trunks and low vegetation at heights from near ground level to several meters. This skink is diurnal.

RANGE.—This species occurs in Samoa.

***Emoia concolor* Duméril**

(Figure 1)

Euprepes concolor Duméril, 1851:62 (type loc.: Fijis (?); type in Muséum d'Histoire Naturelle, Paris).

Emoia samoensis (part) Girard, 1858:264.

Euprepes samoensis (?) Steindachner, 1867:44.

Euprepes resplendens Peters, 1877:416.

Lygosoma samoense (part) Boulenger, 1887:293.

Lygosoma cyanogaster (part?) Boettger, 1893:106.

Lygosoma cyanogaster tongana (part, Fiji Islands) Werner, 1899:375.

Emoia samoense (part) Schmidt, 1923:52.

Emoia samoensis (part) Burt and Burt, 1932:531; (part) Smith 1937:227; (part) Brown, 1956:1487; Greer, 1970:171; (part)

Pernetta and Watling, 1979:236.

Emoia concolor, Pernetta and Watling, 1979:236.

As noted in the introduction, this species has long been regarded as a synonym of *E. samoensis*, the latter having been thought to range from Samoa to Vanuatu and to be the only species of

the complex represented in the Fijis. Only recently has *E. concolor* been recognized as a valid species and name correctly applied to some Fijian populations.

Peters (1877) based his brief description of *E. resplendens* on a single example from Ovalau Island. Several early specimens labeled *L. samoense* of the Godeffroy Museum collections are now in the Zoologisches Museum, Universität Hamburg, so it is reasonable to assume that the type specimen of *E. resplendens* was also transferred to that museum. However, Professor Hans Wilhelm Koeppke (personal communication) states that many of the herpetological types (including *E. resplendens*) and type catalogues were lost or destroyed during World War II. Thus the status of *E. resplendens* (Peters) must be based on the original description.

Peters's count for midbody scale rows (30) and note on color, "metallic gold luster with numerous, dark brown dots arranged in transverse lines," would indeed seem to identify this specimen as an example of *E. concolor*, since this color pattern is exhibited by some examples of *E. concolor* from various islands. Thus, basing our conclusion on Peters's data and color description, we regard *E. resplendens* as a synonym of *E. concolor*. Werner's (1899:375) specimen

from the Fijis, which was referred to *E. cyanogaster tongana*, is almost certainly an example of *E. concolor* although he states that there are only 26 midbody scale rows.

Emoia concolor, though similar to *E. samoensis* in midbody scale rows, is a smaller species than either *E. samoensis* or *E. trossula* and typically has fewer scale rows between the parietals and the base of the tail, and more frequently exhibits a nearly uniform color on the dorsum.

Emoia concolor has a wide range in the Fijis, and there is evidence that some island populations differ sufficiently from one another to warrant recognition as subspecies. However, pending the availability of samples from as yet unexplored islands and larger samples from some already explored we hold such a decision in abeyance.

MATERIAL EXAMINED.—Fiji Is. (without definite locality): MNHN 7084, 7084a (syntypes); AM R6448a-b, 6449a-b, 6450a-c, 6451a-c; MCZ 9133, 9144; BMNH 55.11.7.24, 63.5.11.14-15, 75.12.31.10-13. Eastern Lau Group: AMNH 41750, 40195, 48058, Moala Is.: AMNH 41708. Kadavu Is.: BMNH 82.8.29.169-70; AM R30442, 30445; MCZ 15014, 16943-44; FMNH 3497; CAS 155974-85. Cikobia Is.: AMNH 29007. Vanua Levu Is.: BMNH 87.8.25.41; Pernetta coll. 252, 282. Viwa Is.: Pernetta coll. 117-119, 122-123. Yaduataba Is.: CAS 156002-04. Dravuni Is.: MCZ 16930-40; FMNH 3498a-d. Nagasan Is. (=Yagasa Is.): MCZ 16947-48. Lami Is.: MCZ 48958. Viti Levu Is.: MCZ 16459; FMNH 62796, 69241, 69639, 71764, 71772; BMNH 1940.1.17.7, 1945.11.5.9, 1947.3.1.86; Pernetta coll. 181, 167, 203, 205, 207-90; FM R41, 4, 12, 43; CAS 102361, 156136-37. Matuku Is.: USNM 230221-26. Kori Is.: USNM 230019-21. Ovalau Is.: FMNH 170716, 13641; USNM 230104-05. Taveuni Is.: BMNH 1959.1.2.32. Rotuma Is.: BMNH 97.7.29.8. Gau Is.: Watling coll. 501, 526, 543. Bird Is. (small island near Viti Levu): AM R109939-43.

LECTOTYPE.—MNHN 7084, collected during the voyage of the *Astrolabe* and the *Zeelee*, 1837-1840.

DESCRIPTION OF LECTOTYPE.—Male, 87 mm snout-vent length; rostral broader than high, forming long, nearly straight suture with frontonasal; prefrontals in moderate contact; frontal longer than broad, about as long as frontoparietals and interparietal, in contact with first and second supraoculars; four large supraoculars; interparietal moderate in size; frontoparietals fused; one pair of nuchals; anterior loreal nearly as long as and not much higher than posterior, in contact with second upper labial and supranasal; sixth upper labial enlarged and under eye; some dorsal scales with three or four faint keels; paravertebral rows not enlarged or only slightly enlarged; 34 midbody scale rows; 60 paravertebral rows be-

tween parietals and base of tail; 60 moderately rounded lamellae beneath fourth toe; 16-17 beneath first toe; tail longer than body.

COLOR (IN PRESERVATIVE).—Relatively uniform yellowish olive-green on dorsum and upper lateral surfaces; lower lateral surfaces have bluish tinge and venter dirty ivory.

The following definition, based on a series of more than 50 specimens, provides data on the variation exhibited by this species.

DEFINITION.—An *Emoia* of moderate size, snout-vent length 52.3-88.7 mm for 22 males and 52.8-73.5 mm for 6 females (the sex of the syntype at 87 mm has not been determined, also a unique specimen, FMNH 3497, labeled from Vanuisea on Kadavu Island and measuring about 100 mm, is referred to this species with some reservations); habitus moderately slender; snout moderately tapered, rounded at tip, its length 35-42% of head length and 55-66% of head breadth; head breadth 52-68% of head length and 13-17% of snout-vent length; eye diameter 52-70% of snout length and 30-45% of head breadth; ear diameter $\frac{1}{5}$ - $\frac{1}{2}$ of eye diameter; ear usually with three small, rather pointed lobules anteriorly; rostral broader than high, forming a long, straight or slightly concave suture with frontonasal; supranasals long and narrow, in contact with anterior loreal; prefrontals in moderate contact (rarely very narrowly separated); frontal longer than broad, usually longer than fused frontoparietals, broadly rounded posteriorly, in contact with first and second supraoculars; four large supraoculars; interparietal of moderate length and breadth; parietals in contact posteriorly; one pair of nuchals; anterior loreal somewhat shorter than to nearly as long as posterior and slightly higher, in contact with first and second, second, or first, second, and third upper labials; seven or eight upper labials, sixth (very rarely fifth) enlarged and beneath eye; usually seven lower labials; dorsal scales smooth or with two or three weak striations; paravertebral rows not enlarged or scarcely enlarged; 28-34 (see Table 1) midbody scale rows; 54-63 paravertebral rows between parietals and base of tail; limbs well developed; length of extended hind limb 89-104% of axilla-groin distance and 44-54% of snout-vent length; 46-68 rounded lamellae under fourth toe and 14-18 beneath first toe; rank of adpressed toes from longest to shortest four, three, two through five, one; tail longer than body.

FIGURE 2. *Emoia trossula*.

MEASUREMENTS (IN MM) OF MALE (AM 6448A).—Snout-vent length 73.5; axilla-groin distance 34.8; hind limb length 36.0; head length 19.3; head breadth 11.7; snout length 7.4; eye diameter 4.8; ear diameter 2.0; tail broken.

COLOR (IN PRESERVATIVE).—Dorsal ground color is nearly uniform greenish tan or with a few scattered brown spots or short bars to nearly solid, brownish longitudinal stripes (see Fig. 1); ground color more greenish yellow on lower lateral surfaces; venter more yellowish white or nearly turquoise (pale yellow to lime green in life); top of head and lower limbs often somewhat darker tan than rest of dorsum; sometimes yellow spots on posterior surface of thighs; digits sometimes with dark brown, transverse bands.

NOTE ON REPRODUCTION.—Three hatchlings measure 26.3–28.1 mm in snout-vent length. Gravid females have two eggs.

HABITAT NOTE.—*Emoia concolor* is a lowland species from sea level to 500 m. It occurs both in the relatively open, intermediate-zone woodlands and lowland forests, and in agricultural and suburban areas such as coconut and mango groves.

RANGE.—This species is widely distributed in the Fiji Islands. Steindachner's 1869 reference to

Stuart Island is presumably Unganga Island in the Fijis which some nineteenth century charts call Stuart.

Emoia trossula n. sp.

(Figure 2)

Eumeces samoensis (part) Duméril, 1851:157.

Lygosoma samoense (part) Boulenger, 1887:293; Werner, 1899:375.

Emoia samoense (part) Schmidt, 1923:52.

Emoia samoensis (part) Burt and Burt, 1932:531; (part) Brown 1956:1487; (part) Pernetta and Watling, 1979:236.

This distinctively colored species from the Fijis has long been confused with *E. samoensis*. Even one of the two syntypes of the latter in the National Museum in Paris (MNHN 7070a), although indicated as being from the Samoa Islands in the catalogue, is an example of this species. It exhibits the color pattern and scale counts of the Fijian populations referred to this species (see also p. 44).

HOLOTYPE.—AM R30433, an adult male, collected on Ovalau Island, Fijis, 6 May 1970, by Harold G. Cogger.

PARATYPES.—Fiji Is. (without specific locality): MNHN 7070a (one of syntypes of *E. samoensis*), 5573, 5573a–b; USNM 58155, 58166; AMNH 20927; AM R6446, R8566, A9463; BMNH 75.12.31.6, 62.10.23.4. Ovalau Is.: FMNH 13642,

13644-45; AM R30586, R30616-18; AMNH 40491. Yadauataba Is.: USNM 230301; CAS 156128-29, 155960-62. Kadavu Is.: AM R30446; AMNH 40489; BMNH 82.8.29.185. Aiwa Is.: AMNH 29917-22. Koro Is.: AMNH 40506. Thithia Is.: AMNH 40196. Moala Is.: AMNH 40223. Vatu Vara Is.: CAS 156130; AMNH 29010-11. Gau Is.: AMNH 40503. Buki Levu Is. (possibly part of Kadavu): MCZ 16945. Lakeba Lau Is.: MCZ 16965. Doi Lau Is.: MCZ 16941-42. Tuvuca Is.: AMNH 40539; BMNH 81.10.12.10. Namena Is.: BPBM 1504; AMNH 40441-43, 40445. Taveuni Is.: CAS 155958; BMNH 1938.8.29. Viti Levu Is.: ZMH R01976-77. Rotuma Is.: BMNH 97.7.29.9-10. Gau Is.: Watling coll. 524-25, 541-42. Kia Is. (a small island near Viti Levu): R116160.

BMNH 1860.3.18.8 and 1860.3.18.11, which were purchased from Mr. Cuming, are stated to be from Eumonga and Vanuatu. However, since they agree in most characters with examples from populations of *E. trossula* from the Fijis and not with samples from any of the species known from Vanuatu, we assume that the locality data are probably in error and have referred these two specimens to *E. trossula*, but have not included them in the paratypes.

DIAGNOSIS.—This species differs from other species of the *Emoia samoensis* group in the following combination of characters: (1) 32-40 (rarely less than 34) midbody scale rows; (2) 62-76 paravertebral scale rows between the parietals and the base of the tail; (3) 42-54 lamellae under the fourth toe; (4) snout-vent length for adults 66.5-103.0 mm; (5) some features of color pattern that are generally present, such as short, narrow, greenish white longitudinal dashes on dorsum and upper lateral surfaces. These dashes are more or less in rows occupying the middle region of the concerned scales and are most prominent on the lighter, dorsal transverse bands and above the spaces between the dorsolateral dark blotches.

DESCRIPTION.—A relatively large *Emoia*, snout-vent length 67.0-101.6 mm for 7 mature females and 66.5-103.0 mm for 14 mature males (2 specimens measuring 58.7 and 69.0 mm appear immature); habitus moderately stout with well-developed limbs; snout moderately tapered, rounded at tip, its length 33-39% of head length and 51-65% of head breadth; head breadth 56-60% of head length and 13-17% of snout-vent length; eye moderate, its diameter 60-81% of snout length and 34-48% of head breadth; ear diameter about $\frac{1}{3}$ - $\frac{1}{2}$ of eye diameter, with three or four small, white lobules anteriorly; rostral broader than high, forming a moderate, slightly concave suture with frontonasal; supranasals slightly broader anteriorly than posteriorly, in contact with anterior loreal; prefrontals narrowly separated to moderately in contact; frontal longer than broad, about as long as fused frontopari-

etals, rounded posteriorly, in contact with first and second supraoculars; four large supraoculars; interparietal relatively long and moderately narrow; parietals in contact posteriorly; one pair of nuchals; anterior loreal slightly shorter than to nearly as long as posterior and slightly higher, usually in contact with first and second, second only, or first, second, and third upper labials; six to eight upper labials, sixth (rarely fifth or seventh) largest and beneath eye; usually seven lower labials; scales smooth for adults, a hatchling with faint keels; middorsals only slightly enlarged; 32-38 (very rarely less than 34) midbody scale rows; 61-76 paravertebral rows between parietals and base of tail; limbs well developed, length of extended hind limb 96-109% of axilla-groin distance and 47-53% of snout-vent length; 43-54 rounded lamellae beneath fourth toe and 13-16 beneath first toe; rank of adpressed toes from longest to shortest four, three, two through five, one; tail longer than body.

MEASUREMENTS (IN MM) OF HOLOTYPE, AN ADULT MALE.—Snout-vent length 94.3; axilla-groin distance 48.2; hind limb length 49.1; head length 22.4; head breadth 14.3; snout length 8.6; eye diameter 6.45; ear diameter 2.6; tail length 140.

COLOR (IN PRESERVATIVE).—Ground color of the dorsum and upper lateral surfaces nearly uniform medium brown to greenish olive-brown, or most often marked by irregular, lighter and darker transverse bands and by a series of dark blotches on the dorsolateral surface.

Usually there are few to numerous, narrow, greenish white, longitudinal dashes occupying the median part of each affected scale. These are primarily on the lighter bands and above the dark, dorsolateral blotches, usually in longitudinal rows. The lower lateral surfaces are bluish gray fading into the bluish white of the venter which is lightly to densely spotted or flecked with small, black marks, at least posteriorly.

ETYMOLOGY.—The name *trossula* is from the Latin meaning dandy, and refers to the colorful spotting like a brightly colored coat.

COMPARISONS.—The number of paravertebral rows (62-76) is greater than that of other species of the *E. samoensis* group except for *E. aneityumensis* from Vanuatu which it barely overlaps. Also, the white dashes in the dorsal color pattern (nearly always present) are most prominent in this species. Boulenger (1887:294), Werner (1899:375), and Burt and Burt (1932:531) noted these white markings for some specimens but did not

FIGURE 3. *Emoia campbelli*.

observe that they were primarily limited to Fiji specimens. Nor did they have a sufficiently large series to recognize that in addition to being divisible on the basis of two color patterns, the Fiji samples also show bimodal curves for the number of midbody scale rows and scale rows between parietals and base of the tail.

Emoia trossula is most closely related to *E. samoensis*. They are similar in size, but *E. trossula* differs in color pattern and has a greater number of midbody scale rows and a slightly higher number of paravertebral rows between the parietals and the base of the tail (see Table 1). *Emoia sanfordi* from Vanuatu is also a large species but differs in color pattern and has a much greater number of lamellae. *Emoia concolor* is smaller than *E. trossula* and has a lower number of midbody scale rows.

NOTE ON REPRODUCTION.—Gravid females have two to five large eggs in the oviducts. One hatchling measures 32.3 mm from snout to vent.

HABITAT NOTE.—This species is primarily a semi-arboreal forest form. On Yaduataba Island it was found both in the trees and on the forest floor. Some specimens were also seen asleep on open tree branches. Such habits as well as its relative boldness may have led to its extinction on many islands, possibly due to predation by

mongooses and feral cats. Beckon's notes indicate that in inhabited areas on Taveuni Island this species was found in trees but on Kadavu Island this species was found in the forest, on or near the ground. On Gau Island *E. trossula* was found from the coastal areas up to an elevation of about 650 m in the rain forest.

RANGE.—This species now has a patchy distribution in the Fiji Islands and is almost certainly extinct on the main islands of Viti Levu and Vanua Levu. The two specimens in the Hamburg Museum (ZMH R01976–77) that are recorded from Viti Levu were collected early in the nineteenth century. It is suggested that the introduction of the mongoose in 1887 may have led to this extinction. This theory would appear to be indirectly supported by the fact that *E. nigra*, a primarily terrestrial skink of about the same size as *E. trossula*, is also absent from Viti Levu but common on some other islands on which *E. trossula* still occurs. Thus far *E. trossula* has been recorded from the Fiji Islands.

***Emoia campbelli* n. sp.**

(Figure 3)

HOLOTYPE.—CAS 156256, an adult female collected by John Gibbons in the upper canopy of the cloud forest at Monsasavu



FIGURE 4. Section of "Ant plant" showing chambers in which eggs of *Emoia campbelli* were found.

on the Rairaimatuku Plateau at an elevation of about 750 meters on Viti Levu Island in December 1983.

PARATYPES.—CAS 155967–73, CAS 156257–58, CAS 156710–12 and USPM 46–48 from the same locality as the holotype; Viti Levu Island: ZMH R01978.

DIAGNOSIS.—The species can be distinguished from other species of the *E. samoensis* group on the basis of the following combination of characters: (1) midbody scale rows 30–36 (rarely below 32); (2) scale rows between parietals and base of tail 56–64; (3) fourth toe lamellae 48–54; (4) snout-vent length at maturity 69–98 mm; (5) prefrontals in relatively broad contact; and (6) color pattern: usually large, pale (yellowish in life) blotches along dorsolateral margin, separated by short, irregularly margined, blackish bars. (These spots are small or very faint in two specimens.)

DESCRIPTION.—A moderate sized to relatively large *Emoia*, snout-vent length 70.4–97.8 mm for four males and 68.9–96.0 mm for five females (a female measuring 64.2 mm is apparently immature); habitus moderately stout with well-developed limbs; snout rather strongly tapered, rounded at tip, its length 56–68% of head breadth and 35–42% of head length; head breadth 56–70% of head length and 13–17% of snout-vent length; eye moderate, its diameter 56–72% of snout length and 33–43% head breadth; ear diameter 33–40% of eye diameter; rostral broader than high, forming long, nearly straight suture with frontonasal; supranasals narrowly triangular, in contact with anterior loreal; prefrontals in moderately broad contact; frontal longer than broad, about as long as fused frontoparietals, in contact with first and second supraoculars; four large supraoculars; interparietal moderate; pa-

rietals in contact posteriorly; one pair of nuchals; anterior loreal nearly as long as posterior, in contact with first and second, second and third, or first, second and third upper labials; seven or eight upper labials, sixth (rarely seventh) enlarged and beneath eye; six or seven lower labials; scales smooth; middorsal scales slightly enlarged; 30–36 (rarely less than 32) midbody scale rows; 56–64 paravertebral rows between parietals and base of tail; limbs well developed, length of extended hind limb 88–107% of axilla-groin distance and 45–52% of snout-vent length; 44–56 rounded lamellae under 5th toe; 14–17 under 1st toe; rank of adpressed toes from longest to shortest four, three, two through five, one; tail longer than body.

MEASUREMENTS (IN MM) OF HOLOTYPE.—Snout-vent length 97.8; axilla-groin distance 48.0; length of hind limb 45.6; head length 21.6; head breadth 13.8; snout length 8.9; eye diameter 5.0; ear diameter 1.7; tail length 136.

COLOR (OF FRESHLY PRESERVED SPECIMENS).—Middorsal three or four rows of scales grayish to grayish olive green or light grayish brown, marked by black spots or dashes (in some specimens the black scales form either broken or very irregular transverse bands). Top of head is usually darker (slate brown), occasionally the same as the body; upper lateral surfaces usually marked by small to large (two to eight scales), yellow blotches alternating with black blotches between the nape and the groin (they are evident for some examples of both sexes); lower lateral surfaces mottled grayish tan and bluish green marked by blackish flecks and dashes; venter bright sulfur yellow to greenish yellow, often with a blood red diffusion posteriorly, and on the base of the tail in life (fading in preservative); with small black dashes posteriorly, along midline, on preanals and sometimes base of tail.

ETYMOLOGY.—This species is named for Mr. John Campbell, who collected the first example of this species in the Monasavu area.

NOTE ON REPRODUCTION.—Eggs of this species have been found in the chambers of "ant plants." Figure 4 shows the chambers in a section of one of these plants. One gravid female has two large eggs.

HABITAT NOTE.—Field observations by the junior author indicate that this species uses as shelter primarily, if not exclusively, "ant plants" of the genus *Hydnophytum*, epiphytic in trees in the montane forests. It forages on the branches of

the trees. Only one juvenile has been found on the ground.

RANGE.—This species has thus far been found only on the Nadrau Plateau in the mountains of Viti Levu Island.

COMPARISONS.—*Emoia campbelli* is probably most closely related to *E. concolor* and *E. nigromarginata*. It differs from both in color pattern, a slightly higher number of midbody scale rows, and a somewhat larger size. It also differs from *E. nigromarginata* in the somewhat greater number of lamellae.

The morphological differences separating *E. campbelli* from *E. concolor* are not as great as those separating *E. trossula* from *E. concolor*, and we were at first inclined to regard this population as a montane subspecies of *E. concolor*. However, *E. campbelli*, based on our available sample from the Monasavu area on the Rairaimatuku Plateau (part of the Nadrau Plateau), 750 to 1,200 m elevation, in the montane rain forest, is apparently strictly arboreal, at least in the adult stage. Also it seems to prefer the arboreal "ant plant" as a resting place and even deposits its eggs in cavities of that plant. Furthermore the montane forests of the plateau are effectively isolated from the lowland forest on three sides by high vertical cliffs and by a partially grassland corridor on the fourth side. *Emoia concolor* is a less specialized, primarily lowland species, which is at home in a variety of habitats, many of them much drier than the montane forest (see note on habitat for *E. concolor*). Because of its specialized habitat preference and isolation, we treat *E. campbelli* as a distinct species.

DISCUSSION

Much larger samples were available to us than to earlier authors, and we were able to assess more accurately the limits of variation for many populations and therefore more clearly define species and determine their ranges. As stated in the introduction and the diagnostic key, the populations from the Fijis represent taxa distinct from *E. samoensis* in the Samoa Islands.

Emoia samoensis generally attains a larger size than does *E. concolor* from the Fijis although these two overlap in scale counts and color pattern. *E. trossula* n. sp. is similar in size to *E. samoensis* and *E. sanfordi* from Vanuatu, but differs from these as well as from *E. concolor* in some scale counts (Table 1) and usually in some

features of the color pattern. *Emoia campbelli*, the other new Fiji species, is thus far known only from a population on the Nadrau Plateau in the mountains on Viti Levu Island. For most species of the *E. samoensis* complex the dorsal color tends to vary, but the basic patterns are different. The least variation is characteristic of *E. campbelli* and *E. trossula*. The latter only infrequently exhibits a nearly uniform brown or greenish olive brown color on the dorsum. *Emoia concolor*, as presently diagnosed, exhibits a uniform greenish color, or various patterns of brownish markings. Also, for *E. concolor* at least on Viti Levu, individuals exhibiting a uniform pattern are found almost exclusively in the coastal and open woodlands of the lowlands while those exhibiting varying density of dark spots, often bands or lines, on the dorsum occur primarily in the more dense lowlands and montane forests (see Perretta and Watling 1979). These authors assigned these apparent color morphs to *E. concolor* and *E. samoensis* respectively.

Emoia murphyi is closely related to *E. concolor* and *E. trossula* is closely related to *E. samoensis*.

The following key and table set forth the diagnostic characters and known ranges for the seven species included in this study. Populations in Vanuatu heretofore identified with *E. samoensis* must be reexamined to determine their true taxonomic status and relationship to other species of *Emoia* now recognized as occurring in Vanuatu and the Loyalty Islands.

KEY TO THE SPECIES OF THE *EMOIA SAMOENSIS* GROUP IN THE SAMOA AND FIJI ISLANDS

- 1a. Midbody scale rows 26–36 (rarely greater than 34) 2
- 1b. Midbody scale rows 32–40 (rarely less than 34) 3
- 2a. Fourth toe lamellae 30–39; snout-vent length at maturity 85–121 mm; interparietal very small; dorsal and upper lateral surfaces dark brown to almost black, nearly uniform, with scattered pale spots, or sometimes with vague, irregular transverse bands *E. nigra*
- 2b. Fourth toe lamellae 42–54; snout-vent length at maturity 66–103 mm for 20 specimens; interparietal long; dorsal color pattern greenish olive brown to medium brown usually with darker blotches or

bands and with few to numerous whitish dashes (Fiji Islands) *E. trossula* n. sp.

- 3a. Fourth toe lamellae 34–43; snout-vent length at maturity 46–54 mm; color pattern marked by a golden bronze head, a greenish bronze to greenish blue vertebral stripe about two scale rows in breadth; bordered by a blackish or dark brown band with scattered pale scales; a similar band on the upper labial surface (Fiji Islands)

E. parkeri

- 3b. Fourth toe lamellae 44–83 (very rarely less than 45); snout-vent length at maturity 52–118 mm; color variable but not as above

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- 4a. Fourth toe lamellae 59–82 (rarely less than 63); color of dorsum dull grayish to grayish tan, darker posteriorly with a few vague dark and light spots, especially dorsolaterally (known from Samoa and Tonga islands)

E. murphyi

- 4b. Fourth toe lamellae 44–66 (very rarely greater than 62); color of dorsum usually greenish tan, with or without darker markings

5

- 5a. Midbody scale rows 30–36 (very rarely fewer than 32, mean 33.1); color pattern of middorsal area greenish olive with scattered, dark and light spots or sometimes nearly complete, dark and light bands; dorsolateral area usually marked by a series of large pale to yellowish blotches separated by narrow, blackish bars (mountains of Viti Levu Island, Fijis)

E. campbelli

- 5b. Midbody scale rows 28–35 (rarely greater than 32); color variable but not as above

6

- 6a. Scale rows between parietals and base of tail 54–63 (rarely greater than 60); snout-vent length at maturity 53–88 mm; color pattern of dorsum, four phases: (1) relatively uniform greenish to greenish tan, (2) greenish, marked by few to numerous brown to blackish spots, (3) dark spots in narrow longitudinal lines, or (4) occasionally marked by a series of pale and dark (in preservative usually brownish) more or less complete, transverse bands (Fiji Islands)

E. concolor

- 6b. Scale rows between parietals and base of tail 56–68 (rarely less than 58); snout-vent

length at maturity 78–118 mm; color pattern of dorsum: (1) nearly uniform greenish to greenish tan; or (2) with scattered brownish to blackish spots, sometimes forming transverse bands, very rarely marked by whitish dashes (Samoa)

E. samoensis

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QUATERNARY BARNACLES FROM THE GALÁPAGOS ISLANDS

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ABSTRACT: Quaternary marine deposits on six islands in the Galápagos Archipelago have yielded at least nine species of balanomorph barnacles, seven of which are present in the extant Galápagan fauna. The mid-intertidal species *Tetraclita milleporosa* Pilsbry and the lower intertidal to subtidal species *Megabalanus galapaganus* (Pilsbry) and *Balanus trigonus* Darwin are most common. The whale barnacle *Coronula diadema* (Linnaeus) and the turtle barnacle *Chelonibia testudinaria* (Linnaeus) are represented by unique specimens at separate localities. *Balanus poecilus* Darwin and a shell tentatively identified with *B. calidus* Pilsbry were found at one locality. A species of *Concavus* that might represent *C. (Arossia) panamensis eyerdami* (Henry), and a *Tetraclita* shell bearing marked similarity to that of *T. rubescens rubescens* Darwin were present at single localities. Neither *Concavus* nor *Tetraclita rubescens* is known from the extant Galápagan fauna.

INTRODUCTION

As a participant in the 1964 Galápagos International Scientific Project, I had an opportunity to study the extant cirriped fauna of the Galápagos Archipelago, and to collect a few fossil barnacles from Cerro Colorado on Isla Santa Cruz. Some aspects of the extant fauna were published (Zullo 1966; Zullo and Beach 1973). The lack of adequate fossil material has prevented any serious speculation on the antiquity of the extant fauna and, indirectly, on the antiquity of intertidal and shallow-water habitats in the Galápagos Archipelago.

During February 1982, Carole Hickman, Matthew James, Jere Lipps, and Lois and William Pitt made an extensive survey of fossiliferous marine deposits in the Galápagos. Of the 84 samples taken on seven islands, 12 localities on six islands contained barnacle remains (Fig. 36, 37). Lipps and Hickman (1982) argued that none of the Galápagan fossil localities is older than two million years, and that some types of deposit are only a few hundred years old. This conclusion is

contrary to previous Miocene or Pliocene age estimates for several of these localities (e.g., Dall and Ochsner 1928; Durham 1964), but the completely modern aspect of the fossil barnacle fauna would appear to support a Quaternary age assignment.

PALEONTOLOGY

All of the species represented by fossils are either found today in the intertidal zone or at depths less than 20 m. The mid-intertidal species *Tetraclita milleporosa* Pilsbry, and the low intertidal zone and shelf species *Megabalanus galapaganus* (Pilsbry) and *Balanus trigonus* Darwin are the most abundant fossils. The remaining species, including *Balanus* sp., cf. *B. calidus* Pilsbry, *B. poecilus* Darwin, *Concavus* (*Arossia*) sp., cf. *C. (A.) panamensis eyerdami* (Henry), *Tetraclita* sp. indet., *Chelonibia testudinaria* (Linnaeus), and *Coronula diadema* (Linnaeus) are represented by one or a few specimens from single localities. Quaternary distribution of barnacles mirrors modern distribution patterns. *Tetraclita*

milleporosa and, particularly, *Megabalanus galapaganus* prefer high energy environments and are most abundant and grow to greatest size on windward sides of islands in areas of considerable wave action. *Balanus trigonus*, on the other hand, prefers low energy environments on the leeward sides of islands or in protected areas below wave base. *Balanus calidus* and *B. poecilus* are most common in current-swept areas below wave base.

Table 1 indicates the relationship between fossil barnacle occurrences and orientation of localities with respect to prevailing wind direction. The majority of localities yielding specimens of *Tetraclita milleporosa* and *Megabalanus galapaganus* are on southeast-facing shores that presently bear the brunt of wave energies generated by the southeast trade winds. *Balanus trigonus*, on the other hand, is found predominantly at localities on west-facing, or present leeward shores. Only at CASG locality 61392 does *B. trigonus* occur with *Megabalanus galapaganus*. This apparent contradiction can be explained by the presence of *Balanus* sp., cf. *B. calidus* and *B. poecilus*, both subtidal species, and the small size of the *Megabalanus galapaganus* specimens, typical of subtidal populations. Locality 61392 probably represents a depositional environment below wave base with substantial current action. The two leeward *Tetraclita* localities are notable in that neither has yielded *B. trigonus*, suggesting that local wave energies were sufficient to maintain *Tetraclita* populations, but too high to permit establishment of *B. trigonus*.

ORIGIN OF THE GALÁPAGAN BARNACLE FAUNA

The major objective sought in this study, but not completely attained, was a clue to the time

of origin of the Galápagan barnacle fauna. Clearly, the modern Galápagan fauna was already established in the Pleistocene, and its origins must be looked for in Neogene deposits, if such deposits exist. This conclusion is supported by studies of north temperate and tropical eastern Pacific Cenozoic barnacle faunas. The major faunal break occurs at the Tertiary-Quaternary boundary, with the barnacles of the Pleistocene being essentially of modern aspect, whereas those of the Pliocene are primarily of extinct species-groups that evolved at the end of the Oligocene.

The presence of *Concavus* cannot be adequately explained. The two subspecies of *Concavus* (*Arossia*) *panamensis* (Rogers) range throughout much of the Panamic faunal province (Newman 1982). It is possible that the species has been overlooked in the extant fauna, or was eliminated from the fauna in the recent past.

SYSTEMATICS

Superfamily CORONULOIDEA Newman and Ross
Family CORONULIDAE Leach
Subfamily CHELONIBIINAE Pilsbry
Genus *Chelonibia* Leach

Chelonibia testudinaria (Linnaeus, 1767)

Figures 3, 4

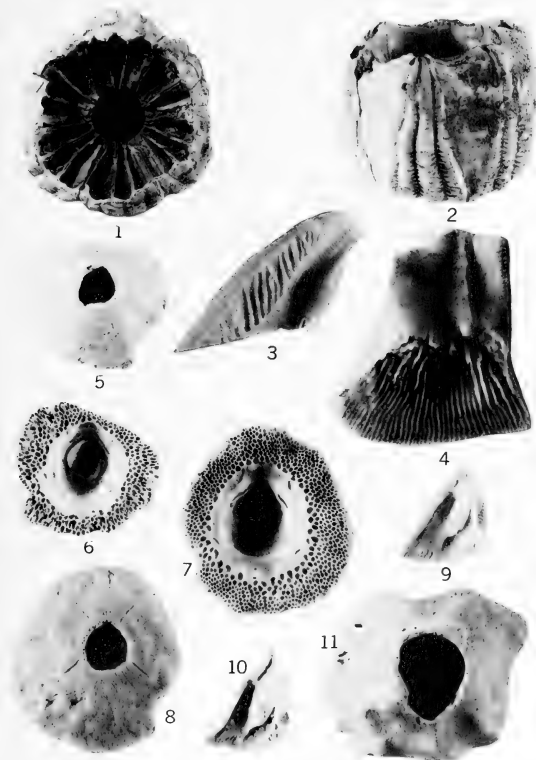
MATERIAL.—One lateral compartment, CASG locality 61281.

DISCUSSION.—The single lateral plate in the collection is 31 mm high and has a basal width of 28 mm. The presence of deep cavities between basal septa and well-developed oblique grooves and ridges on the radial and alar edges of the paries readily identify this specimen with *C. testudinaria*. This common and widely distributed turtle barnacle has been reported from the Pacific loggerhead, green, hawksbill, and ridley turtles. Fossils are known from Miocene and younger

TABLE 1. DISTRIBUTION OF ENVIRONMENTALLY SENSITIVE GALÁPAGAN FOSSIL BARNACLES WITH RESPECT TO LOCALITY ORIENTATION.

| Species | Orientation of localities* | | | | | | | | | | |
|---|----------------------------|-----|----------------------|-----|-----|-----|-----|--------------------|-----|-----|-----|
| | E-facing | | SE-facing (windward) | | | | | W-facing (leeward) | | | |
| | 392 | 387 | 281 | 282 | 285 | 286 | 386 | 388 | 389 | 390 | 391 |
| <i>Tetraclita milleporosa</i> | | X | X | X | | X | X | | | | X |
| <i>Megabalanus galapaganus</i> | X | | X | X | ? | X | | | | | |
| <i>Balanus trigonus</i> | X | | | | | | | X | X | X | |
| <i>Balanus</i> sp., cf. <i>B. calidus</i> | X | | | | | | | | | | |
| <i>Balanus poecilus</i> | X | | | | | | | | | | |

* Locality numbers in table are last three digits of CASG numbers (e.g., 61392).



FIGURES 1-11. Fig. 1, 2. *Coronula diadema* (Linnaeus, 1758), basal and side views of shell, hypotype CASG 61364, CASG locality 61229; $\times 1.3$. Fig. 3, 4. *Chelonibia testudinaria* (Linnaeus, 1767), lateral and interior views of lateral plate, hypotype CASG 61365, CASG locality 61281; $\times 1.6$. Fig. 5-11. *Tetraclita milleporosa* Pilsbry, 1916. Fig. 5, 6. Exterior and basal views of shell, hypotype CASG 61366, CASG locality 61387; $\times 1.6$. Fig. 7, 8. Basal and exterior views of shell, hypotype CASG 61367, CASG locality 61386; $\times 1.6$. Fig. 9. Interior of scutum, hypotype CASG 61368, CASG locality 61286; $\times 2.7$. Fig. 10. Interior of scutum, hypotype CASG 61369, CASG locality 61286; $\times 2.7$. Fig. 11. Exterior of shell rasped by fish, hypotype CASG 61370, CASG locality 61282; $\times 1.6$.

deposits in Mediterranean, Atlantic, and Caribbean regions (Zullo 1982). To my knowledge, this is the first reported fossil occurrence of *Cheilonibia* from the Pacific basin.

Subfamily CORONULINAE Leach
Genus *Coronula* Lamarck

Coronula diadema (Linnaeus, 1767)

Figures 1, 2

MATERIAL.—One complete specimen, CASG locality 61229.

DISCUSSION.—The single specimen is 27 mm in height and its greatest diameter is 31 mm. The well-developed transverse corrugations on the external surfaces of the transverse flanges suggest the ornamentation seen in the Pliocene species *C. barbara* Darwin, but the absence of similar corrugations on the inner surfaces of the flanges and the lack of infilling between radii and the alar plates indicate that the Galápagos *Coronula* is merely a highly corrugated specimen of *C. diadema*.

Coronula diadema, with a modern cosmopolitan distribution on humpback, fin, blue, and sperm whales (Newman and Ross 1976), has been reported from numerous Pliocene and Pleistocene localities in the Pacific basin region.

Family TETRACLITIDAE Gruvel
Subfamily TETRACLITINAE Gruvel
Genus *Tetracilita* Schumacher

Tetracilita milleporosa Pilsbry, 1916

Figures 5–11

Tetracilita porosa var. *communis* Darwin, 1854:329 (in part).
Tetracilita squamosa Pilsbry, 1916:257, pl. 60, fig. 1–1d; Newman and Ross 1976:48.

MATERIAL.—One shell, CASG locality 61386; one shell, CASG locality 61387; one shell, CASG locality 61391; one shell, CASG locality 61281; 21 shells, two partial shells, CASG locality 61282; 28 shells, four compartmental plates, six scuta, and one partial tergum, CASG locality 61286.

DISCUSSION.—The extant tropical American taxa *T. milleporosa*, *T. panamensis* Pilsbry, *T. stalactifera stalactifera* (Lamarck), *T. stalactifera confinis* Pilsbry, and *T. stalactifera floridana* Pilsbry form a group within the genus *Tetracilita* characterized by similarities in shell coloration and opercular plate morphology that readily distinguish them from other *Tetracilita* species and suggest close phylogenetic relationships. It is assumed that *T. milleporosa*, known only from the Galápagos Archipelago, was derived from a

mainland *T. stalactifera* stock. In the eastern Pacific, subspecies of *T. stalactifera* are restricted to Panamic faunal province mainland localities. *Tetracilita panamensis* occurs along the Central American Pacific coast, but is also found on Bay of Panama islands. The intertidal *Tetracilita* of Cocos Island off the coast of Costa Rica appears to be conspecific with *T. panamensis*, but may represent a distinct subspecies.

The opercular plates of *T. milleporosa* are similar to those of *T. stalactifera*, but the shell of the Galápagos species differs in being thicker and having much smaller and more numerous parietal tubes. *Tetracilita milleporosa* approaches *T. panamensis* in thickness and density of small pores, but differs particularly in opercular plate morphology.

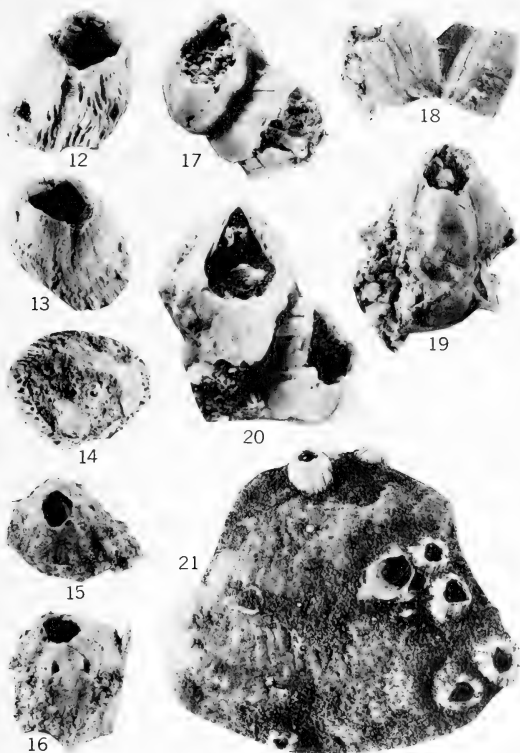
None of the fossils in the present collections shows any deviation from morphologies exhibited by extant *T. milleporosa* populations. The shells (Fig. 5–8) are typical of *T. milleporosa* in being peltate, and in having tiny orifices, obscure sutures, eroded external surfaces exposing infilled parietal tubes, and thickened walls with very small and numerous parietal tubes. A few shells show evidence of rasping by fish (Fig. 11). The well-preserved scuta from CASG locality 61286 (Fig. 9, 10) are typical as well, being about as high as wide, with small, closely set denticulae on the inflected occludent margin, and a relatively short adductor ridge that nearly merges with the lower part of the articular ridge, being separated by only a shallow groove. The tergum is too worn to be of aid in identification.

Tetracilita sp. indet.

Figures 12–14

MATERIAL.—One shell without opercular plates, CASG locality 61286.

DISCUSSION.—A single shell associated with numerous specimens of *T. milleporosa*, from CASG locality 61286, represents a second species of *Tetracilita*. The shell is high conic, with a relatively thin shell wall and correspondingly fewer rows of parietal tubes formed of larger individual tubes. The radii are narrow, but well developed and conspicuous, and the exposed filling of the upper parts of the parietal tubes is red. This shell is remarkably similar to that of *T. rubescens rubescens* which presently ranges between San Francisco, California and Cabo San Lucas, Baja California. The combination of shell features,



FIGURES 12-21. Fig. 12-14. *Tetracitella* sp. indet., lateral and basal views of shell, hypotype CASG 61371, CASG locality 61286; $\times 2.5$. Fig. 15, 16. *Balanus* sp., cf. *B. calidus* Pilsbry, 1916, top and lateral views of shell, hypotype CASG 61372, CASG locality 61392; $\times 2.5$. Fig. 17-19. *Balanus poecilus* Darwin, 1854, CASG locality 61392; $\times 2.5$. Fig. 17, 18. Top and side views of shells, hypotype lot CASG 61373. Fig. 19. Lateral view of shell, hypotype CASG 61374. Fig. 20, 21. *Balanus trigonus* Darwin, 1854, CASG locality 61388. Fig. 20. Top view of shells, hypotype lot CASG 61375; $\times 2.5$. Fig. 21. Shells on *Anomia peruviana* Orbigny, hypotype lot CASG 61376; $\times 1.6$.

particularly the color of the internal filling of the parietal tubes, is unlike that of *T. milleporosa* or any of the known Panamic faunal province

species. The Panamic species, related to or conspecific with *T. stalactifera*, range in color from gray to purple-black, usually lack well-defined

radii, and usually have a conic shell with a small orifice. If this unique specimen is indeed representative of *T. rubescens*, I am at a loss to explain its presence in the Pleistocene Galápagan fauna.

Superfamily BALANOIDEA (Darwin)

Newman and Ross

Family BALANIDAE Darwin

Subfamily BALANINAE Darwin

Genus *Balanus* Da Costa

***Balanus trigonus* Darwin, 1854**

Figures 20, 21

MATERIAL.—Ten shells, CASG locality 61388; two shells, CASG locality 61389; one shell, CASG locality 61390; six shells, CASG locality 61392.

DISCUSSION.—Although shells characteristic of *B. trigonus* were collected at the four localities listed above, no opercular plates were present in the collections. *Balanus trigonus* is found in most of the warm-water regions of the world from the lower intertidal zone to the edge of the shelf, but is most common in those parts of the immediate subtidal and inner-shelf zones that are protected from wave shock. In the Galápagos Archipelago, extant *B. trigonus* is abundant on the leeward sides of islands in the lower intertidal and immediate subtidal.

Considering the widespread distribution and abundance of this species in modern shallow seas, few verifiable reports of fossil *B. trigonus* exist. The species is fairly common in Pleistocene deposits of the Gulf of California region (Ross 1962) and has been identified by William A. Newman (personal communication 1982) from the Pleistocene of Hawaii. To my knowledge, fossil *B. trigonus* has not been reported from the western margins of the Pacific basin. Western Atlantic reports of *B. trigonus* include those of Withers (1953) from the (?)Miocene of Cuba, and of Ross (1965) from the Pliocene Tamiami Formation of Florida. Ross's (1964) report of this species from the Pliocene Yorktown Formation of Virginia was later stated to be in error (Ross 1965). Western Tethyan reports include those of Kólosváry (1957) from the Tortonian (Miocene) of Hungary, and Davadie (1963) from the Pliocene of Italy, the Red Sea, and the Coralline Crag of England.

These fossil occurrences, coupled with the modern distribution of the species, would suggest that *B. trigonus* is an old Tethyan element that has managed to survive to the present. There are

two problems, however, that cause me to question this conclusion. First, many of the aforementioned reports are based on species lists without substantiating descriptions or illustrations. Their validity is placed in question particularly in the knowledge that other students of barnacles who have monographed the faunas of the same regions (e.g., Darwin 1854; Alessandri 1906; Menesini 1966) did not uncover *B. trigonus*. Secondly, although both extinct and extant representatives of the *B. trigonus* complex are common in Neogene and Pleistocene deposits of southern California and the southeastern United States that I have examined (e.g., Zullo 1979), *B. trigonus* is absent. This is particularly odd, because the faunas of these units indicate that hydroclimates were substantially the same or warmer than those in the same regions today, and that depositional environments were fully within the present bathymetric range of *B. trigonus*. The origin and historical biogeography of *B. trigonus* remain in doubt, and their resolution will, in part, be dependent on a thorough evaluation of previously reported occurrences.

***Balanus* sp., cf. *B. calidus* Pilsbry, 1916**

Figures 15, 16

MATERIAL.—One complete shell, CASG locality 61392.

DISCUSSION.—A single shell, lacking opercular plates, is tentatively identified with *B. calidus* based on its coarsely ribbed, volcaniform shell and small orifice. Only a few extant specimens of *B. calidus* were obtained during the 1964 expedition, and all came from shallow, subtidal depths. Off the East Coast of the United States, *B. calidus* is found on the shelf at depths below significant wave action.

***Balanus poecilus* Darwin, 1854**

Figures 17–19

Balanus poecilus Darwin, 1854:246, pl. 5, fig. 3a, b; Henry 1960:142, pl. 2, fig. a, c, d, pl. 5, fig. b–d.

MATERIAL.—Eight shells without opercular plates, CASG locality 61392.

DISCUSSION.—The “west coast of South America, Mus. Cuming; attached to an *Avicula*” was cited by Darwin (1854) as the type and only locality in his original description of *B. poecilus*. The species went unreported until Henry (1960) obtained some individuals of *Pterias sterna* (Gould) from the vicinity of Guaymas in the Gulf

of California. Because of the unusually broad distribution indicated by the recorded occurrences, and because of the ambiguity of the type locality, I requested the aid of J. P. Harding, British Museum (Natural History) in attempting to refine these data through identification of the "*Avicula*" to which the types are attached. Dr. Harding kindly located the type-lot and forwarded the following information provided by S. P. Dance (personal communication August 5, 1965):

The shell to which the type specimens of *Balanus poecilus* Darwin are attached closely resembles a recently described species, *Pteria beilana* Olsson. The type locality for this species is Venado Beach, Canal Zone, Panama. *Pteria peruviana* Reeve may be an earlier name for this taxon but there is not enough material in the British Museum (Natural History) collections to decide this. Whichever name is used for it there can be little doubt that the shell to which the Darwinian barnacles are attached is a member of the Panamic-Pacific faunal province.

Dr. Harding also reported that the specimens bear the label "West coast of America," rather than South America, and as it is known that Hugh Cuming made extensive collections on the west coast of Central America, and especially in Panama during the period 1832-1856 (Keen 1958:2), it seems likely that the types of *B. poecilus* are from the same region.

Based on collections made during the 1964 Galápagos expedition, and previously unreported specimens in the collections of the Allan Hancock Foundation and the California Academy of Sciences, *Balanus poecilus* is found to range throughout the Panamic faunal province. The Allan Hancock Foundation collection includes specimens from off San Pedro Nolasco Island in the Gulf of California, off Jicarita Island and Bahia Honda, Panama, off Gorgona Island, Colombia, and off La Libertad, Ecuador, as well as from the Galápagos off Gardiner Island, near Española.

Genus *Concavus* Newman

Subgenus *Arossia* Newman

Concavus (*Arossia*) sp.,

cf. *C. (A.) panamensis eyerdami* (Henry, 1960)

Figures 22-24

MATERIAL.—Two shells without opercular plates, CASG locality 61390.

DISCUSSION.—The genus *Concavus* is not known to be represented in the extant Galápagan

fauna. According to Newman (1982), modern representatives of this Tethyan Tertiary genus are restricted to the eastern Pacific, ranging from San Francisco, California to Valparaíso, Chile. Newman (1982) established two subgenera for extant species: *Menesiniella* for *C. aquila* (Pilsbry) and *C. regalis* (Pilsbry); and *Arossia* for *C. henryae* Newman, *C. panamensis panamensis* (Rogers), and *C. panamensis eyerdami* (Henry). The Galápagan fossils, with their plicate, but not regularly or strongly ribbed parietes, appear to be assignable to *Arossia* in the absence of the more definitive features of the opercular plates. Within *Arossia*, these fossil shells most closely approach those of *C. panamensis eyerdami* in having a high conic shell with the rostrum higher than wide, a straight carina, and no evidence of beaded growth lines. The preserved reddish-purple coloration of the shell and the closely spaced transverse septa appear to distinguish the fossils from *C. henryae*, the sole representative of *Concavus* in the Peruvian faunal province.

Subfamily MEGABALANINAE Newman

Genus *Megabalanus* Hock

Megabalanus galapaganus Pilsbry, 1916

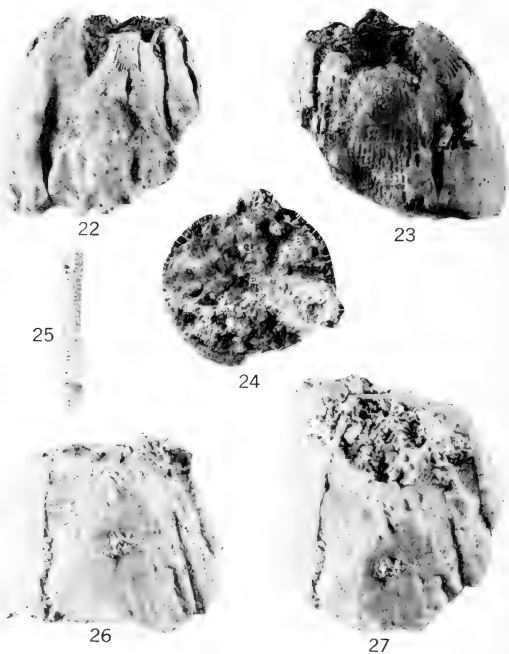
Figures 28-35

Balanus tintinnabulum galapaganus Pilsbry, 1916:70, pl. 12, fig. 1-1b.

MATERIAL.—Eight shells, 5 shell fragments, CASG locality 61281; 2 partial shells, CASG locality 61282; 24 shells, 26 compartmental plates, two bases, four scuta, and one tergum, CASG locality 61286; 2 shells, CASG locality 61392.

DISCUSSION.—After *Tetracrita milleporosa*, shells of *Megabalanus galapaganus* are the most abundant barnacle fossils obtained during the 1982 expedition. The specimens range from recently settled juveniles to mature individuals over 5 cm in height and 4 cm in greatest diameter. Many individuals retain the parietal color or color striping, and the parietal spines characteristic of extant populations. The opercular plates, although somewhat worn, are typical for *M. galapaganus*. The scutum is flat, bears a well-defined adductor ridge, and lacks a definite lateral depressor muscle pit. The tergum has a longer and narrower spur than the closely related species *M. clippertonensis* (Zullo) from Clipperton Island and *M. tanagrae* (Pilsbry) from the Hawaiian Islands (Zullo 1969).

Extant *M. galapaganus* is relatively abundant in low intertidal rocky areas subject to heavy



FIGURES 22-27. Fig. 22-25. *Concavus* sp., cf. *C. (Arossia) panamensis eyerdami* (Henry, 1960), CASG locality 61390; $\times 1.6$. Fig. 22, 23. Lateral views of shell, hypotype CASG 61377. Fig. 24. Basal view of shell, hypotype CASG 61378. Fig. 25. Broken radial sutural edge showing tubes, hypotype CASG 61378. Fig. 26, 27. *Megabalanus* sp. indet., lateral views of shell, hypotype CASG 61379, CASG locality 61285; $\times 2.5$.

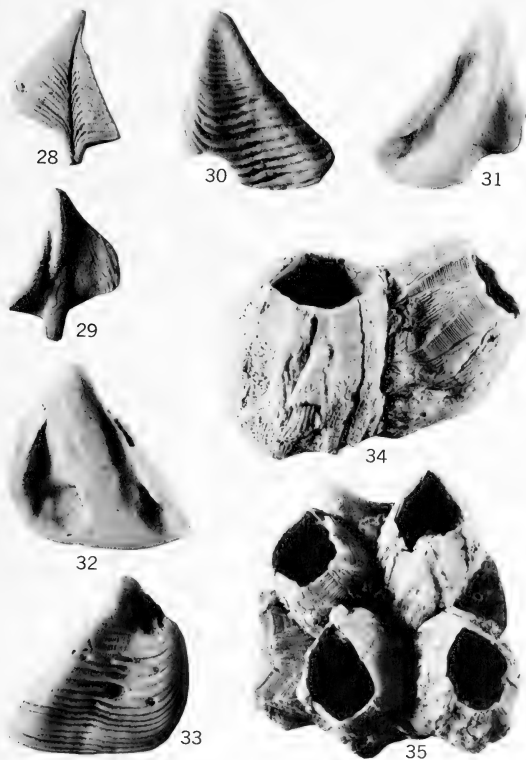
wave shock. It is in this region that the species reaches its maximum size. At subtidal depths specimens are locally abundant on lobster carapaces, gastropod shells, and coral heads, but rarely attain more than 2 cm basal diameter and are usually less than 1 cm high. Pilsbry (1916) based this species on specimens from the intertidal of Española Island. Collections made during the 1964 expedition and augmented by collections from the Allan Hancock Foundation and

the California Academy of Sciences extend the range of *M. galapaganus* not only through most of the Galápagos Archipelago but to Cocos Island (Costa Rica) to the north and Port Utria, Colombia on the South American mainland.

***Megabalanus* sp. indet.**

Figures 26, 27

MATERIAL.—One shell without opercular plates, CASG locality 61285.



FIGURES 28-35. *Megabalanus galapaganus* (Pilsbry, 1916). Fig. 28, 29. Exterior and interior of tergum, hypotype CASG 61380, CASG locality 61286; $\times 1.3$. Fig. 30, 31. Exterior and interior of scutum, hypotype CASG 61381, CASG locality 61286; $\times 1.3$. Fig. 32, 33. Interior and exterior of scutum, hypotype CASG 61382, CASG locality 61286; $\times 1.3$. Fig. 34. Lateral view of shells, hypotype lot CASG 61383, CASG locality 61286; $\times 1.0$. Fig. 35. Top view of shell clump, hypotype CASG 61384, CASG locality 61286; $\times 1.0$.

DISCUSSION.—The single barnacle specimen from CASG locality 61285 differs sufficiently from the typical growth form of *M. galapaganus*

to question its identification. The shell is 15 mm high, 22 mm in carinorostreal diameter, and is low conic, rather than cylindric to subglobose in

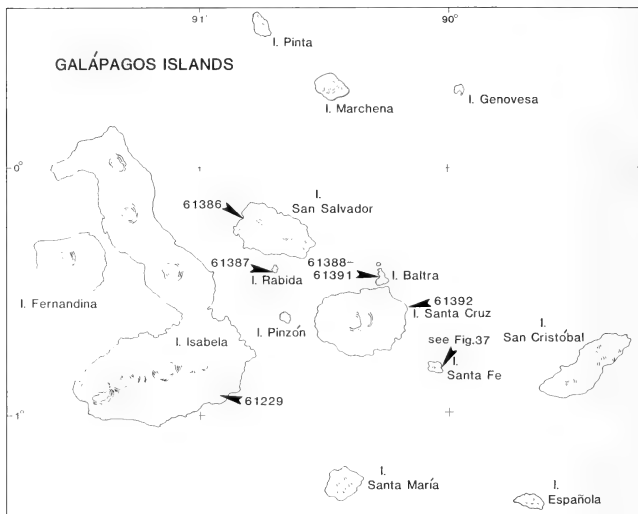


FIGURE 36. Generalized map of CASG Galápagos localities containing fossil barnacles (map provided by J. H. Lipps).

shape. The sub-diamond-shaped orifice is, resultingly, rather small, and the radii are correspondingly narrow. The parietes show no evidence of color or striping, and bear low, rounded, irregular ribs. In the absence of opercular plates, however, there is no way to determine its identity.

LOCALITY DESCRIPTIONS

All barnacle specimens are in the collection of the Department of Geology, California Academy of Sciences, San Francisco (CASG). Locations of collection sites are shown in Figures 36 and 37.

- 61229 Isla Isabela. White to tan, loose, silty sand containing abundant shells at site of airport at Villamil. Collected 3 February 1982. *Coronula diadema*.
 61281 Isla Santa Fe. Beach deposit about 8 m above sea level on southeast shore north of Punta Miedo. Calcareous, sometimes stratified sand up to 2.5 m thick and intermixed with basalt boulders and cobbles. Collected 14

February 1982. *Chelonibia testudinaria*, *Tetraclita milleporosa*, *Megabalanus galapaganus*.

- 61282 Isla Santa Fe. Fossils from top of sedimentary sequence overlain by basalt. Red, tuffaceous, crossbedded sandstone with stratified fossils at top, about 8 m above sea level. Same horizon as CASG locality 61281, but 30 m farther seaward. Collected 14 February 1982. *Tetraclita milleporosa*, *Megabalanus galapaganus*.
 61285 Isla Santa Fe. Terrace deposits of boulders, cobbles, pebbles, and sand containing molluscs and barnacles at top of cliff in small cove at landing site; 3.5–4 m above sea level. Locality is north of CASG locality 61282. Collected 15 February 1982. *Megabalanus* sp. indet.
 61286 Isla Santa Fe. Terrace deposit about 100 m from shore near eastern end of south coast. Loose, white to tan, medium- to coarse-grained sand containing many barnacles. Collected 15 February 1982. *Tetraclita milleporosa*, *Tetraclita* sp. indet., *Megabalanus galapaganus*.
 61386 Isla San Salvador, James Bay. Shelly, basaltic sand in line of trees north of mining camp. Collected 8 February 1982. *Tetraclita milleporosa*.
 61387 Isla Rabida. Storm-tossed shell and bone in small, cliff-

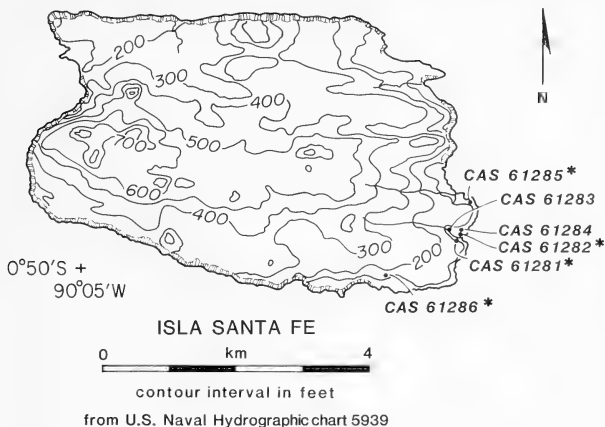


FIGURE 37. Collecting sites on Isla Santa Fe. CASG localities with asterisks yielded barnacles (map provided by J. H. Lipps).

backed cove on south side of island. Collected 9 February 1982. *Tetracita milleporosa*.

61388 Isla Baltra. Bedded to crossbedded, reddish-brown, silty sandstone with abundant *Codakia* shells at basal contact (Unit 4). South shore of Caleta Aeolian, directly south of Punta Noboa. Collected 10 February 1982. *Balanus trigonus*.

61389 Isla Baltra. Crossbedded, white sandstone containing shell debris and abundant pectinids (Unit 1). Locality about 30 m east of CASG locality 61388 along a 100-m stretch of exposure. Collected 10 February 1982. *Balanus trigonus*.

61390 Isla Baltra. Basal 0.5–1.5-m-thick boulder and cobble bed containing abundant coralline algae and casts and molds of molluscs. Same area as CASG locality 61389. Collected 10 February 1982. *Balanus trigonus*, *Concavus* (*Arossia*) sp., cf. *C. (A.) panamensis everdami*.

61391 Isla Baltra. Bulldozed pit (old anti-aircraft gun emplacement) about 170 m back of sea cliff. Collected 10 February 1982. *Tetracita milleporosa*.

61392 Isla Santa Cruz, Cerro Colorado. Fossils from top of limestone shelf on north side of Cerro Colorado. Collected 17 February 1982. *Balanus trigonus*, *Balanus* sp., cf. *B. calidus*, *B. poecilus*, *Megabalanus galapaganus*.

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Pitt, Sacramento, California for providing the specimens, maps, and locality data used in this study, and for their advice during manuscript preparation. Funding for this study was provided by the Marine Sciences Research Program of the University of North Carolina at Wilmington. This paper is contribution number 372 of the Charles Darwin Foundation.

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A SYSTEMATIC REVIEW OF AMPHIZOID BEETLES
(AMPHIZOIDAE: COLEOPTERA) AND THEIR PHYLOGENETIC
RELATIONSHIPS TO OTHER ADEPHAGA

By

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ABSTRACT: Rediscovery of type material for *Amphizoa davidi* Lucas, 1882, the only known Palaearctic amphizoid, is reported, with a lectotype designated, and the type area emended (from Tibet to Szechwan Province, China). A key is provided for identification of adults of the four known amphizoid species. Form and structure, geographical and habitat distributions, and geographical relations with other taxa are described and illustrated for each species. *Amphizoa carinata* Edwards, 1951, is recognized as a junior synonym of *A. lecontei* Matthews, 1872. Through cladistic analysis, using out-group and character correlation criteria, and a review of known Mesozoic fossil material, a hypothesis of phylogenetic relationships among extinct and extant Adephaga is developed, discussed, and related to geologic time. A semi-aquatic, rather than terrestrial, common ancestor is proposed for Adephaga. Amphizoids diverged from their sister-group, which includes all Hydradephaga except halipids, in Triassic time. All extant amphizoid species had differentiated by late Pliocene time, in response to a series of vicariant events. Quaternary climatic and geologic events resulted in changes in geographical distributions of these species and structural, physiological, and behavioral adaptations of their members.

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INTRODUCTION

For several decades, the location of type-material for *Amphizoa davidi* Lucas, 1882, described from Tibet, remained a mystery (Edwards 1951; Kavanaugh 1980; Kavanaugh and Roughley 1981). Although material Lucas studied was known to have been deposited in the Muséum National d'Histoire Naturelle in Paris, several independent efforts to locate specimens of *A. davidi* in appropriate parts of that collection had failed. Equally perplexing was the fact that no additional specimens representing this taxon had been found since its original description.

Amphizoa davidi is an especially important taxon for two reasons. First, it is a member of the small family Amphizoidae, which is considered by many workers to represent an intermediate evolutionary grade between the so-called Geadephaga, or terrestrial Adephaga (i.e., Carabidae, in the broadest sense), and the remaining Hydradephaga, or aquatic Adephaga (i.e., Dytiscidae, Hygrobiidae, Gyrinidae, etc.).

Knowledge of amphizoids is seen as a major key to understanding adephagan evolution and phylogeny; and knowledge of *A. davidi* in particular is critical for understanding Amphizoidae. Second, *Amphizoa kashmirensis* Vazirani, 1964:145, described from the Himalaya of India, has recently been shown to be a dytiscid, referable to genus *Hydronotus* Jakovlev, rather than an amphizoid (Kavanaugh and Roughley 1981). As a result, *A. davidi* is the only known Palaearctic amphizoid; and because no specimens of this species had ever been seen by current workers, doubts had arisen with regard to its familial affinities (Kavanaugh 1980; Kavanaugh and Roughley 1981). What are the phylogenetic relationships between *A. davidi* and the Nearctic species, and what are the zoogeographic implications of this phylogeny and the disjunct distribution of genus *Amphizoa*? Answers to these questions might shed new light on the origins and history of the Holarctic fauna in general and of certain relict, taxonomically isolated taxa in particular.

In early 1983, Terry L. Erwin (U.S. National Museum, Washington, D.C.) discovered several amphizoids pinned in one corner of a Schmidt box labelled "Australian Carabidae" at the Muséum National d'Histoire Naturelle in Paris. Included were a few specimens of *Amphizoa insolens* LeConte from western North America and one specimen (Fig. 1) from Mou-pin, Tibet, the type-locality for *A. davidi*. Suspecting that he had found the long-sought type of *A. davidi*, Erwin arranged for shipment of the specimen to me on loan. Jean Menier, curator at the museum in Paris, provided photocopies of relevant entries in the museum's catalog, specifically for the accession of material from Mou-pin, Tibet, received from Armand David and upon which Lucas's description was based. Subsequently, I have determined that the specimen is the type-specimen of *Amphizoa davidi* Lucas through a study of the specimen itself and the labels it bears (including one with the proper catalog number).

The purposes of this paper are: (1) to report on the rediscovery of type-material for *A. davidi* Lucas; (2) to designate a lectotype for same; (3) to redescribe this material in comparison with Nearctic forms, and illustrate certain characteristics of form and structure for the first time; (4) to update distributional records that have accumulated since Edward's (1951) revision of the family; (5) to propose one new synonymy; (6) to

1



FIGURE 1 *Amphizoa davidi* Lucas: lectotype male, dorsal aspect, total length = 11.4 mm.

provide a revised key to species that reflects new findings; and (7) to initiate consideration of the phylogenetic relationships among extant *Amphizoa* species and the zoogeographic implications of these relationships. A cladistic analysis of relationships among major extant and known extinct adephagan groups is presented as a basis for the intrageneric analysis of *Amphizoa*.

MATERIALS AND METHODS

Descriptions of form and structure, taxonomic conclusions, geographical distributions, and other findings reported here are based on examination of more than 1,250 adult specimens of *Amphizoa* and more than 300 specimens representing other extant adephagan taxa. The following acronyms are used in the text to refer to collections from which specimens were received for study and/or in which specimens are deposited. Curators and collection managers responsible for these collections are also listed, and I thank them sincerely for their help in providing specimens on loan for study.

- BMNH British Museum (Natural History), London SW7 5BD, England; M. E. Bacchus.
- BYUM Brigham Young University Museum of Natural History, Provo, Utah 84602; R. W. Baumann.
- CAS California Academy of Sciences, San Francisco, California 94118; D. H. Kavanaugh.
- CNC Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6; A. Smetana.
- DMad D. Maddison, University of Alberta, Edmonton, Alberta T6G 2E3.
- GCha G. Challet, Orange County Vector Control District, Garden Grove, California 92643.
- GLPa G. L. Parsons, Oregon State University, Corvallis, Oregon 97331.
- GLPe G. L. Peters, Oregon State University, Corvallis, Oregon 97331.
- LGBe L. G. Bezark, California State Department of Food and Agriculture, Sacramento, California 95814.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; A. F. Newton, Jr.
- MNHP Muséum National d'Histoire Naturelle, Paris, 75005 France; J. Menier.
- NSDA Nevada State Department of Agriculture, Reno, Nevada 89504; R. C. Bechtel.
- OSUO Oregon State University, Corvallis, Oregon 97331; J. Lattin, G. L. Peters.
- PUCA Pacific Union College, Angwin, California 94508; L. E. Eighme.
- RERo R. E. Roughley, University of Manitoba, Winnipeg R3T 2N2.
- SJSU San Jose State University, San Jose, California 95114; J. G. Edwards.
- UASM University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.

- UCB University of California, Essig Museum of Entomology, Berkeley, California 94720; J. A. Chemsak and G. Ulrich.
- UCD University of California, Davis, California 95616; R. O. Schuster.
- USNM United States National Museum, Smithsonian Institution, Washington, D.C. 20560; P. J. Spangler, T. L. Erwin.
- UZMH Universitetets Zoologiska Museum, Entomologiska Avdelningen, SF-00100 Helsingfors 10, Finland; H. Silfverberg.

Methods, including techniques for dissection of male and female genitalia and criteria for ranking taxa, are discussed by Kavanaugh (1979). The only measurement used in this paper, standardized body length (SBL), is the sum of three measurements: length of head along midline from apical margin of labrum to a point opposite posterior margin of left eye; length of pronotum along midline from anterior to posterior margin; and length of elytron along midline from apex of scutellum to a point opposite apex of longer elytron.

Line drawings were made with the aid of a camera lucida attached to a Wild Model M-5 stereoscopic dissecting microscope. The scanning electron micrograph (Fig. 2) was obtained using a Hitachi model S-520 SEM (with accelerating voltage = 5 kV and specimen uncoated).

Cladistic analyses were carried out using manual methods (see Phylogeny below for further discussion); but results were compared with those generated using "WAGNER" and "SOKAL" programs from the "Phylogenetic Inference Package" (PHYLIP) for microcomputers created by J. Felsenstein (University of Washington, Seattle), as modified by T. K. Wilson (Miami University, Oxford, Ohio). In general, cladograms obtained using manual and computer-assisted methods were similar. However, placement of individual taxa in cladograms generated by the PHYLIP programs varied markedly, subject to changes in the order in which taxa were listed in the database (and, therefore, compared by computer).

SYSTEMATICS OF AMPHIZOIDAE

Introduction

Edwards's (1951) monograph of Amphizoidae stands as the definitive systematic treatment of this group. His extensive review of the literature and detailed descriptions, comparative studies, and discussions of form and structure serve as a sound basis for all subsequent work on amphizoids.

zoids, as well as for comparisons of members of this group with those of other adepagan taxa.

Because of more liberal institutional lending policies, I was able to borrow type-material that was unavailable to Edwards and designate lectotypes for *Amphizoa insolens* LeConte, *A. josephi* Matthews, and *A. lecontei* Matthews (Kavanaugh 1980). Moreover, a great deal of new material has been collected during the past 30 years. Through loans and my own fieldwork, I have had access to almost five times as many specimens as Edwards studied, many of these from areas in which amphizoids were previously unknown. These new distributional records have important taxonomic and zoogeographic implications. In order to make this report minimally redundant with respect to Edwards's paper, I have limited my descriptive presentations to brief listings and discussions of distinguishing characteristics, except where my findings depart from Edwards's. The reader should consult Edwards (1951) for more detailed descriptive and comparative information on amphizoids, as well as comprehensive coverage of the literature prior to that date.

The format used for presentation of *Amphizoa* species below is as follows: (1) a synonymy (including for each name the author, date, and page citation for original description; status, sex, and depository for holotype or lectotype; type-locality; and literature citations that were not listed by Edwards [1951]); (2) additional comments on nomenclature, type-specimens, and/or type-locality as needed; (3) a brief listing of distinguishing characteristics of adults, with additional discussion of form and structure as needed; (4) habitat distribution; (5) geographical distribution, including distributional summary statement, map illustrating known localities, and formal listing of localities for specimens studied (with area and month[s] of collection, number of specimens studied, and depository[ies] for same); and discussions of (6) geographical variation; and (7) geographical relationships with other *Amphizoa* species.

A Key for Identification of *Amphizoa* Adults

- I. Elytron (Fig. 6b) with blunt but distinct carina on fifth interval, area medial to carina elevated, flat, area lateral to carina slightly concave

- 1'. Elytron (Fig. 3b, 4b, 5b) evenly convex or slightly concave paraterally, without carina 2
- 2(1'). Prosternal intercoxal process (Fig. 11) short, round; body form narrower (Fig. 3a); specimen from southwestern China (Fig. 17) *Amphizoa davidi* Lucas
- 2'. Prosternal intercoxal process (Fig. 12) long, spatulate; body form (Fig. 4a, 5a) relatively broader; specimen from western North America 3
- 3(2'). Elytral silhouette (Fig. 5a) broad basally and distinctly narrowed subapically, elytral surface only faintly rugose in lateral one-half; pronotum (Fig. 9) broadest at base, with lateral margins not or only slightly crenulate
- 3'. Elytral silhouette (Fig. 4a) subovoid, slightly narrowed basally, slightly broader subapically, elytral surface moderately or coarsely rugose in lateral one-half; pronotum (Fig. 8) at least as broad at middle as at base, with lateral margins markedly crenulate
- *Amphizoa striata* Van Dyke
- *Amphizoa insolens* LeConte

Amphizoa davidi Lucas

(Figures 1-3, 7, 11, 13, 17)

Amphizoa davidi Lucas, 1882:157 [incorrect spelling]. **Lectotype** (here designated), a male, in MNHP, labelled: "Muséum Paris, Mou-pin, A. David 1870"/ "398"/ "774 70" [yellow-backed disk]/ "Amphizoa davidis, Lucas" [label double-pierced by pin, hence vertical on pin]; "Type" [red label]/ "Muséum Paris"/ "Lectotype Amphizoa davidi Lucas designated by D. H. Kavanaugh 1983" [red label]. **Type-Locality**.—Pao-hsing, Szechwan Province, People's Republic of China. Edwards 1951:322. Kavanaugh 1980:289.

Amphizoa davidi Lucas [justified emendation]. Edwards 1951:322. Kavanaugh 1980:289. Kavanaugh and Roughley 1981:269. Leech and Chandler 1956:301.

NOTES ON NOMENCLATURE AND TYPE-SPECIMEN.—Mou-pin, Tibet, the area originally cited as type-locality, is now called "Pao-hsing" (30°22'N, 102°50'E). This region is no longer part of Tibet, but rather the western part of Szechwan Province, People's Republic of China.

DISTINGUISHING CHARACTERISTICS.—Size small, SBL male = 11.4 mm; body form (Fig. 1, 3a) narrow; body color piceous, with antennae, maxillary and labial palpi, and tarsi rufopiceous; head (Fig. 2) finely and densely punctate; pronotum (Fig. 2) coarsely and densely punctate, with

areas between punctures convex, granulate in appearance; elytra finely and densely punctate, slightly rugose at base and in lateral one-fourth; pronotum (Fig. 7) broadest at base, with lateral margins arcuate at middle, markedly sinuate anterior to basal angles, not crenulate, median longitudinal impression present but faintly impressed; prosternal intercoxal process (Fig. 11) short, round; posterolateral angle of proepisternum and posteromedial angle of proepipleuron about evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 3a) moderate in width basally and distinctly narrowed subapically, elytra (Fig. 3b) evenly convex, without carinae; elytral striae complete but faintly impressed and finely punctate; front tibia with posterodorsal groove present on apical three-fourths, with fringe setae in groove very short and restricted to apical one-half; male median lobe (Fig. 13) with shaft slender at middle, evenly arcuate ventrally, apex slightly deflected ventrally, left paramere narrow basally, with vestiture restricted to apical one-fourth; female unknown; specimen from southwestern China (Fig. 17).

Edwards's description of *A. davidi* (1951:322) was an English translation of the original description in French (Lucas 1882). Based on my examination of the type-specimen, additional comments and certain amendments to the original description seem appropriate. Lucas described the type of *A. davidi* as "noir mat . . . avec les palpes . . . d'un brun teinté de ferrugineux. Les antennes . . . d'un brun ferrugineux brillant" (i.e., dull black, with reddish-brown antennae and palpi). In my view, the specimen is as dull as adults of *A. insolens* and *A. striata* but less dull than adults of *A. lecontei*. Its body color is piceous, not black as in *A. insolens* adults; and its antennae and palpi are rufopiceous, not reddish-brown. The median longitudinal impression (median furrow), which was described as "ne presente pas" (i.e., absent), is present and as deeply impressed as in *A. striata* adults, less so than in *A. lecontei* and *A. insolens* members. Lucas described the scutellum as "tres finement chagriné" (very finely granulate); but because this character state is shared with adults of the other *Amphizoa* species, it is of no taxonomic use. According to the original description, the elytral striae are "les parcourant obsoletement accusées et non ponctuées" (obsolete and

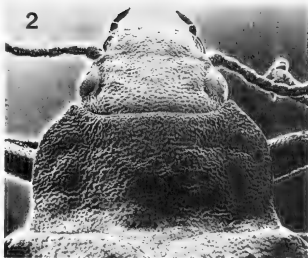


FIGURE 2. *Amphizoa davidi* Lucas: scanning electron micrograph of head and pronotum, dorsal aspect, magnification = 25 \times (specimen uncoated).

impunctate); but they appear to be complete and clearly (although very shallowly) impressed. Due to dense punctation of the entire elytral surface, it is difficult to distinguish the fine punctures which are found in the striae.

Close examination of the elytra of the lectotype of *A. davidi* has revealed a previously unrecorded feature. Due to the relatively faint development of macrosculpture on the elytral surface of this specimen, I found small but distinctly foveate punctures on the third, fifth, seventh, and ninth intervals. No setae appear to be associated with these punctures. Identical punctures were subsequently found in adults of all three Nearctic *Amphizoa* species, although they are much less obvious in Nearctic specimens, least so in *A. striata* adults. Similar, but seta-bearing, punctures are found among adults of a broad spectrum of tribes and genera of Carabidae. The presence of such setiferous punctures on odd-numbered elytral intervals (except the first) in amphizoids suggests that this may be an ancestral (plesiotypic) adephagan trait. Absence of setae from the punctures may be an apotypic trait associated with development of an aquatic lifestyle. Absence of the punctures themselves (such as is seen in adults of the other hydradephagan groups) may represent a more highly evolved trait. However, a majority of carabid groups also lack some or all of these punctures; so the evolution of this character has been complex and homoplastic, no matter how the polarity of its states is interpreted.

HABITAT DISTRIBUTION.—Unknown.

GEOGRAPHICAL DISTRIBUTION.—This species is known only from the type-locality in southwestern China (Fig. 17), in the Min River drainage, an upper tributary of the Yangtze River. This watershed flows first south, then east more than 2,000 km to the Pacific Ocean, at 30°N latitude, and has no Himalayan drainage component.

Past mislocation of the type-locality (i.e., Tibet rather than Szechwan, China) has apparently led collectors astray. Several workers, all with knowledge of the habits and habitat preferences of Nearctic amphizoids, have collected in various parts of the Himalayas (e.g., India, Nepal, Tibet, Sikkim) in recent years without finding representatives of this species. This suggests that the range of *Amphizoa* in the Palearctic Region may not extend west to include the main Himalayan ranges. Furthermore, the People's Republic of China has been closed to most western collectors for decades (and until very recently); and this may account for the lack of additional specimens in European or North American collections during this century.

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The known range of this species is allopatric with respect to ranges of all other known species of *Amphizoa*.

***Amphizoa insolens* LeConte**

(Figures 4, 8, 14, 18, 28)

Amphizoa insolens LeConte, 1853:227. Lectotype (designated by Kavanaugh 1980) male in MCZ. **Type-Localities.**—Sacramento, California. Edwards 1951:323, 1954:19. Hatch 1953:194. Kavanaugh 1980:290. Leech and Chandler 1956:301.

Dysmathes sahlbergii Mannerheim, 1853:265. Location of type-specimen unknown. **Type-Localities.**—Sitka, Alaska. Edwards 1951:323. Kavanaugh 1980:291. Synonymized by Sallé 1874:222.

Amphizoa josephi Matthews, 1872:119. Lectotype (designated by Kavanaugh 1980) male in BMNH. **Type-Localities.**—Vancouver Island, British Columbia. Edwards 1951:323. Hatch 1953:194. Kavanaugh 1980:290. Synonymized by Horn 1873:717.

NOTES ON NOMENCLATURE AND TYPE-SPECIMENS.—The problem with location of the holotype of *Dysmathes sahlbergii* Mannerheim was discussed by Kavanaugh (1980).

DISTINGUISHING CHARACTERISTICS.—Size varied (small, medium, or large), SBL male = 10.9–13.6 mm, female 11.1–15.0 mm; body form moderately broad (Fig. 4a); body black, with antennae, maxillary and labial palpi, and tarsi black

or rufopiceous; head finely and densely punctate; pronotum medially with coarse, sparse punctures with areas between punctures flat, laterally with punctures coarser, denser, confluent, surface markedly gnarled; elytra finely and densely punctate, markedly rugose at base and in lateral one-half; pronotum (Fig. 8) as broad (or broader) at middle as (than) at base, with lateral margins arcuate at middle, moderately or markedly sinuate anterior to basal angles, markedly crenulate, median longitudinal impression deeply impressed; prosternal intercoxal process (Fig. 12) slightly elongate, spatulate; posterolateral angle of proepisternum and posteromedial angle of proepipleuron abut evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral midlhouette (Fig. 4a) subovoid, slightly narrowed basally, less narrowed subapically, elytra (Fig. 4b) evenly convex, without carinae; elytral striae complete but faintly impressed (difficult to define laterally because of macrosculpture) and finely punctate; front tibia with posterodorsal groove restricted to apical one-half or two-thirds, with fringe setae in groove restricted to apical one-third or one-half; male median lobe (Fig. 14) with shaft slightly thickened at middle, evenly arcuate ventrally, apex slightly deflected ventrally and extended apicodorsally, left paramere narrow basally, with vestiture restricted to apical one-third; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with stylar region short, with vestiture of only a few scattered, minute setae; specimen from western North America (Fig. 18).

Among specimens studied, I observed greater variation in pronotal shape than that reported by Edwards (1951). Although many adults of *A. insolens* have pronota broadest at the middle, in most they are equally broad at middle and base. There is also notable variation among individuals with respect to tibial grooves and associated fringe setae ("hairs" of Edwards 1951). These structures are discussed more fully below in my treatment of *A. lecontei*. In *A. insolens* adults, the posterodorsal groove on the front tibiae is varied in length, either restricted to the apical one-half of the tibia or extended basally to occupy the apical two-thirds of the tibia. Fringe setae in this groove are restricted to the apical one-third of the tibia in most individuals, but several adults were seen with fringe setae also at the middle of the tibia or even on the apical part of the proximal one-half. As noted by Edwards

(1951:324), *A. insolens* adults have the least completely developed complement of fringe setae among extant amphizoids (see further discussion in section on Zoogeography and Evolution).

HABITAT DISTRIBUTION.—Members of this species are most often found at the edges of cold, swift-flowing streams, under rocks or in coarse gravel at shoreline, clinging to exposed roots beneath undercut banks, or in floating debris that has collected in backwater eddies. Adults are often found in greatest numbers at the bases of waterfalls, which represent a first stretch of quiet water after a steep drop downstream. The occasional occurrence of these beetles in ponds or lakes, where they are almost always found near the inlets of torrential streams, probably results from their being washed downstream and does not represent permanent residence in such standing bodies of water.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 18) extends from southern Yukon Territory and southeastern Alaska south to the San Bernardino, San Gabriel, and San Jacinto mountains of southern California, and from the Pacific Coast, including the Queen Charlotte Islands and Vancouver Island, east across the Columbia Plateau and Great Basin to western Alberta, central Montana, western Wyoming, central Idaho, and eastern Nevada.

I have examined 398 males and 360 females from the following localities:

CANADA

Alberta: Banff National Park, Banff [May] (1; CAS). **British Columbia:** Yoho National Park, Kicking Horse River (20.9 km W of Field) [June] (2; USNM); other localities, Ainsworth Hot Springs [July] (1; USNM), Fernie [Aug.] (1; CAS), Haines Highway (km 92.1) [July] (1; UASM), Inverness [July–Aug.] (2; USNM), Kaslo [June] (1; USNM), Kay Falls [July] (1; CAS), Kuskanook (Kootenay Lake [530 m] [Oct.] (1; RERo), Kwinizta (Telegraph Point) [June] (2; UASM), Nicomen Ridge [July] (1; CAS), North Bend [June] (1; USNM), Prince Rupert (north slope of Mount Hayes near base [120 m] [July] (1; CAS), Revelstoke (25.7 km W) [July] (1; CAS), Seltat Creek (Haines Highway km 78.5) [June] (1; UASM), Skagit (40 km E of Hope) [July] (1; RERo), Stanley [June] (1; CAS), Stawamus River (2 km S of Squamish on Highway 99) [July] (1; CAS), Wynndel [Aug.] (10; CAS, OSUO); Queen Charlotte Islands, Graham Island (Ghost Creek drainage 7.3 km NW of Rennell Sound Road [240 m], Juskatla area, Nebria Peak at Lower Nebria Lake [620 m] [July] (11; CAS), Moresby Island (3 km NE of Jedway [6–50 m], Mount Moresby at High Goose Lake [640 m] [July–Aug.] (2; CAS); Vancouver Island, Tyee (4.9 km NW) [June] (2; UASM). **Yukon Territory:** Upper Frances River (at Route 10) [June] (3; DMAd).

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Alaska: Juneau [June] (1; CAS), Lituya Bay (9.7 km N [240–590 m] [Aug.] (21; CAS). **California:** El Dorado County, Pino Grande ([1,370 m] [July] (3; UCD), Pollock Pines [July] (1; UCD), Riverton [July] (2; CAS, UCD), Whitehall area [June] (1; CAS), Fresno County, Barton Flat ([1,580 m] [May] (1; UCB), Hackberry Meadow [May] (1; CAS), Inyo County, Lone Pine (12.9 km N) [June] (1; CAS); Kings Canyon National Park, Bubbs Creek Canyon ([3,200 m] [July] (1; CAS); Lake County, Bartlett Springs [June] (1; CAS); Lassen County, Susan River (12.9 km N of Susanville on Highway 36) [Aug.] (1; CAS); Los Angeles County, Coldwater Canyon [Aug.] (2; CAS), Little Jimmy Creek [June] (1; GChA), Los Angeles area (1; USNM), San Antonio Creek [June] (6; GLPe), Madera County, Boggy Meadows ([1,830 m] [July] (10; CAS, NSDA, SJSU); Mariposa County, Sweetwater Creek ([1,220 m] [July] (2; CAS); Mono County, Twin Lakes [Aug.] (4; USNM); Nevada County [Aug.] (1; CAS), Sagehen Creek (near Hobart Mills) [Aug.] (9; UCD), Truckee [Aug.] (1; CAS); Placer County, Emigrant Gap ([1,620 m] [June] (1; UCD), Shirttail Creek (below Yellow Pine Reservoir) [May] (1; BYUM), Plumas County, North Fork Feather River ([910 m] [Apr.] (1; CAS); Riverside County, San Jacinto Mountains (Idelwild) [July] (6; CAS); San Bernardino County, Camp Baldy [July, Sep.] (9; CAS, UCD), Cienega Seco (6.4 km E of Barton Flats on Highway 38) [Aug.] (1; GChA), Mill Creek (0.16 km E of Forest Falls [1,650 m] [May] (4; CAS), San Geronimo Mountain ([2,130 m] [Sep.] (22; CAS), San Mateo County, Tunitas Creek [Aug.] (1; UASM); Santa Clara County, Corte Madera Creek [Apr.] (1; CAS), Los Gatos [June] (1; CAS), San Francisco County (Stanford University Campus) [July] (1; USNM), San Jose [Sep.] (1; CAS), Uvas Creek (Sveadal, Uvas County Park, Uvas Meadows) [Mar.–May, July–Aug.] (11; LGBe, SJSU); Santa Cruz County, Boulder Creek [Apr.] (1; SJSU), Castle Rock State Park [May] (1; LGBe); Sequoia National Park ([610–910 m] [May–June] (7; CAS, UCD), Ash Mountain (Kawah Powerhouse #3) [June–July, Sep.] (22; UCB, UCD), Cahoon Meadow ([2,290 m] [Aug.] (1; CAS), Giant Forest [Aug.–Sep.] (1; CAS), Paradise Valley ([910–2,130 m] [May, July] (2; CAS), Potwisha ([610–1,520 m] [May, July] (5; CAS, UCD, USNM), Wolverton ([2,130–2,740 m] [June] (1; CAS); Shasta County [July] (1; USNM), Castle Crags [July] (4; CAS), Lost Creek (at Twin Bridges Road [1,450 m] [Aug.] (3; CAS), McArthur–Burney Falls State Park ([910 m] [June–Sep.] (36; CAS, OSUO, SJSU), Old Station ([1,220 m] [Sep.] (2; CAS), Viola ([1,370 m] and 6.4 km W) [June] (3; CAS, NSDA); Sierra County, Sierraville (8 km S [1,830 m] [Aug.] (1; CAS); Siskiyou County [July] (7; CAS), Big Flat Campground [Aug.] (6; CAS), Cement Creek (S of Callahan [1,220 m] [Aug.] (1; CAS), East Fork of South Fork Salmon River (headwaters at Cecilville/Callahan Road [1,830 m] [July] (1; CAS), McCloud [June] (4; CAS, USNM), Mount Shasta (Panther Creek [2,440 m] [July] (1; CAS), Shasta Springs (Shasta Retreat [730 m] [July] (14; CAS), Taylor Lake Road ([1,750 m] [Aug.] (1; CAS), Yreka area (1; USNM); Tehama County, Soap Creek ([610 m] [July] (1; CAS); Trinity County, Boulder Creek (at Goldfield Campground [1,070 m] [July] (5; CAS), Doe Gulch (1.6 km W of Altoona Mine on Ramshorn/Castella Road [1,230 m] [Aug.] (1; CAS), Emerald Lake ([1,680 m] [Aug.] (1; CAS), Rarick Gulch Creek (8 km S of Dedrick [640 m] [Aug.] (1; CAS), Swift Creek ([1,520 m] [May] (12; PUCA); Tulare County, California Hot Springs [July] (7; LGBe), Franklin Creek ([2,500–2,990 m] [July] (1; CAS), Kaweah [June–Aug.] (10; CAS), Mineral King [Aug.] (2; CAS), South Fork Kaweah River [July] (2; USNM); Tuolumne

County, Herring Creek ([1,980 m]) [Aug.] (1; CAS); Yosemite National Park, Yosemite Valley (Lower Merced River) [June] (3; CAS); county unknown, Alpine Lake (1; CAS). **Idaho:** Blaine County, Petit Lake Creek (4.8 km WSW of Highway 93 on Twin Lakes Trail [2,130–2,440 m]) [Aug.] (1; CAS); Boise County, Rocky Bar ([1,830 m]) [June] (1; CAS); Elmore County, South Fork Boise River (4.8 km N of Pine at Dog Creek [1,460 m]) [Aug.] (1; CAS); Nez Perce County, Waha [June] (1; CAS); Shoshone County, Wardner [July] (6; CAS, OSUO); county unknown, Twin Creek Forest Camp ([1,520 m]) [July] (2; OSUO). **Montana:** Cascade County, Belt Creek (27.4 km S of Monarch on Highway 89 [2,100 m]) [July] (4; CAS); Glacier National Park [July, Sep.] (5; CAS, SJSU, UCD); Howe Creek [July] (4; SJSU), St. Mary Lake [July] (3; CAS), Swiftcurrent Creek (at Many Glacier Ranger Station) [Aug.] (3; SJSU), Two Medicine Lake [July] (7; CAS); Sweetgrass County, Big Timber Creek (at Half Moon Campground [2,230–2,290 m]) [July] (4; CAS). **Nevada:** Elko County, Lamoille Creek (near headwaters) [June] (1; BYUM), Thomas Creek (12.9 km SE of Lamoille at Thomas Creek Campground [2,320–2,380 m]) [Aug.] (1; CAS); Lander County, Hilltop [Aug.] (1; NSDA), Skull Creek [Sep.] (3; NSDA); Washoe County, Galena Creek (17.7 km W of Highway 395 on Highway 27 [2,290 m]) [July] (3; CAS), Third Creek (at Highway 28 [2,210 m]) [July] (22; CAS), Whites Creek (near Reno) [Oct.] (1; NSDA); White Pine County, Taft Creek ([2,130–2,440 m]) [July] (3; CAS). **Oregon:** Baker County, Pine Creek (16.1 km W of Baker [1,220 m]) [June–July, Sep.] (17; CAS, OSUO, USNM); Benton County, Marys Peak (Parker Creek at Road 1245 and Road 1296) [June] (9; GLPe, OSUO, SJSU), Yew Creek (14.5 km E of Alsea) [May] (1; OSUO); Clackamas County, Brightwood [May] (1; OSUO); Deschutes County, Indian Ford Creek (8 and 9.7 km NW of Sisters) [May–July, Sep.–Oct.] (81; GLPe, OSUO, SJSU), Squaw Creek (Highway 20 at Sisters [980 m]) [Aug.] (1; CAS); Hood River County, Mount Hood (Sand Creek) [July] (4; CAS); Jefferson County, Camp Sherman [Aug.] (2; UCD), Metolius (9; OSUO), Metolius River [June] (2; OSUO); Klamath County, Deming Creek (17.7 km NE of Bly) [June] (4; GLPa); Lane County, McKenzie River (8.4 km W of McKenzie Bridge [350 m]) [May] (2; CAS), South Fork McKenzie River [Sep.] (1; OSUO); Linn County, H. J. Andrews Forest (Mack Creek at Road 1553 [810 m]) [May] (1; CAS), North Santiam River (near Idanha) [May] (1; OSUO); Multnomah County, Bonneville [July] (1; BYUM), Horsetail Falls ([120 m]) [May, July] (8; CAS, GLPe, OSUO), Multnomah Falls [July] (5; CAS, OSUO); Walla Walla County, Lostine River ([1,310 m]) [Aug.] (1; OSUO), Wallowa Lake ([1,830 m]) [June–July] (9; CAS, OSUO, USNM), West Fork Wallowa River (at Sixmile Meadow [1,830 m]) [July] (1; CAS); Wasco County, Bear Springs (40 km W of Maupin [980 m]) [May] (1; OSUO). **Washington:** (1; OSUO); Chelan County, Buck Creek [Aug.] (1; SJSU); Clallam County, Soleduck River [Sep.] (3; CAS, SJSU); King County, Fall City [July] (1; OSUO), Greenwater River (1; OSUO), North Bend [July] (1; CAS), Seattle [July] (1; OSUO), Snoqualmie (1; OSUO), Snoqualmie Pass [Sep.] (2; OSUO), Tokul Creek (at Tokul) [July] (4; CAS, GLPe, OSUO, UCD), Wellington [July] (4; CAS, USNM), White River (8 km W of Greenwater on Highway 410 [490 m]) [Aug.] (35; CAS); Kitsap County, Seabeck [Aug.] (1; OSUO); Kittitas County, Iron Creek Pass ([1,520 m]) [Aug.] (2; OSUO); Lewis County, Horse Creek (near Longmire) [July] (1; CAS); Mason County [June] (2; OSUO), Pebble Ford Creek [June] (1; OSUO), Skokomish River [May] (1; OSUO); Mount Rainier National Park, Longmire [July] (2; CAS); Narada Falls ([1,370 m]) [July] (1; CAS), Paradise River

([1,490 m]) [June] (1; USNM); Olympic National Park, Deception Creek (at Dosewallips Trail [960 m]) [July] (1; CAS), Olympic Hot Springs ([760 m]) [June–July] (9; CAS, OSUO), Pass Creek (at Dosewallips Trail [560 m]) [July] (1; CAS), Sol Duc Hot Springs [Aug.] (2; USNM), Upper Twin Creek (at Dosewallips Trail [670 m]) [July] (2; CAS); Pierce County, Goat Creek (6.4 km E of Ashford on Highway 706 at Nisqually River [900–910 m]) [July] (4; CAS), Poch Creek (Carbon River Canyon) [Aug.] (1; OSUO); Whatcom County, Mount Baker (3.3 km E of Picture Lake on Highway 542 at Bagley Creek [670 m]) [Aug.] (1; CAS); Yakima County, Glenwood (2.7 km N [700 m]) [May] (2; CAS), Mount Adams (Bird Creek [1,370–2,130 m]) [July] (44; CAS, OSUO, USNM), Naches River (6.9 km SE of Cliffdell on Highway 410 [740 m]) [July] (1; CAS), White Pass [June] (2; SJSU); county unknown, Mount Adams ([1,830–2,440 m]) [July] (3; CAS). **Wyoming:** Yellowstone National Park, Gardiner River (at Mammoth Hot Springs) [Aug.] (1; OSUO). **Locality unknown:** (2; CAS, USNM).

GEOGRAPHICAL VARIATION.—Although considerable intrapopulational variation is evident for several characters, the only character in which I observed variation associated with distribution is body size. Adults from southern California, at the southern range limit for *A. insolens*, are the largest specimens I have seen. The smallest adults are from coastal Alaska, at the extreme northern range limit of the species. Adults from intermediate areas are intermediate in size, but the pattern is not strictly clinal. For example, adults from the area around Portland, Oregon, are larger than those from the Mount Rainier, Washington, area; and adults from interior localities (e.g., Alberta, Montana, and Wyoming) are almost as small as Alaskan specimens and clearly smaller than specimens from west coast localities at equivalent latitudes. Hence, the pattern is one of decreasing size from south to north and from west to east, with minor exceptions to the pattern in a few areas (such as Portland).

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The known range of *A. striata* (Fig. 19) is completely within the range of *A. insolens* (Fig. 18). Nevertheless, the two taxa may not be microsympatric. The only record of their co-occurrence (perhaps in different streams) is at North Bend, King County, Washington.

The geographical ranges of *A. insolens* and *A. lecontei* (Fig. 20) overlap broadly: from south-central and southeastern British Columbia, east to southwestern Alberta (Banff National Park) and northwestern Montana (Glacier National Park), and south to northeastern Oregon (Wallowa Mountains) and central Idaho (Sawtooth Mountain system). Ranges of these species appear to overlap also in northwestern British Co-

lumbia/southern Yukon Territory. Adults of both species have been found together in several localities (see respective locality lists).

Amphizoa striata Van Dyke

(Figures 5, 9, 15, 19, 28)

Amphizoa striata Van Dyke, 1927b:197. Holotype male in CAS. **Type-Localities.**—North Bend, King County, Washington. Edwards 1951:324. Hatch 1953:194. Kavanaugh 1980:291. Leech and Chandler 1956:301.

DISTINGUISHING CHARACTERISTICS.—Size large, SBL male = 13.1–14.2 mm, female 13.2–14.9 mm; body form very broad (Fig. 5a); body dark brown or piceous, with antennae, maxillary and labial palpi, and tarsi piceous or rufopiceous; head very finely and densely punctate; pronotum coarsely, moderately densely punctate over entire surface, with areas between punctures flat; elytra finely and densely punctate, slightly rugose in lateral one-third; pronotum (Fig. 9) broadest at base in most individuals (as broad at middle as at base in a few individuals), with lateral margins slightly or moderately arcuate at middle, not sinuate or slightly sinuate anterior to basal angles, slightly or moderately crenulate, median longitudinal impression present but faintly impressed; prosternal intercoxal process moderately elongate, spatulate; posterolateral angle of propisternum and posteromedial angle of propopleuron about evenly to form smooth prothoracic margin (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 5a) very broad basally, markedly narrowed subapically, elytra (Fig. 5b) convex, except slightly concave in lateral one-half posterior to humeral area, without carinae; elytral striae complete but faintly impressed, coarsely punctate; front tibia with posterodorsal groove extended along entire length, with fringe setae in groove restricted to apical two-thirds or four-fifths of tibia; male median lobe (Fig. 15) with shaft distinctly thickened at middle, slightly bulged ventrally, apex slightly deflected ventrally, not extended apicodorsally, left paramere broad basally, with vestiture restricted to apical one-fourth; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with stylar region medium in length, with dense vestiture of minute setae; specimen from western North America (Fig. 19).

HABITAT DISTRIBUTION.—Members of this species have been found in cool (but not cold), slow-flowing streams (Edwards, pers. comm.) and

in roadside ditches. Their distribution in such streams is similar to that of members of *A. insolens*.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 19) extends from southern Vancouver Island and the Olympic Peninsula and Cascade Range of northern Washington, south to southwestern Oregon, and east to Yakima County, Washington, and Wasco County, Oregon (both east of the Cascade Range).

I have examined 73 males and 63 females from the following localities:

CANADA

British Columbia: Vancouver Island, Duncan (Koksilah Creek) [Aug.] (5; MCZ, OSUO, USNM), Little Qualicum Falls Provincial Park (Little Qualicum River) [Aug.] (4; CAS, OSUO).

UNITED STATES OF AMERICA

Oregon: Benton County, Sulphur Springs (9.7 km NW of Corvallis) [May] (2; GLPe); Clackamas County, Colton [Aug.] (1; CAS); Jackson County, Little Applegate River (7.2 km S of Ruch [520 m]) [May] (1; CAS); Lincoln County, Deer Creek (12.9 km S of Toledo) [June] (1; OSUO); Wasco County, Tygh Valley [June] (1; OSUO). **Washington:** Clallam County, La Push [July] (1; OSUO); King County, Bothell (North Creek, Swamp Creek) [May–July] (12; CAS, GLPe, OSUO, SJSU, UCD), North Bend [July] (3; CAS), Seattle (Swamp Creek) [July, Sep.] (10; BYUM, CAS, OSUO, SJSU, UCD), Swamp Creek [May–Aug.] (71; GLPe, OSUO); Kitsap County, Bremerton [Apr.] (1; NDSA); Kittitas County, Parke Creek (near Kittitas) [Aug.] (1; LGBe); Mason County, South Fork Snohomish River [July] (2; OSUO); Snohomish County, Hazel (Stillaguamish Club) [May] (1; OSUO), Swamp Creek [Sep.] (5; SJSU); Yakima County, Satus Creek (near Toppenish [610 m]) [Aug.] (7; CAS, UCD, USNM); county unknown, Pack Forest [Aug.] (1; OSUO), "Pishi R." [July] (1; CAS).

GEOGRAPHICAL VARIATION.—Although intrapopulation variation is evident in body size, pronotal shape, and several other characters, I found no characters in which variation is associated with distribution.

GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—Refer to discussions under this heading for *A. insolens* and *A. lecontei*.

Amphizoa lecontei Matthews

(Figures 6, 10, 12, 16, 20, 28)

Amphizoa lecontei Matthews, 1872:121. Lectotype (designated by Kavanaugh 1980) male in BMNH. **Type-Localities.**—Vancouver Island, British Columbia [doubtful record, see comments below], Edwards 1951:327, 1954:19. Hatch 1953:195. Kavanaugh 1980:290. Leech and Chandler 1956:301.

Amphizoa planata Van Dyke, 1927a:98. Holotype female in CAS. **Type-Localities.**—Beaver Creek, Alberta. Edwards 1951:327, Hatch 1953:195. Kavanaugh 1980:291. Synonymized by Van Dyke 1927b:197.

Amphizoa carinata Edwards, 1951:326. Holotype male in CAS.

Type-Locality.—Conejos River near Menkhaven, Conejos County, Colorado. Kavanaugh 1980:289. Leech and Chandler 1956:301. **NEW SYNONYMY.**

NOTES ON NOMENCLATURE AND TYPES.—The lectotype of *A. lecontei* is supposed to have been collected on Vancouver Island, British Columbia, as noted both in Matthews's original description and on labels affixed to the specimen. However, I have not seen any other specimens from the island nor from the adjacent coastal mainland. Because the present type-locality appears to be well outside the known geographical range of *A. lecontei* (see Fig. 20 and text below), it is probable that the lectotype is mislabeled and that the type-locality should be emended. However, I choose not to do so at this time, pending further field efforts on Vancouver Island.

DISTINGUISHING CHARACTERISTICS.—Size medium, SBL male = 11.7–12.7 mm, female 12.2–14.0 mm; body form moderately broad (Fig. 6a); body dark brown or piceous (specimens from Arizona almost black), with antennae, maxillary and labial palpi, and tarsi piceous or rufopiceous; head very finely and densely punctate; pronotum medially with coarse, sparse punctures, with areas between punctures flat, laterally with punctures coarser, denser, more or less confluent, surface unevenly rugose in appearance; elytra finely and densely punctate, with punctures confluent over large areas, moderately rugose in lateral one-half; pronotum (Fig. 10) broadest at base in most individuals (as broad at middle as at base in a few individuals), with lateral margins slightly or moderately arcuate at middle, not or slightly sinuate anterior to basal angles, slightly or moderately crenulate, median longitudinal impression faintly or deeply impressed; prosternal intercoxal process moderately elongate, spatulate or sublanceolate; posterolateral angle of proepisternum and posteromedial angle of proepipleuron either about evenly to form continuous posterior prothoracic margin or proepipleuron is distinctly shorter than proepisternum and the two do not abut evenly, posterior prothoracic margin therefore with distinct jog (see Edwards 1951:321, "Plate 4"); elytral silhouette (Fig. 6a) broad basally, markedly narrowed subapically, elytron (Fig. 6b) with blunt but distinct carina on fifth interval, area medial to carina elevated, flat, area lateral to carina slightly concave; elytral striae complete but faintly impressed, coarsely punctate; front tibia with posterodorsal groove ex-

tended along entire length or restricted to apical four-fifths, with fringe setae in groove restricted to apical one-half or two-thirds of tibia; male median lobe (Fig. 16) with shaft distinctly thickened at middle, slightly bulged ventrally, apex slightly deflected ventrally, not extended apico-dorsally, left paramere broad basally, with vestiture restricted to apical one-fourth; female coxostylus ("coxite" of Edwards 1951:321, see his "Plate 4") with stylar region long and slender, with dense vestiture of minute setae; specimen from western North America (Fig. 20).

There is considerable intrapopulational variation in the development of tibial grooves and associated fringe setae among adults of all *Amphizoa* species; for this reason, I have experienced considerable difficulty in trying to interpret tibial characters that Edwards used to distinguish *A. lecontei* and *A. carinata* adults. I have found no differences between specimens Edwards identified as *A. carinata* and specimens of *A. lecontei* from various localities throughout its range in development of tibial grooves or in length or distribution of fringe setae, except such as can be attributed to intrapopulational variation.

Edwards also described and illustrated differences in shape of valvifers and paraprocts between *A. lecontei* and *A. carinata* females. Among my own dissections of females from within the range of *A. carinata* and from other localities for *A. lecontei*, I found only the *lecontei* form illustrated by Edwards (1951:321, "Plate 4"). I have also examined material dissected by Edwards, including the specimen that he illustrated for *A. carinata*. Although his drawing is a true representation of form of the valvifers and paraprocts of the latter specimen, other specimens from the same series differ from it in form and are, in fact, similar to other females of *A. lecontei*. It appears, therefore, that *A. lecontei* and *A. carinata* females are similar in form of valvifers and paraprocts, and that the *A. carinata* specimen illustrated by Edwards is atypical in this regard.

HABITAT DISTRIBUTION.—Members of this species are found in cool or cold, slow- or fast-flowing streams, in the same microhabitats as those described above for *A. insolens* members. However, they are more common in stretches of slow-moving water and streams that drop less steeply than are members of the latter species.

GEOGRAPHICAL DISTRIBUTION.—The known range of this species (Fig. 20) extends from south-

ern Yukon Territory south along the Rocky Mountain system to the Chuska Mountains of northeastern Arizona and Sangre de Cristo Range of northern New Mexico, and from the Wallowa Mountains of northeastern Oregon and Independence Mountains of northeastern Nevada east to the Bighorn Mountains of northcentral Wyoming and Front Range of central Colorado.

I have examined 190 males and 202 females from the following localities:

CANADA

Alberta: Banff National Park, Banff (and at Cascade River) [May, July–Aug.] (5; CAS, USNM); other localities, Beaver Creek [May] (4; CAS, USNM), Blairmore [Aug.] (1; CAS), Edmonton (1; OSUO), Happy Valley [Aug.] (2; CAS, USNM), Lundbreck [Aug.] (1; CAS), Mill Creek (72.4 km W of Fort Macleod) [Aug.] (2; USNM), Whitecourt (21 km SE on Highway 43) [May–June] (2; RERo). **British Columbia:** Creston (Goat River) [July–Aug.] (16; CAS, GLPe, OSUO), Fernie (Lizard Creek) [July] (1; CAS), Golden [Apr.] (1; CAS), Midday Valley (near Merritt) [July–Aug.] (4; CAS), Stanley [June] (1; CAS), Vernon (1; USNM). **Yukon Territory:** Haunka Creek (Highway 8 N of Atlin, British Columbia) [July] (1; UASM).

UNITED STATES OF AMERICA

Arizona: Apache County, Lukachukai Creek (8 km NE of Lukachukai at Wagon Wheel Campground [2,250–2,260 m]) [May, July–Aug.] (21; BMNH, CAS, MCZ, UASM, USNM). **Colorado:** (2; MCZ): Archuleta County, Pagosa Springs area (2,440–2,740 m) [Aug.] (2; MCZ), Upper San Juan Valley (2,130–3,200 m) [Aug.] (6; MCZ, USNM); Boulder County, Coal Creek (3.2 km E of Wondervu) [May] (1; CAS), Lefthand Creek (9.7 km WSW of Highway 36 [2,010 m]) [Aug.] (12; CAS); Conejos County, Menkhamen (Conejos River) [June] (2; CAS); Jackson County, Cameron Pass (2,740–2,930 m) [Aug.] (5; CAS, SJSU), Gould (Michigan River near Cameron Pass) [Aug.] (2; BYUM); Larimer County, Virginia Dale [June] (1; USNM); Pueblo County, Beulah [Aug.] (4; MCZ); San Miguel County, South Fork San Miguel River (2,590 m) [July] (12; MCZ). **Idaho:** Adams County, New Meadows [June] (2; CAS, OSUO); Bear Lake County, Bloomington Creek (11.1 km SW of Bloomington [2,130 m]) [Aug.] (2; CAS); Camas County, Carrie Creek (57.9 km ESE of Ketchum [2,100 m]) [Aug.] (13; CAS), Little Snake Creek [Sep.] (1; GLPe), South Fork Boise River (22.5 km E of Featherville at Skeleton Creek [1,550 m]) [Aug.] (2; CAS); Cassia County, Goose Creek [July] (2; GLPe), Magic Mountain (Rock Creek at Ranger Station [1,890 m]) [July] (5; OSUO); Clark County, Birch Creek [July] (1; GLPe); Elmore County, South Fork Boise River (4.8 km N of Pine at Dog Creek [1,460 m]) [Aug.] (3; CAS), Wood Creek (1.6 km S of Pine [1,370 m]) [Aug.] (16; CAS); Valley County, Bear Valley [July] (1; GLPe). **Montana:** Cascade County, Dry Fork Belt Creek (at Henn Gulch [1,620 m]) [July] (9; CAS); Chouteau County [Aug.] (1; OSUO); Glacier National Park [July–Sep.] (10; CAS, SJSU), Kintla Lake [June] (1; CAS), Swiftcurrent Creek (at Many Glacier Ranger Station [1,460 m]) [June–Aug.] (32; CAS, SJSU). **Nevada:** Elko County, North Fork Humboldt River [Oct.] (1; BYUM). **New Mexico:** Taos County, Red River (6.6 km W of Red River [2,580 m]) [June] (1; CAS). **Oregon:** Baker County, Cornucopia (14.5 km NW of Halfway) [July] (1; GLPe), Richland area ([1,220 m]) [June] (1; CAS); Grant

County, Clear Creek (3.2 km W of Granite) [Aug.] (1; GLPe); Wallowa County, Bear Creek (at Boundary Camp) [Sep.] (1; USNM), Lostine River (16.1 km S of Lostine [1,310 m]) [July–Aug.] (7; CAS, OSUO, UCD, USNM). **Utah:** Box Elder County, Clear Creek (at Clear Creek Campground) [Mar.] (1; BYUM), George Creek Campground [Apr.] (1; BYUM); Emery County, Huntington Creek (at Stuart Ranger Station) [July] (1; BYUM); Garfield County, Steep Creek [Aug.] (1; BYUM); Kane County, East Fork Virgin River (7.9 km NE of Glendale [1,860 m]) [June] (2; CAS); Salt Lake County, City Creek [June–July] (14; USNM); Piute County, Beaver Creek (below national forest boundary) [May] (1; BYUM); Sevier County, Mount Marvine (0.2 km N of Johnson Valley Reservoir at Sevenmile Creek [2,590 m]) [Aug.] (15; CAS); Summit County, Tryon Lake (1; BYUM); Utah County, Hobbie Creek ([1,830 m]) [July–Aug.] (29; BYUM, CAS, NSDA, SJSU), Provo ([1,490 m]) (1; CAS); Wasatch County, Little South Fork Provo River [July] (1; BYUM), Lost Lake Campground (2,990 m) [Aug.] (1; CAS), Upper Provo River (5.5 km E of Hailstone Junction on Highway 89A/150 [1,890 m]) [Aug.] (35; CAS), West Fork Duchesne River [Aug.] (1; BYUM); Weber County, Ogden [July] (2; USNM), Weber River (Highway 30 at Mountain Green [1,510 m]) [Aug.] (3; CAS); county unknown, Uinta Mountains [June] (2; BYUM), “Wasatch” [June] (1; USNM). **Washington:** Pend Oreille County, Sullivan Lake [Aug.] (2; CAS, OSUO); Stevens County, Crystal Falls [Aug.] (1; CAS). **Wyoming:** Big Horn County, Granite Creek (12.9 km SW of Granite Pass on Highway 14 [2,380 m]) [July] (2; CAS); Converse County, LaPrele Creek (61.2 km SW of Douglas on Highway 91 at Camel Creek Campground [2,530 m]) [July] (7; CAS); Grand Teton National Park, Colter Bay [Aug.] (1; SJSU), Delta Lake (2,730 m) [July] (1; SJSU); Johnson County, South Fork Clear Creek (25.7 km W of Buffalo on Highway 16 [2,350 m]) [July] (7; CAS), Tie Hack Camp [Aug.] (2; SJSU); Sheridan County, Little Tongue River (20.9 km WSW of Dayton on Highway 14 [2,380 m]) [July] (5; CAS); Sublette County, Hoback River (3.2 km NW of Bondurant [2,100 m]) [Aug.] (28; CAS); Teton County, Jackson (1; USNM); Washakie County, Tensleep Creek (17.7 km NE of Tensleep on Highway 16 [1,890 m]) [July] (1; CAS); Yellowstone National Park, Grand Canyon of the Yellowstone (above Tower Falls) [Aug.] (1; MCZ), Indian River Campground [Aug.] (1; USNM), Spirea Creek [Aug.] (2; SJSU).

GEOGRAPHICAL VARIATION.—In his original description of *A. carinata*, Edwards (1951:327) suggested that this form might represent “merely a geographical subspecies” of *A. lecontei*, but added that “it seems probable that no intergradation occurs between these populations.” However, subsequent collections from geographically intermediate areas demonstrate intergradation, and the incongruence found among geographical variation patterns of different characters has led me to treat *A. lecontei* and *A. carinata* as conspecific. Nonetheless, the pattern of variation in *A. lecontei* merits description.

Mature (i.e., non-teneral) adult specimens from northeastern Arizona are black whereas mature specimens from other parts of the species range are piceous or dark brown.

Characters of pronotal shape, including shape of lateral margins, of apical and basal angles, and relative width at base versus at middle, are all highly varied among adults of *A. lecontei*. All character states cited by Edwards as unique for *A. carinata* adults fall within the range of variation seen among *A. lecontei* adults from other geographical areas. Edwards described the median longitudinal impression as deep in *A. carinata* adults but shallow and indistinct in *A. lecontei* adults. Specimens with pronotal characteristics of the *carinata* form predominate in the region from southcentral Wyoming, south through Colorado and northern New Mexico, east through northeastern Arizona, and north through south and central Utah. Adults with the typical *lecontei* form predominate in all other areas.

Specimens with prominent excavations of the prosternum anterior to the front coxal cavities, described by Edwards as a feature unique to *A. carinata* adults, are found in localities throughout the range of *A. lecontei*, although always in lower numbers than specimens from which these excavations are lacking. Furthermore, not all specimens exhibiting other features characteristic of *A. carinata* have these excavations (e.g., most specimens from Arizona). Similarly, the relationship between the proepisternum and proepipleuron described and illustrated by Edwards (1951:321, "Plate 4") does not hold up as a distinguishing feature of *A. carinata* adults. Samples from localities in southcentral Wyoming, northern Colorado, northern New Mexico, northeastern Arizona, and southern and east-central Utah include specimens exhibiting both states of this character, as well as intermediates between these extremes.

In most adults from northeastern Arizona, northern New Mexico, and Colorado, the prosternal intercoxal process is slender, elongate, and sublancoate, whereas it is slightly broader, shorter, and spatulate in adults from other areas.

Several of the characters noted above are useful for describing the *carinata* form. Its geographical range is centered at the southern extreme of the range of *A. lecontei*, in northeastern Arizona, and extends northwestward (through Utah) and northeastward (through New Mexico, Colorado, and southcentral Wyoming). In successively more northern populations within this range, the *carinata* form is represented by a lower percentage of individuals. However, adults demonstrating one or more *A. carinata* traits are found in low

numbers throughout the range of *A. lecontei*; adults that are intermediate between the *A. carinata* and typical *lecontei* forms (for one or more characters) are abundant in northern parts of the range of the *A. carinata* form and present in low numbers throughout that range. Given this pattern, there appears to be insufficient reason for retaining the name *A. carinata* even at subspecific rank.

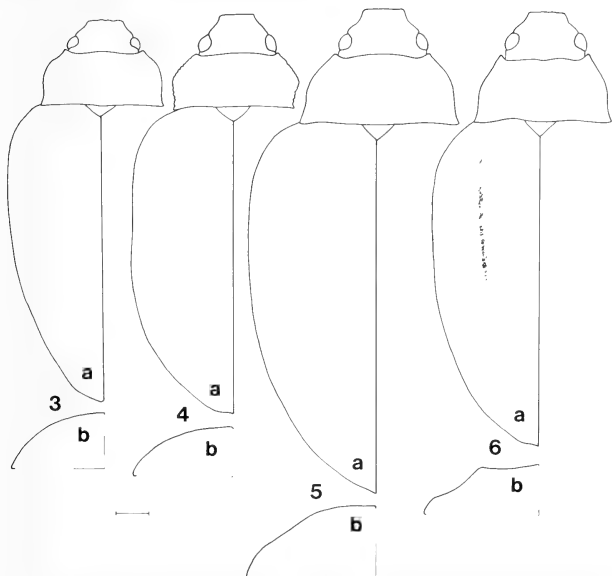
GEOGRAPHICAL RELATIONSHIPS WITH OTHER SPECIES.—The geographical ranges of *A. lecontei* and *A. insolens* overlap extensively over a broad north/south area (see above under this heading for *A. insolens*); and adults have been collected together in several localities (e.g., at Swiftcurrent Creek, Glacier National Park, Montana; see also respective locality lists).

Based on material I have examined, the ranges of *A. lecontei* and *A. striata* are allopatric. If, however, *A. lecontei* is represented on Vancouver Island, the original type locality for the species, then these two species are at least macrosympatric in that area.

Phylogeny

Prerequisite to understanding the evolutionary and distributional histories of the species of *Amphizoa* is formulation of a hypothesis of phylogenetic relationships among them. Cladistic analysis is the best available technique for elucidation of these relationships (Hennig 1966; Kavanaugh 1972, 1978a). Briefly, the analytical procedure is as follows. (1) For each character, the direction of its evolution (i.e., the so-called "polarity" of the transformation of its different character states) is determined, from most primitive (plesiotypic) to most derived (apotypic) state or states. (2) Taxa are then grouped together, solely on the basis of shared derived (synapotypic) character states, into successively more inclusive groups. (3) Because synapotypy is accepted as evidence for common ancestry, and because degree of phylogenetic (cladistic) relationship is equivalent to relative recency of common ancestry, the hypothetical branching pattern of phylogenetic relationships inferred is simply the grouping sequence read in reversed order (i.e., from most to least inclusive).

The crucial step in cladistic analysis is determination of the polarity of transformations of character states for each character. Several criteria have been proposed and/or used (Ball 1975;



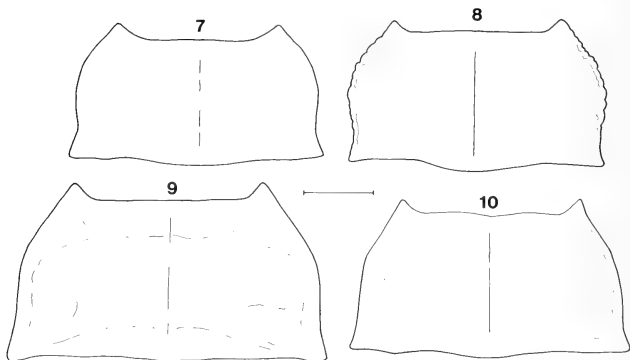
FIGURES 3-6. Body form (a = dorsal aspect, right elytron omitted; b = cross-sectional dorsal silhouette of left elytron at point one-third of elytral length from base); scale line = 1.0 mm. Figure 3, *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 4, *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 5, *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 6, *Amphizoa lecontei* Matthews (Upper Provo Canyon, Utah).

Ross 1974; Ekis 1977; Kavanaugh 1978b; Crisci and Stuessy 1980; Watrous and Wheeler 1981; and references therein) to determine which states are relatively plesiotypic and which are relatively apotypic. Of these, only two have intrinsic merit.

First, and most important, is the so-called "out-group" criterion, which can be stated as follows: for a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic [=plesiotypic] state (Watrous and Wheeler 1981). This criterion is relatively straightforward and easy to apply, except when an appropriate out-group is difficult to recognize or when more than one character state is represented in the out-group.

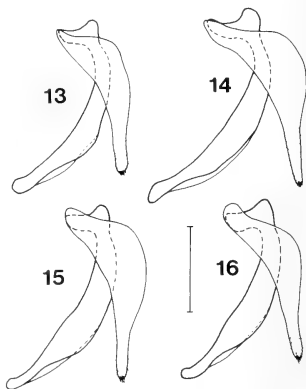
Recently, Maddison, Donoghue, and Maddison (1984) proposed a practical method for out-group analysis using parsimony criteria which should prove useful even when phylogenetic relationships among out-group components are inadequately known.

The second criterion, "character correlation" (Ekis 1977; Hennig 1966; Kavanaugh 1978b), can be stated as follows: characters for which the polarities of transformation series have been determined with confidence can be used to infer polarities in transformations of other characters in which evolutionary sequence is less easily inferred. This is the criterion of choice only when the out-group criterion cannot be applied on its

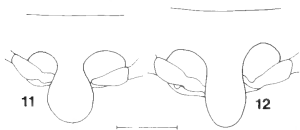


FIGURES 7-10. Pronotum, dorsal aspect; scale line = 1.0 mm. Figure 7. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 8. *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 9. *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 10. *Amphizoa lecontei* Matthews (Upper Provo Canyon, Utah).

own. Without formally recognizing it, Watrous and Wheeler (1981) invoked the character correlation criterion in order to recognize functional in-groups and functional out-groups where conventional (i.e., their so-called "taxonomic") in-groups and out-groups proved useless. In practice, a tentative phylogenetic tree (cladogram) is constructed based on one or more characters for which character-state polarities are well established. Depending on the structure of the cladogram derived, it may be possible to recognize a functional out-group (e.g., the most basal divergent lineage in the cladogram), which can be used in analysis of other characters. The distribution of states of another character, polarity of which cannot be determined by reference to the out-



FIGURES 13-16. Median lobe and left paramere of male genitalia, left lateral aspect; scale line = 1.0 mm. Figure 13. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 14. *Amphizoa insolens* LeConte (Indian Ford Creek, Oregon). Figure 15. *Amphizoa striata* Van Dyke (Swamp Creek, Washington). Figure 16. *Amphizoa lecontei* Matthews (Swiftcurrent Creek, Montana).



FIGURES 11, 12. Prosternal intercoxal process, ventral aspect; scale line = 1.0 mm. Figure 11. *Amphizoa davidi* Lucas (Pao-hsing, China). Figure 12. *Amphizoa lecontei* Matthews (Lukachukai Creek, Arizona).

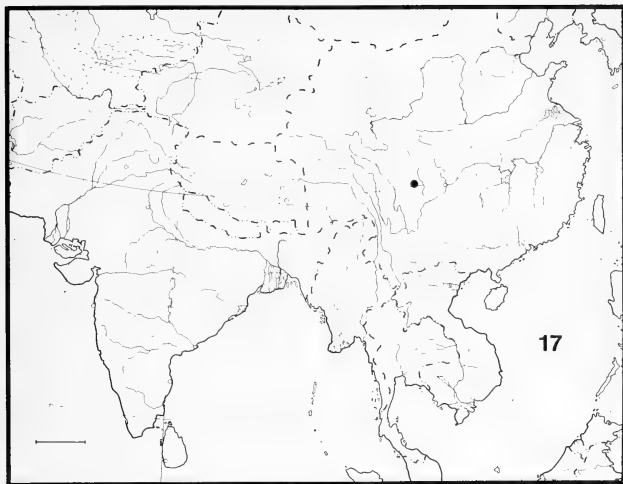


FIGURE 17. Map of geographical distribution of *Amphizoa davidi* Lucas.

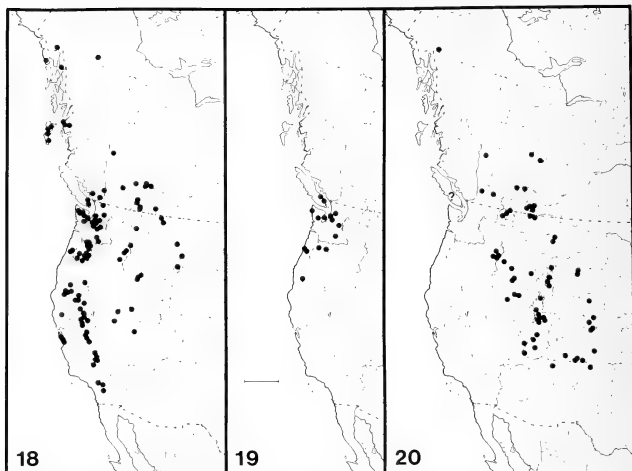
group criterion using the conventional (taxonomic) out-group, is then determined over the tentative cladogram. A derivative out-group correlation may then be possible, making use of the functional out-group recognized using other characters.

The choice of a suitable out-group for *Amphizoa* is not a simple one. Although amphizoids have long been considered to represent an evolutionary grade between the Geadephaga and the more specialized groups of Hydradephaga (LeConte 1853; Edwards 1951), their phylogenetic relationships with other adephagan groups are not clearly understood. Among the Adephaga are both terrestrial and aquatic groups, each with generalists, specialists, and hyperspecialists (Erwin 1979) in their ranks. Structural, functional, and behavioral diversity within the suborder is great, and independent evolutionary trends, some in opposite directions, are numerous. Character state distributions of many important characters are so complex within the suborder, at least in

our present understanding of them, that the logical out-group for amphizoids, the Adephagaminus-Amphizoidae, is not a particularly useful group for cladistic analysis. I have, therefore, tried to limit the scope of the out-group to some subgroup of Adephaga to maximize the usefulness of the out-group criterion as a tool in analysis.

Phylogenetic relationships of amphizoids

To many workers (Edwards 1951, and references therein), amphizoids appear to represent a primitive grade of dytiscoid evolution. Amphizoids lack structural adaptations of highly specialized swimmers (Hlavac 1975; Evans 1982), such as dytiscids. In fact, they are much more efficient as runners on land than as swimmers in water. Characteristics of thoracic and male and female genitalic structure and numerous other features approximate what could be expected in a suitable common dytiscoid ancestor. Among



FIGURES 18–20. Map of geographical distribution. Figure 18. *Amphizoa insolens* LeConte. Figure 19. *Amphizoa striata* Van Dyke. Figure 20. *Amphizoa lecontei* Matthews.

extant forms, no other hydradephagan adults appear to represent the early Mesozoic grade of dytiscoid evolution (Ponomarenko 1977) as well as amphizoids. But are amphizoids related only to the dytiscoids, and if so, to which most closely?

Several more particular affinities have been proposed for amphizoids. Horn (1881) and a few later authors have suggested close relationship with hygrobiids. Might the latter alone serve as a suitable out-group? Probably not. Evidence linking hygrobiids with amphizoids is minimal and likely based on symplesiotypic traits (Hammond 1979).

Bell (1966) suggested that amphizoids, living in habitats where swimming is hazardous, may have evolved from more advanced dytiscids, with their apparent plesiotypic characteristics representing secondary loss or reduction of swimming adaptations. However, characteristics of prothoracic (Hlavac 1975) and pterothoracic structure (Ponomarenko 1977; Evans 1982, also in

press) support a phylogenetically more remote (basal) relationship between amphizoids and dytiscids. Although a suitable out-group for amphizoids must include dytiscids, extant forms of the latter represent a more highly specialized grade of adephagan evolution and are probably not sufficient as an out-group.

Several lines of evidence suggest that Trachypachidae form a monophyletic group with the dytiscoid families, including all the hydradephagan groups except, perhaps, haliplids and gyrrinids (Bell 1966, 1967, 1982; Crowson 1981; Evans 1977, 1982; Hammond 1979; Forsythe 1981; Roughley 1981). This relationship is established on the basis of numerous supposed synapotypic features (Hammond 1979; Roughley 1981; Evans 1982) involving characters of antennal pubescence, locomotory function and structure (of legs, wings, and associated structures), male and female genitalic structure, and female reproductive system. If trachypachids are

closely related to amphizoids and other dytiscoids, then they should be included in any suitable out-group for analysis.

Determination of apotypic states of at least several characters linking trachypachids with dytiscoids is based on the assumption, either stated or implied, that the common adephagan ancestor was terrestrial rather than aquatic in habits (Crowson 1955, 1981; Bell 1966, 1967, 1982; Evans 1977, 1982, also in press; Hammond 1979; Forsythe 1981; Roughley 1981). However, this contention is not universally accepted. Erwin (1979) suggested that the Adephaga arose from an aquatic neuropteroid ancestor similar to extant amphizoids, at least in habits. Based on review of both Palaeozoic and Mesozoic fossil beetles, Ponomarenko (1977) proposed an aquatic origin of Adephaga, probably in late Permian time, from aquatic schizophoroid Archostemata. In fact, his separation of fossil specimens of Adephaga from those of Schizophoridae of that age was admittedly somewhat arbitrary (Ponomarenko 1977). Perhaps this distinction is one of grade rather than clade.

Crowson (1981) and Ponomarenko (1977) agree on both the time (Late Permian) and source group (Archostemata: Schizophoridae) for the probable origin of Adephaga. They differ, however, in their views on the ancestral adephagan habitat (whether terrestrial or aquatic), which by extension, could have been inherited from either terrestrial or aquatic schizophoroid ancestors, both of which are known from Permo-Triassic time.

Amphizoids are only semiaquatic in habits. Adults are able to carry on most if not all life functions (e.g., feeding, locomotion, oviposition) at least as well out of water as in it and based on my fieldwork, do so routinely in nature. At least under laboratory conditions, eggs and larvae also thrive out of water, and pupation occurs on land. These habits are reflected by structure. Adults lack special adaptations for fast swimming and are barely able to move freely underwater except by clinging to substrata. Their most effective mode of locomotion in water is passively drifting with stream currents. Here I use the term "semiaquatic" to refer to the combination of amphibious habits, structure that is relatively unspecialized for aquatic life, and ineffective swimming capability that is characteristic of extant amphizoids.

If the ancestral adephagan was a terrestrial organism, then amphizoids may represent, at least structurally, a first stage in adephagan adaptation to aquatic life. Primitive (plesiotypic) character states for Hydradephaga, including amphizoids, should be represented among their near terrestrial (i.e., geadephagan) relatives, including the Mesozoic Eodromeinae and Protorabinae (Ponomarenko 1977), both living and extinct Trachypachinae (Bell 1966, 1982; Evans 1977, 1982; Ponomarenko 1977; Roughley 1981), and living basal-grade Carabinae, such as Notiokasiini, Nebriini, and Opisthiini. It might, therefore, be a waste of effort to include other extant hydradephagan groups in the out-group for cladistic analysis because their members may demonstrate only relatively apotypic character states associated with more advanced stages of specialization to aquatic life.

Alternatively, if the common adephagan ancestor were aquatic, then plesiotypic character states should be associated with aquatic rather than terrestrial organisms. Any suitable out-group for cladistic analysis of amphizoids would have to include extinct aquatic groups, such as the Mesozoic Parahygrobiidae, Coptoclavidae, and Liadytidae (Ponomarenko 1977), as well as other living dytiscoids (Hygrobiidae, Dytiscidae, and Noteridae). If, however, the common adephagan ancestor were only semiaquatic, similar in both habits (Erwin 1979) and structure to living amphizoids, then extant dytiscoids might again be too specialized to be useful in out-group comparisons.

Composition of a suitable out-group for analysis of extant *Amphizoa* species depends, at least in part, on the evolutionary hypothesis proposed to account for the origin and initial radiation of Adephaga—whether from a terrestrial, aquatic, or semiaquatic common ancestor. Faced with a choice from among five conflicting hypotheses (none of which he could reject with available evidence) to explain the relationships of trachypachids with other Adephaga, Bell (1982) called for additional efforts to discover new evidence bearing on the question. Perhaps a similar call for additional data is most appropriate here as well. However, even a preliminary cladistic analysis of *Amphizoa* species at this time requires selection of an out-group for comparative purposes; such a selection requires a choice among alternative hypotheses for adephagan origin. In

my view, evidence favors the origin of Adephaga from a semiaquatic common ancestor for reasons outlined below.

Evidence from the fossil record

Thanks to Ponomarenko's (1977, and other papers cited therein) outstanding work on late Palaeozoic and Mesozoic beetle fossils, information about the early stages of adephagan evolution is now available. It is evident, for example, that a significant aquatic radiation of schizophorid Archostemata, presumptive ancestors of Adephaga, had occurred by Permo-Triassic time (Ponomarenko 1977). By early Mesozoic time, the adephagan radiation was already diverse. Forms that, structurally, could have given rise to all major extant adephagan groups—gyrinoids, haliploids, dytiscoids, and caraboids—were represented in the Jurassic fauna of Asia. However, the aquatic adephagan component was clearly more diverse and more advanced (i.e., more similar to extant forms) than the terrestrial component of that time. The carabid fauna, for example, did not take on a modern aspect (i.e., one in which middle- and higher-grade carabids are evident) until mid- to late-Cretaceous time (Ponomarenko 1977). This suggests that the aquatic radiation of Adephaga preceded that of terrestrial groups.

Much can also be learned about plesiotypic (primitive) versus apotypic (derived) character states for Adephaga from study of the diverse and beautifully preserved Mesozoic fossil material illustrated by Ponomarenko (1977). For example, it is clear, from review of these fossil specimens and out-group comparisons with schizophorid fossil material, that contribution to the lateral wall of the mesocoxal cavity by the metepisternum is plesiotypic in Adephaga. This trait was widespread among extinct (and extant) Archostemata as well as the extinct eodromeine trachypachids, protorabine carabids, triaplids, and some (but not all) Mesozoic dytiscoid groups. Among extant forms it is restricted to Amphizoidae, some Dytiscidae, and members of genus *Spanglerogyrus* among Gyrinidae. Similarly, the form of hind coxae seen among extant trachypachids, dytiscids, amphizoids, hygrobids, gyrenids, and halipids—in which the lateral coxal wing extends laterally to the elytral epipleuron, completely separating thoracic from abdominal

sclerites (i.e., the "incomplete" form of Bell 1967, or "interrupted" form of Roughley 1981)—appears to be plesiotypic, based on out-group comparisons with schizophorids and Mesozoic fossil adephagans.

In form and structure of hind coxae, relationships of mesepimera and metepisterna to mesocoxal cavities, and every other structural detail that can be observed in the fossil material, amphizoids appear to demonstrate the character state that can be interpreted as plesiotypic in relation to a semiaquatic ancestor and divergent lines of more specialized forms. Liadytids (Ponomarenko 1977), which probably represent a basal grade of Mesozoic dytiscoids, have hind coxae more specialized (hence, apotypic) for rapid swimming than amphizoids, and coptoclauids (Ponomarenko 1977) have metepisterna excluded from lateral walls of mesocoxal cavities by anterolateral extensions of the metasternum. Amphizoids are very similar in appearance and structure to Mesozoic eodromeine trachypachids, except that their metacoxae are slightly larger and more closely contiguous medially than the latter. Presumably, eodromeines were terrestrial beetles, not aquatic or semiaquatic.

Perhaps the only known form more similar to eodromeines than amphizoids is *Necronectulus* (Ponomarenko 1977), described from a single, legless specimen of Early Jurassic age from Asia. Its metacoxae were typical of those in eodromeines, but nothing is known of its distal leg structure. Based on body structure and form of antennae, Ponomarenko suggested that it could have been either terrestrial or aquatic in habits, but he favored the latter view. Possibly, it represents the first stage of adaptation to purely terrestrial life among Adephaga, although the earliest known eodromeines predate the only known occurrence of *Necronectulus* in the fossil record.

In summary, I suggest that a review of Mesozoic fossil material provides two insights. First, character states demonstrated by extant amphizoid adults can, in almost every instance, be interpreted as plesiotypic in relation to respective character states in known Mesozoic and extant aquatic Adephaga, as well as extant trachypachids and carabids. Second, there is little with which to distinguish amphizoids and eodromeine trachypachids, except their habitats. If this similarity is based on synapotypic features, then adephagan relationships could be as illustrated in Figure 21a or 21b. If it is based on symple-

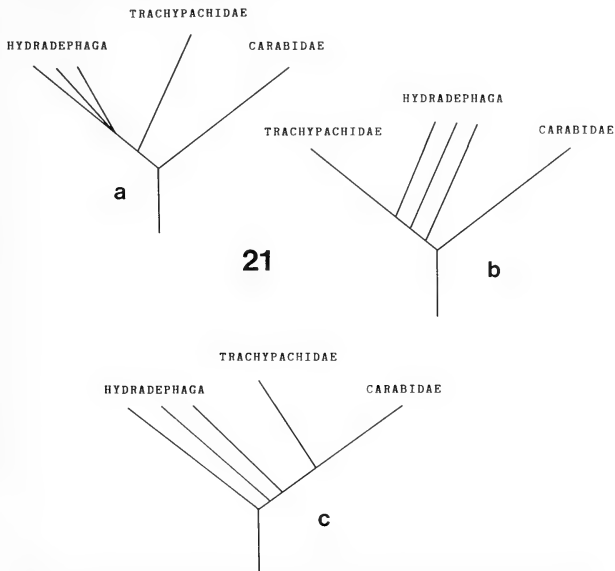


FIGURE 21. Illustrations of alternative hypotheses of phylogenetic relationships among Hydradephaga, trachypachids, and carabids.

siotypic features, then adephagan groups could be related as in Figure 21c.

Evidence for relationship between amphizoids and trachypachids

As noted above, several workers (Bell 1966, 1982; Evans 1977, 1982; Hammond 1979; and Roughley 1981) have provided evidence in support of close relationship between trachypachids and the dytiscoids, including amphizoids, hygrobids, noterids, and dytiscids. All of these authors presumed a terrestrial origin for Adephaga. Hammond (1979) listed 7 and Roughley (1981) 10 (for a total of 14 different) proposed synapomorphies uniting these groups. Each should be considered separately, in light of all available data about extant and fossil forms.

1. Antennal pubescence. Both Hammond and Roughley considered the glabrous antennae of adult hydradephagans to be apotypic, with the plesiotypic state—antennae pubescent—associated with carabids (i.e., terrestrial forms). The condition in trachypachids—glabrous, except for an apical whorl of setae on each antennomere and fine pubescence on antennomere 11 only—was considered synapotypic with the condition found among Hydradephaga. Most Coleoptera have flagellar antennomeres covered with a dense coat of short sensory setae, as do adults of most other insect orders; and presence of such pubescence would appear to be plesiotypic for Adephaga. If we assume an aquatic or subaquatic ancestry for the suborder, however, presence of pubescence could be interpreted as apotypic in

carabids; pubescence on antennae of trachypachids, albeit greatly restricted, could be synapotypic for trachypachids and carabids.

2. Open procoxal cavities with postcoxal bridge. This combination of two characters (i.e., (a) procoxal cavities open or closed and (b) postcoxal bridge absent or present) is difficult to interpret. Most workers agree that open procoxal cavities represent the plesiotypic state of the first character (a). However, presence or absence of a postcoxal bridge (b) is more difficult to interpret. A bridge has been reported from trachypachids and dytiscoids and cited as a synapotypy for these groups. However, Hlavac (1975) and Hammond (1979) noted the presence of a bridge in adults of *Carabus*, *Hiletus*, and the nebriniine genus *Leistus*, whereas no bridge is evident in members of related carabid groups, including other nebriniine genera (i.e., *Nebria* and *Pelophilus*). Presence or absence of a postcoxal bridge does not appear to be a reliable character for demonstrating phylogenetic relationships among Adephaga.

3. Prosternal process. Roughley (1981) proposed a similarity (synapotypy) among trachypachids and Hydradephaga in length and shape of the prosternal intercoxal process. I disagree with this contention. The process in both trachypachids and amphizoids (Fig. 11, 12) is very similar to that in Nebriniini, Notiokasiini, and other basal-grade carabids in size and shape and unlike more specialized aquatic adephagans such as dytiscids and hydrobiids. I regard this character as symplesiotypic in trachypachids, amphizoids, and carabids, apotypic in higher dytiscoids.

4. Prosternal-metasternal contact. Roughley (1981) suggested that contact between the prosternal intercoxal process and the anteriormost portion of the metasternum was possible in trachypachids as in most dytiscoids and, further, that this represented a synapotypic feature. As with character 3 (prosternal process) above I disagree with this interpretation. Contact between prosternum and metasternum is no greater in either trachypachids or amphizoids than in nebriniines or other basal-grade carabids. The condition in amphizoids, trachypachids, and basal-grade carabids is surely symplesiotypic.

5. Coadaptation of posterior border of pronotum and anteriorly truncate elytra. Hammond (1979) proposed that coadaptation of the posterior pronotal margin and elytral base among

trachypachids and hydradephagans represents a synapotypic feature. It is true that pronota and elytra are very closely juxtaposed in trachypachids and most dytiscoids, but no more so than in a number of carabid groups (e.g., omophronines, amarines, and some migadopines, bembidiines, pterostichines, and harpalines). Close, relatively inflexible association of prothoraces and pterothoraces and a continuous, evenly arcuate, uninterrupted lateral silhouette (also including the head in many instances) is broadly characteristic of aquatic beetles. Assuming an aquatic origin for Adephaga, this form may represent the plesiotypic condition. Apparent support for this interpretation is provided by Ponomarenko's (1977) numerous illustrations of Mesozoic Adephaga. Among beetles illustrated, including eodromeine trachypachids and protorabine carabids, a form typical of extant trachypachids predominates. This evidence suggests that early carabids were more similar in form to extant trachypachids than to a majority of extant carabids. Perhaps the relatively narrow-waisted, flexibly-joined carabids are apotypic rather than plesiotypic in this regard, with members of groups such as omophronines and amarines having acquired a trachypachid-like form secondarily, as an adaptation to particular, specialized biotopes.

6. Metacoxal cavities interrupted ("incomplete," Bell 1966). As discussed above, metacoxae of trachypachids, amphizoids, and other Hydradephaga (both extinct and extant) are similar in form and lateral extent to those seen in Archostemata, including presumptive schizophoroid ancestors of Adephaga. The main difference between these adephagan metacoxae and archostematan metacoxae is that the former, unlike the latter, are countersunk into the body wall (i.e., into the basal abdominal sterna), so that they appear to divide the first (basal) visible sternum into two lateral parts. Continuity of this sternum internal to the metacoxa (i.e., dorsally) can be confirmed by dissection. I agree with Ponomarenko (1977) that this form of metacoxae is plesiotypic in Adephaga, rather than apotypic as suggested by most recent workers (Bell 1966, 1967, 1982; Evans 1977, 1982; Hammond 1979; Forsythe 1981). Evans (1977, 1982), Forsythe (1981), Hammond (1979), and others have constructed and/or reviewed various hypotheses to explain why trachypachids should have metacoxae preadapted for aquatic life, and why car-

abids should have even partially immobilized coxae for rapid running. Again, these workers assumed a terrestrial origin of Adephaga. In light of both out-group comparisons with Archostemata and form and structure of known Mesozoic Adephaga, it seems simplest to suggest that trachypachids have legs adapted for aquatic life because their ancestors were aquatic, and carabids have immobilized coxae because, like trachypachids, their ancestors lived in the water and such coxae are advantageous there. Carabid leg structure is adapted to terrestrial life, but it still reflects the constraints of ancestry.

7. Metacoxal fusion. Roughley (1981) stated that "in trachypachids and Hydradephaga the metacoxae are fused medially, the fusion being marked by a single internal intercoxal septum continuous with the metafurca and the median sternal ridge." My own dissections do not substantiate the extent of fusion Roughley reported. In both trachypachids and amphizoids, the medial walls of the metacoxae are not fully fused to form a single septum, but are merely very closely approximated, slightly more so in amphizoids than in trachypachids. Roughley is correct in noting the close association between the metacoxae and the metafurca and median sternal ridge in adults of these groups. In the carabids examined, the metafurca is positioned far forward in relation to the metacoxal base medially. It is unclear, however, which of these conditions (states) is apotypic. Presumably the state seen in trachypachids and Hydradephaga is an adaptation to "aquatic existence" (Roughley 1981:276). Again, assuming an aquatic ancestry, the state seen in carabids could be apotypic, rather than plesiotypic as Roughley and others have suggested.

8. Similarities in wing venation and folding. According to Hammond (1979), hindwings of trachypachids and dytiscoids share numerous features (e.g., wing folding pattern, position of oblongum cell in relation to apical and posterior wing margins). Adephaga are characterized by having an exceptionally strong spring mechanism for wing folding, which is aided, in a majority of groups, by one or another kind of abdominal movement. Almost complete reliance on the spring mechanism alone is seen among the related, basal-grade carabid tribes Nebriini, Opisthiini, Notiophilini, Carabini, and Cicindelini. Hammond (1979) interpreted this latter condition as (probably) plesiotypic for Adephaga;

but he noted that this hypothesis requires that increased reliance on abdominal movements, and development of special structures associated with same, occurred independently in several adephagan lineages. Again, without information from direct out-group comparisons with other Coleoptera, especially Archostemata, it is difficult to recognize the most plesiotypic condition with any confidence. Although they may represent only a basal grade of carabid evolution, nebrini, opisthiini, and the other groups listed above may also form a monophyletic assemblage that diverged from other carabids at an early evolutionary stage, members of which are characterized by sole reliance on the spring mechanism for wing folding.

9. Subcubital binding patch of hindwing. Both Hammond (1979) and Roughley (1981) cited presence of this binding patch, posteriorly near the apex of the hindwing, as a synapotypic feature uniting trachypachids with dytiscoids. Absence of such a binding patch from hindwings of carabids, halipids, and gyrinids was seen as a plesiotypic condition. Not all dytiscoids, however, have the binding patch; in all *Systolosoma* (Trachypachidae) adults that I examined, the patch was nonpigmented and very poorly defined, if it could be claimed as present at all. A subcubital binding patch is absent from hygrobiid wings and from wings of members of some bidessine, hydrovatine, and hyphydrine dytiscid genera. Hammond (1979) noted a marked association between small body size and absence of the binding patch in the dytiscid groups cited above. He suggested functional reasons why the subcubital binding patch might not be necessary in small beetles and proposed that its absence represented a secondary loss in the above dytiscid groups. Size considerations do not, however, account for the absence of the patch from hygrobiid hindwings nor its reduction or absence from *Systolosoma* adults. Although I see no reason to doubt that presence of the subcubital binding patch is an apotypic feature in Adephaga, I suggest that its absence from hygrobiid and carabid hindwings may also represent secondary losses. If this is correct, presence of the binding patch may, in fact, be synapotypic for Adephaga, with its secondary loss having evolved independently in some or all members of the dytiscid, trachypachid, carabid, and halipid lineages.

10. Male genitalia with long, apically nar-

rowed parameres. Parameres of trachypachid males and of at least some dytiscoid group males are very similar in length, shape, and vestiture. Hammond (1979) suggested that the long, apically narrowed form seen in males of these groups represented a synapotypic feature. However, males of certain carabid groups, including carabines, cythrines, pamborines, and cicindelids also have parameres resembling those of trachypachids in form. It seems simpler to suggest that this condition represents a plesiotypic rather than apotypic condition, with the great diversity of forms seen among extant carabids having evolved through several independent, apotypic trends diverging from the basic form.

11. Size and armature of internal sac. Roughley (1981) and other workers have assumed that presence of a well-developed internal sac found in the median lobe of the aedeagus, such as in carabid males, represents the plesiotypic condition among Adephaga; he further suggested that presence of an armature of setae and spines, on or in the sac, is also plesiotypic. Without knowledge of these characteristics in proposed schizophoroid common ancestors of Adephaga, nor even in extant archostematan males (such as in *Omnia* species), it is difficult to interpret differences in size and development of the internal sac among extant Adephaga in a cladistic sense. As Roughley suggested, it is also possible that the small, slightly developed internal sac of trachypachids and dytiscoids represents the plesiotypic adephagan condition. Male gyrinids, which appear to be only distantly related to other Adephaga, based on many other characters (Evans 1982; Ponomarenko 1977), also have a slightly developed internal sac. This suggests that the large, well-developed internal sac of carabids represents an apotypic, rather than plesiotypic, condition.

Some basal-grade carabid males (e.g., nebrines, notiokasiines, and opisthiines) lack evident armature on the internal sac. Although associated spines and/or setae are found in males of some basal-grade carabids and are widespread among those of middle- and high-grade carabid groups, I see no reason to suggest that their occurrence represents a plesiotypic condition among Adephaga, and I do not consider their absence to be synapotypic for trachypachids and dytiscoids.

12. Dilator muscle of vagina. The presence of this muscle in a majority of dytiscoids examined

(Burmeister 1976) led Roughley (1981) to suggest that its occurrence represents a synapotypic feature among dytiscoids (including amphizoids) and trachypachids. Its absence from carabid females was considered plesiotypic. The source of Roughley's data for trachypachids and amphizoids (Roughley 1981, table 1) is unclear; but I assume that these data are from his own dissections because Burmeister (1976) did not present data for these groups (see his table 1, p. 216). Assuming that Roughley is correct, and this muscle is present in trachypachids and amphizoids as well as in haliplids, gyrinids, hydrobiids, and most dytiscids, but not in carabids (Burmeister 1976), it would seem simpler to suggest that its presence is plesiotypic, and its absence (in carabids and a few dytiscids) apotypic among Adephaga. As with the previous character, it will be useful to examine extant archostematan as a possible out-group test of alternative hypotheses.

13. Giardina bodies. Roughley (1981) suggested that the nature of so-called "Giardina bodies," which contain extrachromosomal DNA and appear in oögonia at the preoocyte stage of oögenesis, might represent a synapotypic feature for dytiscoids and trachypachids. He noted that these bodies "appear to be of a different type in Dytiscoidea than in other insects." They have been found in female representatives of Gyrinidae, Hydrobiidae, and some Dytiscidae studied. For example, they occur in Colymbetinae, Laccophilinae, and some (e.g., *Hydaticus*, *Dytiscus*), but not all (e.g., *Eretes*, *Cybister*), dytiscines, and are absent from the few hydroporines studied. More significantly, however, their presence (or absence) remains unknown for noterids, haliplids, amphizoids, trachypachids, and carabids. Roughley's primary intent was to initiate a survey of the occurrence of Giardina bodies among Adephaga—to introduce a new character into adephagan systematics. Available data cannot support the hypothesis that presence of a particular type of Giardina body is synapotypic for dytiscoids and trachypachids.

14. Ligula absent from labium of larva. Hammond (1979) cited this character state as a possible synapotypic feature uniting trachypachids and dytiscoids; but he noted that a ligula is absent from larvae of various carabid groups (e.g., *Brachinus*, *Gehringia*, and lebiines) as well. Distribution of this characteristic among extant Adephaga is not yet fully known, nor have detailed out-group comparisons with archostema-

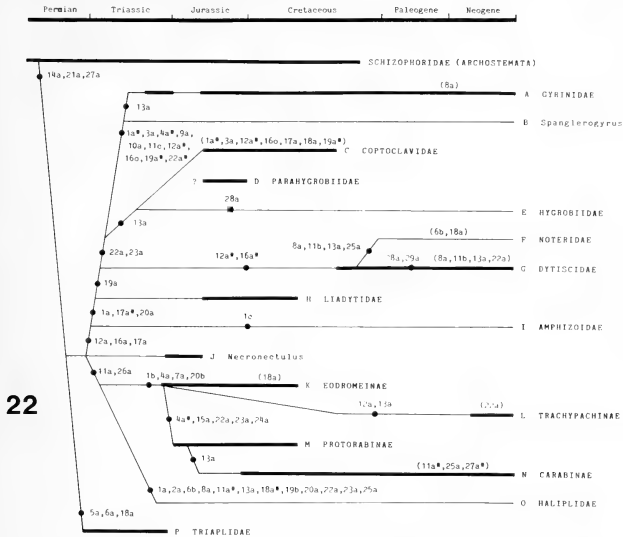


FIGURE 22. Reconstructed phylogeny of Adephaga, including both extinct and extant groups. Time is represented by the horizontal axis; but neither position nor gap width on the vertical axis is intended to reflect divergence considerations. Thickened portions of tree branches indicate known temporal occurrence in the fossil record. Number and letter symbols placed adjacent to solid dots refer to synapotypic features presented in Table 1 and discussed in the text. Symbols in parentheses refer to apotypic features found in some, but not all, members of the lineage directly below them.

tan larvae been made. Therefore, significance of the co-occurrence of this feature among dytiscoids and trachypachids cannot be properly evaluated. It may represent another symplesiotypy for Adephaga.

In summary, there is little, if any, unequivocal evidence to support strict monophyly of a group including dytiscids, hygrobiiids, amphizoids, and trachypachids but excluding carabids. This view is based on a re-evaluation of character polarities proposed and/or supported by Hammond (1979), Roughley (1981), and several other workers (e.g., Bell, Crowson, Evans, and Forsythe, as previously cited). These workers may be correct in their interpretations. Nonetheless, I offer an alternative interpretation of data and relationships as perceived from my studies of nebrinae and

other basal-grade carabids over the past few years; I hope that these interpretations and conclusions will be rigorously tested by current and future colleagues.

A hypothesis of adephagan phylogeny

The hypothesis of adephagan relationships that I have used below as a basis for out-group comparison in cladistic analysis of amphizoids is illustrated in Figure 22. Some relationships proposed are highly speculative in relation to available data, and relatively few characters have been adequately studied and applied to a cladistic analysis of Adephaga. Consequently, the monophyly of certain groups proposed is not substantiated, or is inadequately substantiated,

by synapotypic features at present. Nevertheless, I hope that others will be encouraged to challenge proposed relationships through a search for additional apotypic features that support or refute the phylogenetic hypothesis. In this regard, a comprehensive comparative study of larval structure, including what can be gleaned from review of fossil material, will undoubtedly provide extremely valuable data.

In both comparisons made and conclusions drawn, I have accepted adaphagan family limits as presently defined. Some of the family-group taxa so delimited may not represent strictly monophyletic groups, and better understanding the phylogenetic relationships among some of these so-called "families" (e.g., dytiscids and noterids) will require further cladistic analyses of member subgroups and relationships among them. Familial status of certain taxa known only from fossils (e.g., liadytids, parahygrobiids, and coptoclavids) is unclear, but I have accepted proposed familial ranking for each herein to facilitate comparisons with extant taxa of familial rank.

Based mainly on Ponomarenko's (1977) review of Mesozoic fossil material, I have also tried to relate the branching sequence of the proposed cladogram to geologic time (but not specifically to events in Earth history). Among possible sources of error in establishing timing of divergent events in adaphagan phyletic history are: (1) that fossil occurrence of a group provides only a minimum estimate of the time of its origin, and disappearance or absence of a group from the known fossil record does not rule out its existence at a particular time or place; and (2) that the geographical distribution of currently available material which represents the Mesozoic (and early Cenozoic) adaphagan fauna is highly biased. Almost all useful specimens are from Asia, and some groups, such as amphizoids, hygrobiids, and haliplids, may well have evolved in other areas and much earlier than the known fossil record suggests.

Of the five hypotheses of adaphagan relationships reviewed by Bell (1982), that of Ponomarenko (1977) is most similar to the one proposed here. Ponomarenko suggested that the common adaphagan ancestor gave rise to three major, independent lineages, which Bell (1982) termed the "haliplomorph," "dytiscomorph," and "carabomorph" ancestral lineages, respectively. According to Ponomarenko, extant haliplids may

be descendants of the Triassic haliplomorph group, Triaplidae; gyrynids diverged, probably in Lower Triassic time, from the common ancestor of other dytiscoids (including amphizoids, hygrobiids, dytiscids, and a number of extinct Mesozoic forms); and extant carabids and trachypachids are descendants of a common, terrestrial carabomorph ancestor, which also evolved in, or just before, the Triassic.

The only major difference between Ponomarenko's hypothesis and that illustrated in Figure 22 involves the relationship of haliplids to other Adephaga. I doubt that any close phylogenetic relationship exists between haliplids and triaplids. Evidence cited by Ponomarenko as linking these two groups more likely represents convergence. Instead, several synapotypic features link haliplids with caraboids, and triaplids probably have no extant descendants or near relatives.

Several other relationships proposed here are noteworthy. The recently discovered gyrynid genus *Spanglerogyrus* (Folkerts 1979) appears to be a relict form less closely related to other extant gyrynids than is the Upper Triassic form, *Triadogyrus* (Ponomarenko 1977) (see details below). Nothing is known about external structure of parahygrobiid adults, and placement of this group in the cladogram is problematic at present. Some evidence exists to link hygrobiids with the extinct coptoclavids rather than with other extant dytiscoids. Both coptoclavids and hygrobiids appear to be more closely related to gyrynids than to dytiscids and amphizoids. The Lower Jurassic form, *Necroneotulus* (Ponomarenko 1977), known from only a single specimen without legs, shares apotypic features with no known adaphagan lineage. I have, therefore, indicated its derivation from an unresolved trichotomy with the dytiscomorph and carabomorph lineages. It may be related to either of these lines, but evidence for one or the other affinity is currently lacking.

Evidence in support of relationships proposed in Figure 22 is presented in Table 1. Code letters used for taxa in the table are the same as those used in Figure 22. Coding of character states, both in Figure 22 and Table 1, is as follows: (1) each character is represented by a unique, Arabic number; (2) the plesiotypic state of each character is represented by the letter *a*; (3) independently derived apotypic states are represented by different letters (*a*, *b*, etc.), where states *a* and *b*

evolved independently from state *o*; (4) sequentially derived apotypic states are represented by a letter (*a*) or a letter plus asterisk (*a**), where state *a* evolved from state *o* and state *a** evolved from *a*; and (5) apotypic states that include a combination of independently and sequentially derived conditions are represented by letters (*a*, *b*, etc.) and letters with different symbols (*a**, *a#*, etc.), where states *a* and *b* evolved independently from state *o*, and both *a** and *a#* evolved independently from state *a*. Polarities of transformation for 25 of the 29 characters used for cladistic analysis were determined by means of the out-group criterion. The character correlation criterion was used to determine polarities for characters 4 (antennal pubescence), 27 (gonostyli of female ovipositor), 28 (thoracic defense glands), and 29 (pygidial defense gland cells). Implications of the distributions of states of the characters presented in Table 1 in relation to the cladogram in Figure 22 are as follows.

Character 1. General habitat. If a semiaquatic lifestyle, similar to that of extant amphizoids, is accepted as plesiotypic for Adephaga, then a fully aquatic lifestyle may have evolved only twice: in a lineage including all Hydradephaga except amphizoids and haliplids, and in haliplids. A more highly evolved lifestyle, one specializing in water surface activity apparently evolved twice—once in gyrimids, and again in some coptoclauids (see Ponomarenko 1977). Haliplids and amphizoids swim with an alternating (walking) leg motion. In the former group, this trait may reflect a semiaquatic (or even terrestrial) ancestry and independent adaptation to fully aquatic life. Adaptation to passive drifting in streams shown by amphizoids is no doubt an apotypic feature.

Character 2. Food habits/feeding. Ponomarenko (1977) suggested that triaplids and haliplids shared herbivorous feeding habits, but he noted also that this trait could have been plesiotypic in triaplids. If the relationship of haliplids to caraboids proposed here is correct, then algal feeding must be apotypic in haliplids.

Character 3. Compound eyes. Both gyrimids and a majority of known coptoclauids have compound eyes divided into dorsal and ventral portions. Based on other characteristics, this co-occurrence appears to be convergent in the two groups. In all extant gyrimids, except *Spanglerogyrus* adults, the dorsal and ventral eye portions are moderately or broadly separated by an an-

terior extension of the gena. In *Spanglerogyrus* adults, the eye portions are broadly contiguous, with their division marked by only a thin septum. This feature, in combination with others listed below, suggests a very ancient divergence of this monobasic group from the main line of gyrimid evolution.

Character 4. Antennal pubescence. As noted above, this character is problematic. Other authors (e.g., Roughley 1981) have suggested that absence of antennal pubescence is apotypic, a trait evolved in association with the change to an aquatic lifestyle. Yet terrestrial trachypachids lack antennal pubescence (except on antennomere 11) and aquatic gyrimids have pubescence (but of a peculiar form and distribution). If, as I suggest here, presence of antennal pubescence is an apotypic feature where it occurs in Adephaga, then this trait may have evolved only twice: once in the lineage including trachypachids and carabids, and again in gyrimids. The minimal pubescence seen in extant trachypachids can be interpreted as a first step in a transformation series leading to the condition found in a majority of carabids.

Character 5. Orientation of mouthparts. Ponomarenko (1977) suggested that apparent opisthognathy seen in triaplid fossil specimens may reflect a grazing style of feeding, characteristic of a variety of herbivorous beetle groups. The known occurrence of opisthognathy among schizophoroid Archostematan Adephaga is such that it must be apotypic for triaplids.

Character 6. Prosternal intercoxal process. Most extant and extinct Archostemata and Adephaga have a well-developed prosternal intercoxal process. Known triaplids appear to have lacked such a process, at least externally. This probably represents an apotypic feature. In relation to those of other groups, haliplids, omophronine carabids, and some noterids have intercoxal processes markedly expanded and strikingly similar in form and degree of contact with the mesothorax. However, adult haliplids and noterids have open procoxal cavities, whereas omophronines have them closed. While this difference may be significant, Bell (1967) pointed out that the type of procoxal closure found in omophronines was apparently unique to them. Hence, it is likely that the immediate ancestor of omophronines had open procoxal cavities. Shape of the prosternal intercoxal process is just

| Character | | Taxa and character state distributions | | | | | | | | | | | | | | | |
|-----------|---|--|----|-------|---|---|------|------|---|---|---|---|---|---|-------|----|---|
| | | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P |
| 1. | General habitat Semiaquatic, o Aquatic, a Aquatic, surface, a* Terrestrial, b Semiaquatic, passive drifter, c | a* | a* | a, a* | a | a | a | a | ? | c | ? | b | b | b | b | a | ? |
| 2. | Food habits/feeding Predaceous, o Herbivorous (on algae), a | o | o | o | o | o | o | o | o | o | o | o | o | o | o | a | ? |
| 3. | Compound eyes Undivided, o Dorsoventrally divided, a | a | a | o, a | ? | o | o | o | o | o | o | o | o | o | o | o | o |
| 4. | Antennal pubescence Without pubescence, o Only antennomere 11 pubescent, a Pubescence widespread, a* | a* | a* | ? | ? | o | o | o | ? | o | ? | ? | a | ? | a* | o | ? |
| 5. | Orientation of mouthparts Prognathous, o Opisthognathous, a | o | o | o | ? | o | o | o | o | o | o | o | o | o | o | o | a |
| 6. | Prosternal intercoxal process Narrow, o Absent, a Broad, b | o | o | o | ? | o | o, b | o | o | o | o | o | o | o | o | b | a |
| 7. | Protibial antenna cleaner Absent, o Present, a | o | o | o | ? | o | o | o | o | o | ? | a | a | a | a | o | ? |
| 8. | Scutellum Visible externally, o Concealed, a | o, a | o | o | ? | o | a | o, a | o | o | o | o | o | o | o | a | o |
| 9. | Mesothoracic length Short, o Long, a | a | a | o | ? | o | o | o | o | o | o | o | o | o | o | o | o |
| 10. | Mesocoxal shape Round, o Laterally expanded, a | a | a | o | ? | o | o | o | o | o | o | o | o | o | o | o | o |
| 11. | Ventral mesocoxal articulation Absent, o Coxal lobe, sternal stop, a Coxal peg, sternal socket, a* Coxal groove, sternal ridge, b Coxae otherwise immobilized, c | c | c | ? | ? | o | b | o, b | ? | o | ? | ? | a | ? | a, a* | a* | ? |
| 12. | Metasternal transverse ridge Present, laterally extended, o Present, laterally reduced, a Absent, a* | a* | a* | a, a* | ? | a | a* | a* | a | a | o | o | a | o | o | o | o |
| 13. | Relationship of metepisternum to mesocoxal cavity Forms part of lateral wall, o Excluded from lateral wall, a | a | o | a | ? | a | a | o, a | o | o | o | o | a | o | a | a | o |
| 14. | Metacoxal position Free of abdomen, o Countersunk into abdomen, a | a | a | a | ? | a | a | a | a | a | a | a | a | a | a | a | a |
| 15. | Metacoxal width Wide, o Narrow, a | o | o | o | ? | o | o | o | o | o | o | o | o | a | a | o | o |

TABLE 1. CONTINUED.

| Character | Character state | Taxa and character state distributions | | | | | | | | | | | | | | | |
|-----------|---|--|----|-------|---|----|------|------|----|---|---|------|------|---|-------|----|---|
| | | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P |
| 16. | Metacoxal length Short, o Medium, slightly expanded anteriorly, a Long, markedly expanded anteriorly, a* | o | o | o, a | ? | a | a* | a* | a | a | o | o | o | o | o | o | o |
| 17. | Metacoxal fusion Not fused medially, o Partially fused medially, a Extensively fused medially, a* | a* | a* | a, a* | ? | a* | a* | a* | a* | a | o | o | o | o | o | o | o |
| 18. | Metacoxal femoral plates Absent or small, o Present, moderately large, a Present, very large, a* | o | o | o, a | ? | o | o, a | o | o | o | o | o, a | o | o | o | a* | a |
| 19. | Legs, distal modifications for swimming Absent, o Slight modifications, a Extensive modifications, a* Femoral modifications only, b | a* | a* | a, a* | ? | a | a | a | o | o | ? | o | o | o | o | b | ? |
| 20. | Legs, fringe setae Present, slightly developed, o Present, well developed, a Absent, b | a | a | a | ? | a | a | a | a | o | ? | b | b | b | b | a | ? |
| 21. | Hindwing apex in repose Spirally rolled, o Folded, a | a | a | ? | ? | a | a | a | ? | a | ? | ? | a | ? | a | a | ? |
| 22. | Hindwing, subcubital binding patch Present, o Absent, a Absent, suboblongum patch present, a* | a* | a* | ? | ? | o | a | o, a | ? | a | ? | ? | o, a | ? | o | o | ? |
| 23. | Oblongum cell position Posteroapical, o Near center of wing, a | a | a | ? | ? | a | o | o | ? | o | ? | ? | o | ? | a | a | ? |
| 24. | Male median lobe, internal sac Short, slightly developed, o Large, better developed, a | o | o | ? | ? | o | o | o | ? | o | ? | ? | o | ? | a | o | ? |
| 25. | Male genitalia, parameres Symmetrical in length and shape, o Asymmetrical in length and shape, a | o | o | ? | ? | o | a | o | ? | o | ? | ? | o | ? | o, a | a | ? |
| 26. | Male genitalia, ring sclerite Split posterodorsally, o Complete posterodorsally, a | o | o | ? | ? | o | o | o | ? | o | ? | ? | a | ? | a | a | ? |
| 27. | Female ovipositor, gonostylus Distinct, o Fused with gonocoxite, a Apparently distinct, a* | a | a | ? | ? | a | a | a | ? | a | ? | ? | a | ? | a, a* | a | ? |
| 28. | Thoracic defense glands Absent, o Present, a | o | o | ? | ? | a | o | a | ? | o | ? | ? | o | ? | o | o | ? |
| 29. | Pygidial defense gland cells Type I cells absent, o Type I cells present, a | o | o | ? | ? | o | o | a | ? | o | ? | ? | o | ? | o | o | ? |

one of several similarities (see below) among noterids, haliplids, and omophronines that appear to represent convergences, based on data from other characters.

Character 7. Protibial antennal cleaner. Several authors (e.g., Hammond 1979) have suggested that absence of a protibial cleaning organ may be an apotypic feature among hydradephagans. Also among carabid groups (e.g., paussines) in which specialized antennal structure precludes grooming by means of a protibial cleaning organ, such an organ is absent. I see no evidence, however, to suggest that presence of a protibial cleaning organ is plesiotypic among Adephaga, and I view its occurrence as an apotypic feature linking trachypachids and carabids.

Character 8. Scutellum. A scutellum is visible externally in extant and extinct Archostemata and in Adephaga, except noterids, haliplids, omophronine carabids, some gyrinids, and some dytiscids. Because the distributions of apotypic states of several other characters are incongruous with the distribution of a concealed scutellum among Adephaga (i.e., character correlation criterion), there is little evidence to suggest that this trait is synapotypic for any two or more of the exceptional taxa. It probably evolved independently in each, although its co-occurrence among noterids and certain dytiscids may reflect close phylogenetic relationship.

Character 9. Mesothoracic length. A significant increase in length of the mesothorax is seen in extant and fossil gyrinids, including adults of *Spanglerogyrus* and the inadequately known Triassic fossil form, *Triadogyrus*. This feature appears to be autapotypic (i.e., uniquely derived) in gyrinids.

Character 10. Mesocoxal shape. Distribution of states of this character is identical with that in character 9. No doubt, the two characters are closely correlated. Among known Adephaga, only gyrinids have laterally expanded mesocoxae. Even coptoclavids, which share several other features with gyrinids, had round mesocoxae typical of the remainder of the suborder.

Character 11. Ventral mesocoxal articulation. Evans (1977) reviewed various structural means found among Adephaga for ventral articulation of mesocoxae with the metasternum. He noted that amphizoids, hygrobiids, and some dytiscids evidently lack special structural means of ventral articulation. Carabids and extant trachypachids (i.e., adults of both *Trachypachus* and *Systolo-*

soma species) have a coxal lobe/sternal stop mechanism, but noterids and those dytiscids with evident ventral articulations have a sternal ridge/coxal groove arrangement. Gyrinids have mesocoxae that are practically immobilized by a unique structural arrangement which is probably independently derived. It seems that the absence of ventral articular structure is plesiotypic in Adephaga, and therefore, that articular structures evolved independently in (1) noterids and some dytiscids, and (2) the lineage including trachypachids and carabids. A special coxal peg/sternal socket arrangement is found in haliplids and omophronines (Evans 1977), although position of the socket is different in members of the two groups. This is yet another similarity between these groups, but it probably evolved independently in each from the coxal lobe/sternal stop arrangement seen in other caraboids.

Character 12. Metasternal transverse ridge. Evans (1977) discussed this structure (also known as the "metasternal suture"), its functional significance, and its distribution among Adephaga. Its presence appears to be plesiotypic and its loss or lateral reduction apotypic within the suborder. The single known *Necronectulus* specimen has a well-developed transverse ridge. Presence of the laterally reduced ridge in amphizoids and hygrobiids suggests that, if the cladogram is correct, its loss has occurred three times independently: in dytiscids and noterids, in gyrinids, and in some (but not all) coptoclavids. Eodromeines apparently had well-developed, laterally extended transverse ridges, like extant carabids, and so the laterally reduced ridge found in extant trachypachids probably represents reduction convergent with that in the dytiscomorph lineage. Steiner and Anderson (1981) reported presence of a metasternal ridge in adults of *Spanglerogyrus*. In my own examination of representatives of this genus, I found the structure in question to be wholly part of the metacoxa rather than the metasternum. I suggest that the suture (or ridge) at the base of the metacoxa in *Spanglerogyrus* adults is autapotypic among them and not homologous with the metasternal ridge found among Adephaga as listed in Table 1.

Character 13. Relationship of metepisternum to mesocoxal cavity. As noted earlier, the plesiotypic condition among Adephaga is that in which the metepisternum contributes to the lateral wall of the mesocoxal cavity. Among extant forms, this condition is found only in amphizoids, some

dytiscids, and adults of the gyrinid genus, *Spanglerogyrus*. Although this condition may have been achieved secondarily in members of *Spanglerogyrus*, it is more likely that it represents yet another feature suggesting ancient ancestry for this unique genus. Exclusion of the metepisternum from the mesocoxal cavity appears to have evolved at least seven times: in (1) gyrinids (after divergence of *Spanglerogyrus* from the main lineage), (2) the lineage including hygrobiids and coptoclauids, (3) noterids, (4) some dytiscids, (5) trachypachines [this is the feature that distinguishes them from eodromeines], (6) carabids [again, this feature distinguishes extant carabids from protorabines], and (7) haliplids. This structural change must be highly advantageous mechanically for it to have become fixed in so many different lineages making use of both terrestrial and aquatic habitats.

Character 14. Metacoxal position. In all known Adephaga, the metacoxae are countersunk into the base of the abdomen so that they divide the first visible abdominal sternum externally into two triangular lateral portions. This feature distinguishes Adephaga from other Coleoptera, including Archostemata. It is, no doubt, a synapotypic feature.

Character 15. Metacoxal width. The narrowed metacoxae found in protorabines and all extant carabids (except gehringiines) are clearly apotypic. The condition found in rhyssodines is not equivalent to the plesiotypic state, because the metacoxae extend laterally only to the posterolateral corner of the metasternum, just as in carabids. The metepisterna are hidden posteriorly under the elytral epipleura, but they are completely laterad of the lateral margins of the metacoxae.

Evans (1977) noted that, unlike those in dytiscids, gyrinids, and other Hydradeephaga, metacoxae of haliplids have a lateral coxal condyle, as do carabid metacoxae. I agree this feature indicates close affinity with a presumed terrestrial ancestor, namely carabids. However, a coxal condyle is also present, although not as well developed, in extant trachypachines and amphizoids, but not in hygrobiids and other dytiscoids. Presence of a coxal condyle may represent the plesiotypic condition among Adephaga. The laterally extended metacoxae of haliplids may represent either the plesiotypic adephagan condition or secondary acquisition of a similar condition as part of an adaptation of metacoxae for a new

function (see further discussion under character 18).

Character 16. Metacoxal length. Slight to moderate expansion of metacoxae anteriorly, and attendant reduction in size of the metasternum, is seen in amphizoids, liadytids, hygrobiids, and some coptoclauids. In dytiscids and noterids, metacoxae are greatly expanded anteriorly. Based on distributions of states of other characters, it is likely that the trend for anterior expansion, which was initiated in the common dytiscoid ancestor, has been reversed at least twice independently: in gyrinids and in some coptoclauids.

Character 17. Metacoxal fusion. This character was discussed above in consideration of the relationship between amphizoids and trachypachids. Based on character states represented in extinct and extant Archostemata and Mesozoic Adephaga, it is clear that the unfused metacoxae are plesiotypic. As noted by Evans (1977) and others, the metacoxae of haliplids are not fused medially. It is therefore likely that at least partial medial fusion of metacoxae represents a synapotypic feature for Hydradeephaga exclusive of haliplids (and *Necronectulus*, if its members were aquatic). A trend for more extensive medial fusion of metacoxae may have evolved only once—in the common ancestor of all dytiscomorphs except amphizoids. If so, then this trend was also reversed at least once, in the ancestor of some (but not all) coptoclauids. Eodromeine trachypachids appear to have had more widely separated metacoxae than extant trachypachids. Hence, a trend toward increased medial continuity, if not fusion as suggested by Evans (1977) and Roughley (1981) for extant trachypachids, probably represents a development independent of that in Hydradeephaga.

Character 18. Metacoxal femoral plates. Ponomarenko (1977) described posteroventral extensions of metacoxae, which he termed femoral plates, in triaplids, some coptoclauids, and some eodromeines among Mesozoic fossil forms. He noted that such plates could be rather easily broken off and, therefore, that their distribution may have been taxonomically more extensive than present fossil material illustrates. He also suggested that presence of metacoxal plates may be plesiotypic for Adephaga. Such structures are apparently unknown among schizophoroid Archostemata, however, and among extant forms, femoral plates are found only in noterids and haliplids. In my view, it is simplest to consider

presence of femoral plates as apotypic where they occur among Adephaga. There is little or no evidence to suggest that this feature is synapotypic for any two or more of the extinct and/or extant groups whose members are known to possess them.

Haliplid metacoxal femoral plates are much larger, both posteriorly and laterally expanded, than those of noterids and the extinct groups listed above, including triaplids. The role of these plates in haliplid respiration has been well documented (Hickman 1931). It is unlikely that they served this highly specialized function in triaplids, coptoclauids, or eodromeines, and no respiratory role has been suggested for them among noterids.

Character 19. Legs, distal modifications for swimming. Based on comparisons with Archostemata and Mesozoic Adephaga, it appears that distal leg structure in amphizoids represents the plesiotypic state among Adephaga. Special structural modifications of femora, tibiae, and/or tarsi as adaptations for rapid swimming are considered apotypic. Relatively slight modifications of this kind have apparently evolved twice independently: in the common ancestors of (1) noterids and dytiscids and (2) hygrobiids, coptoclauids, and gyrinids. In each of these groups, structure of distal leg parts is quite distinctive in detail. Gyrinids and members of the extinct genus *Coptoclava* (Ponomarenko 1977) are similar in that their middle and hind legs are (or were) markedly flattened and expanded. This feature is probably apotypic relative to more conservative leg modification, but distributions of states of other characters suggest that it is not synapotypic for these two groups.

Middle and hind legs of haliplids show no special structural adaptations for swimming. Haliplid hind femora are unique in that they are markedly narrowed basally—a feature probably evolved to facilitate leg movement within the narrow space between abdominal venter and metacoxal femoral plates.

Character 20. Legs, fringe setae. Unfortunately, some of the most important extinct Mesozoic groups are known only from specimens without distal leg parts. Among these are Triaplidae and genus *Necronectulus*. Hence, it is difficult to know whether or not ancestral Adephaga had legs bearing fringe setae (or so-called “swim-

ming hairs”). Assuming a semiaquatic ancestry, the condition found in extant amphizoids, in which fringe setae are present but short and limited in distribution, could be considered the plesiotypic condition. Absence of fringe setae would then be synapotypic for trachypachids and carabids. If the cladogram in Figure 22 is correct, then more extensive development of fringe setae would also be apotypic. But this feature would have had to have evolved at least twice independently: in (1) the common ancestor of all Hydradephaga except amphizoids, and (2) haliplids. Fringe setae are longer and more extensively distributed in haliplids than in amphizoids—this is perhaps associated with a slightly better developed aquatic lifestyle.

Character 21. Hindwing apex in repose. Members of all Adephaga groups examined have the hindwing apex folded, rather than spirally rolled as in Archostemata. This feature is probably synapotypic for the suborder Adephaga.

Character 22. Hindwing, subcubital binding patch. If presence of the subcubital binding patch is synapotypic for suborder Adephaga (hence, plesiotypic within Adephaga, see above), then loss of the patch has evolved at least five times: in (1) the common ancestor of carabines and (probably) protorabines, (2) haliplids, (3) trachypachids of genus *Systolosoma*, (4) some dytiscids, and (5) the common ancestor of gyrinids, hygrobiids, and (probably) coptoclauids. Gyrinid specimens examined have a narrow patch of short setae or long microtrichia along the posterior margin of the oblongum cell that may aid in wing folding as an alternative to or replacement for the subcubital patch.

Character 23. Oblongum cell position. Hammond (1979) noted that the oblongum cell is positioned closer to the posterior margin of the wing apex in trachypachids, amphizoids, noterids, and dytiscids than in other Adephaga and considered this to represent a synapotypic feature for the groups noted. Position of the oblongum cell in archostematan hindwings, however, is also close to the posterior margin of the apex, just as in amphizoids and other taxa noted by Hammond. I conclude that this feature is plesiotypic, and further, that a more anterior and basal placement of the cell is apotypic. If this view is correct, then the apotypic state could have evolved as few as three times: in (1) cara-

birds, (2) haliplids, and (3) the common ancestor of hygrobiids, coptoclauids, and gyrinids.

Character 24. Male median lobe, internal sac. As noted above, it is likely that a large, well-developed internal sac, such as is found in most carabid males, is apotypic among Adephaga. Males of basal-grade rhyssodid lineages have larger internal sacs than those of more highly evolved lineages, but this trend appears to reverse that seen among carabids in general.

Character 25. Male genitalia, parameres. Based on comparisons with genitalia of extant Archostemata, it appears that the plesiotypic form of parameres among Adephaga demonstrates symmetry in both length and shape. Asymmetrical parameres are found in noterids, haliplids, and most, but not all, carabids. Based on the distribution of this feature in relation to character-state distributions of other characters, it is likely that asymmetry of parameres evolved in each of these groups independently.

Character 26. Male, ring sclerite. The ring sclerite (Kavanaugh 1978b) and associated structures probably represents the sclerotized remains of the ninth abdominal segment (the genital segment, or urite X of Jeannel 1941), and it serves as a rim for attachment of muscles from the base of the median lobe. In all Hydradephaga examined, except haliplids, the ring is split postero-dorsally in the midline, into what might be termed "hemitergites," but is continuous anteroventrally (see Edwards 1951, "Plate 2"). This condition is shared with Archostemata males examined. In trachypachids, carabids, and haliplids, however, the ring is complete posterodorsally as well as anteroventrally—a feature that is probably synapotypic for these three groups.

Character 27. Female ovipositor, gonostylus. Bell (1982) and others have suggested that the apparent absence of a gonostylus (or stylomere two) from ovipositors of female trachypachids, isochoetous carabids, and hydradephagans may represent a synapotypic feature uniting these groups. In fact, a majority of basal-grade carabid groups (e.g., opisthiines, notiokasiines, nebriniines, and notiophilines) also have females in which a gonostylus is either absent from the ovipositor or fused with the gonocoxite (stylomere one) so as to appear absent. I agree with Bell that this feature is apotypic, but suggest that it is synapotypic for the suborder Adephaga rather than

just for a subgroup of that taxon. The structures that have been called gonostyli (or second stylomeres) in female carabines, cychrines, cicindelids, and a majority of intermediate- and advanced-grade carabids are probably not homologous with the gonostyli of female Archostemata and Polyphaga.

Character 28. Thoracic defense glands. Forsyth (1968, 1970) noted that, among Adephaga, only hygrobiids and dytiscids possess thoracic defense glands in addition to the pygidial defense glands common to all Adephaga. Presence of such thoracic glands is no doubt apotypic in hygrobiids and dytiscids, but based on the character correlation criterion, I agree with Forsyth that this similarity represents convergence rather than common ancestry.

Character 29. Pygidial gland cells. In a series of papers describing the structure of pygidial and other defense glands among Adephaga, Forsyth (1968, 1970, 1972) provided numerous excellent characters, while making detailed comparisons among members of included taxa, but he did not consider states of these characters from a cladistic perspective. The relationships he suggested were based on simple similarity, rather than on synapotypy, and I have been unable to recognize patterns of synapotypy among the mass of data he provided for included adephagan taxa.

Forsyth (1968) recognized two types of secretory cells (Type I and Type II cells) in the pygidial glands of dytiscids. Apparently, only Type II cells are found in these glands in other Adephaga, and presence of Type I cells in dytiscid pygidial glands must be autapotypic.

Summary of phylogenetic reconstruction. Several final points should be made in reference to the proposed cladogram and data provided in Table 1. First, the monophyly of a lineage including all Adephaga except triaplids is unsupported at present by evidence in the form of synapotypic features. We know too little about triaplid structure and lifestyle to recognize features in which their proposed sister-group may be considered specialized (i.e., apotypic). I also failed to discover any synapotypic feature uniting Trachypachinae with Eodromeinae. However, eodromeines probably represent the ancestral stock from which both trachypachines and carabids evolved. A group including trachypachines and eodromeines but excluding carabids would

therefore be paraphyletic, which may explain why synapotypic features for such a group are lacking.

Monophyly of a group including both extinct and extant trachypachids, carabids, and halipids is supported by fewer and less compelling synapotypic features than might be desirable. The only proposed synapotypies for this group are the following: (1) mesocoxal ventral articulation by means of a coxal lobe and sternal stop or derivative of this arrangement, and (2) male genitalia with ring sclerite complete posterodorsally. Nonetheless, available evidence supports a closer phylogenetic relationship between halipids and carabids than between the former and other Hydradephaga.

As can be seen in Table 1, noterids share apotypic features (e.g., see characters 8, 11, and 13) with some, but not all, dytiscids. This suggests a close relationship between noterids and only some dytiscids. It is therefore possible that if Dytiscidae (in the broad sense) is a monophyletic taxon (and there is considerable doubt in this regard; Roughley, pers. comm.) then it would be a paraphyletic taxon if noterids were excluded and/or recognized as a separate family. On the other hand, dytiscids possess thoracic defense glands and Type I secretory cells in their pygidial defense glands, whereas noterids studied to date have neither of these features. Available evidence is therefore equivocal with regard to the question of relationship between noterids and dytiscids. However, I suggest that noterids and dytiscids should be taken together as a monophyletic unit of greater inclusiveness, whether at the familial or some higher taxonomic level, to assure that appropriate comparisons are made in future studies.

The proposed relationship between hygrobiids and coptoclavids also requires further comment. Among characters used in this study, I found no apotypic states that distinguish all members of either group from all members of the other. Some coptoclavids have apotypic features not shared with hygrobiids, but the reverse does not apply, except perhaps for the presence of thoracic defense glands in hygrobiids (but coptoclavids may also have had such glands). Hygrobiids are most similar to certain members of Necronectinae (Ponomarenko 1977). Together, these groups appear to represent a basal grade of coptocladid evolution, and I predict that future studies will indicate that hygrobiids and coptoclavids should be included in a single family.

Phylogenetic relationships of amphizoid species

Based on assumed adepagan phylogenetic relationships as illustrated in Figure 22, a cladistic analysis was conducted to ascertain relationships among extant amphizoid species. A total of 14 selected characters was used. For each, the out-group criterion was used to establish polarity (from plesiotypic to most apotypic) of character-state transformation. Characters and character-state distributions among amphizoid species are presented in Table 2, and the cladogram that results from analysis of these data is illustrated in Figure 23. Format and coding for characters and character states used in Table 2 and Figure 23 are as explained above for Table 1 and Figure 22.

If the hypothesis of phylogenetic relationship proposed—namely that *Amphizoa davidi* is the sister-group of the other three species, and that *A. insolens* is the sister of the group including *A. striata* and *A. lecontei*—is correct, then the following comments are appropriate.

Character-state distributions of all characters analyzed are compatible with each other over the cladogram, except for character 3 (sinuation of the lateral margin of the pronotum). Development of a deep sinuation basolaterally is evident in adults of *A. davidi* and *A. insolens*. Although nothing is presently known about habitat requirements and/or tolerances of *A. davidi* members, those of *A. insolens* are often found in swift-flowing, more precipitous streams than are members of *A. striata* or *A. lecontei*. A deep sub-basal sinuation of the lateral pronotal margin is also found in certain dytiscids (e.g., members of genus *Hydronebrius* Jakovlev and of the *cordatus* group of *Agabus*), which also live in fast-flowing streams. This suggests that the apotypic state of this character (i.e., lateral margin deeply sinuate sub-basally) may be associated with adaptation to life in swift-flowing streams, and distributions of states of other characters suggest that this feature evolved independently in *A. davidi* and *A. insolens*. An alternative, equally parsimonious interpretation of the distribution of character states is that a deep, sub-basal sinuation evolved among members of the common ancestor of extant *Amphizoa* species and is therefore synapotypic for the genus. An evolutionary reversal then occurred in members of the common ancestor of *A. striata* and *A. lecontei*. If this interpretation

TABLE 2. DISTRIBUTIONS OF STATES OF SELECTED CHARACTERS AMONG MEMBERS OF *Amphizoa* SPECIES (See Text for Discussion of Character Coding).

| Character Character state | Taxa and character state distributions | | | |
|--|--|-----------------|----------------|-----------------|
| | <i>davidi</i> | <i>insolens</i> | <i>striata</i> | <i>lecontei</i> |
| 1. Macrosculpture, elytra Not rugose or slightly rugose basally, punctures distinct, o Markedly rugose basally, punctures distinct, a Slightly rugose basally, punctures confluent, b | o | a | o | b |
| 2. Pronotum, shape Widest at base, o Width at middle and base equal, a | o | a | o | o |
| 3. Pronotum, sinuation of lateral margin Absent or shallow, o Deep, a | a | a | o | o |
| 4. Pronotum, lateral margin Not crenulate, o Slightly crenulate, a Markedly crenulate, a* | o | a* | a | a |
| 5. Prosternal intercoxal process, shape Elongate, spatulate, o Short, circular, a | a | o | o | o |
| 6. Elytra, silhouette (dorsal aspect) Moderately broad basally, narrowed subapically, o Subovoid, slightly narrowed basally, less narrowed subapically, a Very broad basally, narrowed subapically, b | o | a | b | b |
| 7. Elytra, silhouette (cross-sectional aspect) Evenly convex, o Convex medially, slightly concave laterally, a Carinate, flat medially, concave laterally, a* | o | o | a | a* |
| 8. Male median lobe, shaft thickness Slender at middle, o Slightly thickened at middle, a Markedly thickened at middle, a* | o | a | a* | a* |
| 9. Male median lobe, ventral margin Evenly arcuate, o Slightly bulged, a | o | o | a | a |
| 10. Male median lobe, shape apex Slightly deflected ventrally, o Extended apicodorsally, a | o | a | o | o |
| 11. Male left paramere, shape Narrow basally, o Broad basally, a | o | o | a | a |
| 12. Male parameres, vestiture Restricted to apical one-fourth, o Restricted to apical one-third, a | o | a | o | o |
| 13. Female ovipositor, length of coxostylus Short, o Medium, a Long, a* | ? | o | a | a* |
| 14. Female ovipositor, vestiture of coxostylus Dense, evenly distributed setae, o Sparse, scattered setae, a | ? | a | o | o |

is correct, then absence of a deep sinuation from adults of the last two species mentioned represents yet another synapotypy for these taxa.

Among the characters used in this analysis (and

others used for descriptive purposes only), no apotypic feature was found to unite all members of *A. striata*, although six (or seven, see above) synapotypic features support a sister-species re-

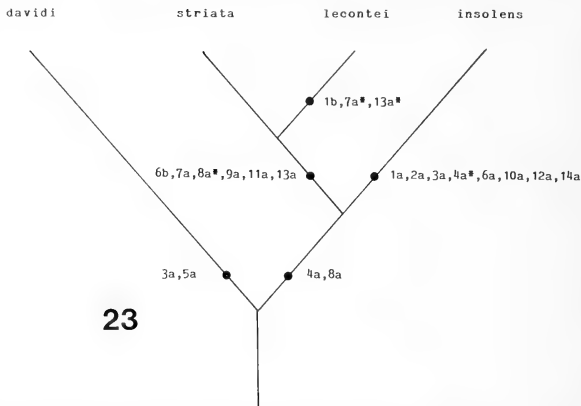


FIGURE 23. Reconstructed phylogeny of species of *Amphizoa*. Number and letter symbols placed adjacent to solid dots refer to synapotypic features presented in Table 2 and discussed in the text.

lationship for *A. striata* and *A. lecontei*. Adults of *A. striata* are distinctly larger than most members of other amphizoid species; but it was not possible, using the out-group criterion, to affirm that this represents an apotypic feature.

Zoogeography and Evolution

In this section, I briefly review the present geographical and habitat distributions of amphizoids and then discuss what can now be inferred about the zoogeographic and evolutionary history of this group.

Present pattern of amphizoid distribution

The present pattern of geographical distribution of Amphizoidae is disjunct across the northern Pacific Basin, with three species (Fig. 18–20) restricted to western North America and one (Fig. 17) to central China. This pattern reflects a vicariance relationship, with the Palaearctic species recognized as the sister-group of the three Nearctic forms.

Among North American species, the distribution of *A. insolens* (Fig. 18) is mainly coastal (i.e., east to the Sierra Nevada and Cascade

Range), with range extensions east into mountain ranges of the Great Basin in Nevada, Oregon, and Idaho, and to the Northern Rocky Mountains of Idaho, Montana, Alberta, British Columbia, and Yukon Territory. The sister-group of this species includes *A. lecontei*, restricted to the Rocky Mountain region (Fig. 20), and *A. striata*, restricted to western Oregon, western and central Washington, and Vancouver Island, British Columbia (Fig. 19). A vicariance relationship is apparent between *A. lecontei* and *A. striata* across the northern Great Basin and Columbia Plateau. However, because the ranges of *A. striata* and *A. insolens* overlap extensively, *A. insolens* and its sister-group are not strictly vicariant at present.

The habitat distribution of extant amphizoids is apparently quite limited. Members of all three Nearctic species are confined to cool or cold streams. Members of *A. striata* are found in slow-flowing, relatively warm streams, those of *A. lecontei* in cooler or cold, moderate- to fast-flowing streams, and those of *A. insolens* in cold, fast-flowing or cascading streams. Habitat is unknown for *A. davidi* members; however, the type-locality of this species is in a region occupied by vegetation types that Wolfe (1979) called “no-

tophyllous broad-leaved evergreen forest" and "mixed broad-leaved evergreen and coniferous forest." Western North American vegetation types with apparently equivalent temperature requirements include "mixed coniferous forest," "mixed evergreen forest," and "California woodlands" (in part) (Griffin and Critchfield 1972). These vegetation types are almost completely restricted to areas in California at present, and members of *A. insolens* are found in streams associated with such forests. I suggest that the habitat of *A. davidi* members will be found to be similar to that for *A. insolens* members, although the former may prefer slightly warmer and slower-flowing streams than the latter.

Mesozoic events and the origin of amphizoids

According to the hypothesis of adephegan phylogenetic relationships proposed above and illustrated in Figure 22, amphizoids are the sister-group of all other Hydradephaga, except halipids. If this is correct, then divergence of these sister-groups probably occurred at about the Permian-Triassic boundary, and certainly no later than Upper Triassic time. Although there are no amphizoid fossil specimens known from that time, fossils representing a diverse array of other hydradephagan taxa document a relatively extensive radiation of the structurally more advanced sister-group of amphizoids by Upper Triassic and Jurassic time.

In the Triassic, the supercontinent of Pangaea was still intact (Smith, Briden, and Drewry 1977), and climate was apparently warm and equable over the entire landmass (Hallam 1981). Local climatic anomalies, associated with physiography and/or relative proximity to the ocean, may have provided some diversity of habitats, but there is no evidence for broad, latitudinally limited climatic zones such as occur on continents at present. Both early and late Palaeozoic glaciations have been recognized (Tarling 1978), with most of these associated with high latitude positions of the continents affected. No major glaciations appear to have occurred during all of the Mesozoic, however, probably because the continents were all positioned at relatively low latitudes.

At present, we have no information from which to infer the geographical and habitat distributions of amphizoids during early Mesozoic time. Again, these beetles are not known from the fossil

record; their sister-group includes both extinct groups, presently known only from Mesozoic Asia, and extant groups with widely disjunct (e.g., Hygrobiidae) or worldwide (e.g., Dytiscidae and Gyrinidae) distributions. Because (1) there is extensive sympatry at the familial level and (2) comprehensive hypotheses of phylogenetic relationships within families have not yet been formulated, it is currently impossible to recognize vicariance relationships between amphizoids and their sister-group. Hence, amphizoids could have been either widely distributed in Pangaea or geographically restricted to some unknown part of that supercontinent.

Structurally, extant amphizoids appear to have diverged little, if at all, from the hypothetical common ancestor of all Hydradephaga (excluding halipids). It is their sister-group, whose extant descendants include hygrobiids, dytiscoids, and gyrinoids, that evolved rapidly away from the presumed ancestral form and lifestyle in adapting to a more fully aquatic existence. How then were amphizoids able to survive presumed early competition with members of their advanced sister-group, whereas other lineages within their sister-group (e.g., liadytids and most copoclauids) appear to have been replaced by more highly evolved forms? Amphizoids may have persisted in geographical isolation from their sister-group for an extended period. Eventually, a shift of habitat—namely to faster-flowing water—may have reduced the potential for competition with other, more rapidly diversifying Mesozoic hydradephagan groups. Even to the present, dytiscoids and their allies have exploited lotic habitats in only a limited manner, especially in geographical areas where amphizoids now occur. There is no reason to suggest that amphizoids also became adapted to cool- or cold-water habitats so early in their history. Such habitats may have been available locally, but as noted above, climate was generally warm and equable throughout Pangaea (Hallam 1981) at that time. Cool- or cold-water specialization would seem to have been a risky adaptive strategy at that time—one that could well have led to extinction during or before early Cenozoic time (see below).

At present, there is no way to infer what (if any) effect Mesozoic plate-tectonic processes, resulting in fragmentation of Pangaea, may have had on the Mesozoic amphizoid fauna. Of potentially greater impact, however, were eustatic changes in Jurassic and Cretaceous time that re-

sulted in formation of epicontinental seas in Eurasia (the so-called "Turgai Sea," late Middle Jurassic through Oligocene) and North America (mid-to-late through latest Cretaceous) (Hallam 1981). Because there appear to have been continental connections between eastern North America and western Europe on one hand and western North America and Asia on the other, two new land masses were formed, which Cox (1974) called "Euramerica" and "Asiamerica," respectively. Fossil evidence suggests that biotas subsequently evolved independently on each landmass (Cox 1974; Hallam 1981), resulting in increased endemism in each area by the end of the Mesozoic. The geographical range of extant amphizoids is confined to land area derivatives of Asiamerica, and it is tempting to suggest that amphizoids were at least present on that landmass, if not also restricted to it, during Cretaceous time.

Tertiary events and amphizoid radiation

As just noted, there is no evidence to suggest that the late Mesozoic distribution of amphizoids extended outside an area including eastern Asia and western North America (Fig. 24), although a more extensive distribution was certainly possible. The first direct land connection between these areas occurred well before the end of the Cretaceous, as a consequence of spreading of the North Atlantic (Hallam 1981), and persisted continuously until late Miocene time (Hopkins 1967). Then, between 10 and 12 million years before present (mybp), a trans-Beringian seaway developed, which linked the North Pacific and Arctic basins but interrupted the exchange of terrestrial and freshwater (aquatic) biota between North America and Asia. A land connection was re-formed in Pliocene time and permitted renewed biotic exchange until about 3.5–4.0 mybp, at which time the trans-Beringian seaway opened again (Hopkins 1967). In Quaternary time, the Beringian land connection was re-established during several, if not each, of the major glaciations, and further biotic exchange is known to have occurred during this period (Repenning 1967). Finally, the seaway opened for the last time more than 11,000 years ago, and it has remained a substantial barrier to east-west biotic movement since that time.

Paleobotanical and other evidence indicates that early Cenozoic climates were as warm and equable as those of the Mesozoic. Then, in late

Eocene time, an abrupt cooling occurred in the northern hemisphere. This cooling trend leveled off in Oligocene time; but cool conditions have persisted, with both major and minor fluctuations (e.g., the various Pleistocene glaciations), to the present. Another set of events that had a profound effect on climate, especially in western North America, were the episodes of orogenic and volcanic activity in Miocene and Pliocene times. This activity produced topographic relief that resulted in local and regional rain-shadow effects, increased diversity of microclimates, and increased seasonality.

Geographical regions of Asia and North America that are now occupied by extant *Amphizoa* species appear to have shared closely related floras in early Tertiary time. These floras were of the evergreen sclerophyllous broad-leaved and mixed mesophytic forest types (Leopold and MacGinitie 1972). Floral affinities between Asia and western North America were very close in Paleocene and early Eocene time. However, by middle-to-late Eocene time, floras of the Rocky Mountain region were quite distinctive. Leopold and MacGinitie (1972) suggested that edaphic conditions associated with local volcanic activity may have stimulated selection for xeric-adapted vegetation. Although affinities between floras of southeastern Asia and the Pacific coast of North America decreased more gradually, they were nonetheless very slight indeed by late Miocene time (Wolfe and Leopold 1967). Differentiation of the North American floras appears to have been closely related to general cooling begun in late Eocene time and to middle through late Tertiary orogenic activity in the Pacific Northwest region.

Two features that seem to characterize development of the North American floras more than contemporary floras of southeastern Asia include wholesale selective elimination of broad-leaved evergreen elements, and recruitment of subtropical and temperate elements from Neotropical floras (Wolfe 1978). The first feature is no doubt related to decreasing temperatures and/or increased seasonality in the region; the second may simply indicate that derivative Neotropical elements were already well suited to life in arid regions and could readily move into such habitats as they appeared and expanded.

The historical factors that resulted in the vicariance relationship observed between *A. davidi* and the three Nearctic species may be the same

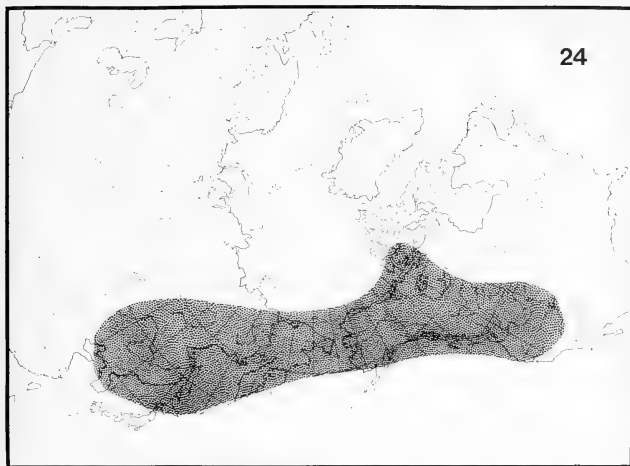
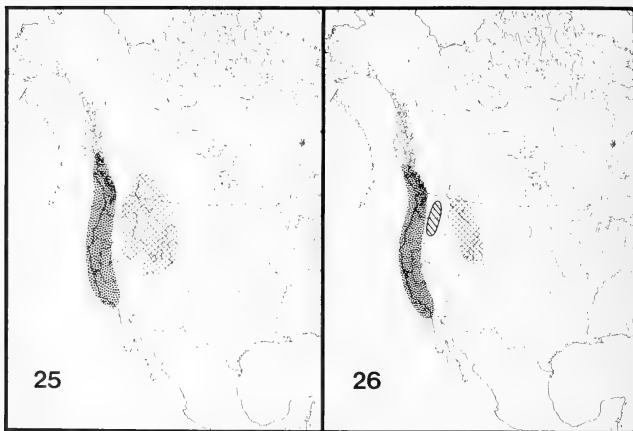


FIGURE 24. Hypothetical distribution of ancestral amphizoid stock, late Cretaceous to middle Eocene time.

factors that led to initial isolation of ancestral stocks and thereby permitted differentiation to proceed. These factors may include: (1) the general cooling trend that began abruptly in late Eocene time, which resulted in the elimination of subtropical and warm temperate vegetation types and their biotic associates from the Beringian region by late Miocene time; (2) Miocene orogenic and volcanic activity, particularly in western North America, which resulted in latitudinal and altitudinal climatic zonation, increased climatic and habitat diversity, and development of physiographic and local climatic barriers to north-south and east-west continuity of biotic distribution; and (3) opening of the trans-Beringian seaway in late Miocene time, which effectively severed faunal continuity between Asia and North America for about two million years. Any of these factors, either singly or in combination, could have effected a division of the geographical range of the common ancestor of extant amphizoids into Asian and North American isolates, and all three point to a middle-to-late Miocene age for the vicariance event in question.

Because extant Nearctic and Palaearctic amphizoids all appear to be cool-adapted, it is likely that their common ancestor was also cool-adapted rather than that such an adaptation was acquired independently in the two lines. If this is correct, then it is another indication that isolation of respective ancestral stocks occurred after initiation of the late Eocene cooling trend, hence in Miocene time. Because there do not appear to have been any extensive areas of cool-temperate climate in the northern Pacific region prior to late Eocene or Miocene time, it is unlikely that amphizoids had specialized at an earlier time for life in a cool climate.

As noted above, a vicariance relationship is not readily apparent between *A. insolens* and its sister-group, including *A. lecontei* and *A. striata*, due to rather extensive sympatry. However, present distribution patterns of these species are at least suggestive of an initial split of the ancestral Nearctic stock into eastern and western vicars, the latter represented at present by *A. insolens*, the former by its sister-group (Fig. 25).



FIGURES 25, 26. Hypothetical distributions of amphizoid ancestral stocks. Figure 25. Late Miocene to early Pliocene time; ancestral stocks of *A. insolens* (stippled areas) and *A. striata* and *A. lecontei* (cross-hatched area). Figure 26. Middle Pliocene to end of Tertiary; ancestral stocks of *A. insolens* (stippled area), *A. lecontei* (cross-hatched area), and *A. striata* (obliquely hatched area).

The present range of *A. insolens* is primarily centered in and west of the Sierra Nevada and Cascade Range. Present populations in mountain ranges of the Great Basin, in the northern Rocky Mountains, and in Yukon Territory, could be viewed as representing more recent dispersal eastward from areas along the Pacific Coast.

Development of the Cascade Range and Sierra Nevada was a gradual process (King 1977) that apparently had little effect on Pacific Northwest biota before late Miocene time. At that time, differences between floras east and west of the divide first became apparent (Wolfe 1969). Floras east of the divide began to include elements adapted to drier summers and increased seasonality, while composition of the western flora continued to reflect a more humid, somewhat less seasonal climate. From late Miocene time to the present, topographic relief has continued to increase, resulting in greater seasonality and aridity in the east, and increasingly greater differences between trans-montane climates and associated biotas.

Based on proposed phylogenetic relationships among extant Nearctic amphizoid taxa and respective habits of their members at present, it seems likely that Nearctic amphizoids were adapted for life in cool (but not cold), slow- to only moderately fast-flowing, lowland or lower-montane streams during late Miocene time. Consequently, development of the extensive north-south trending Sierra-Cascade mountain system served as a barrier that effectively isolated the ancestors of *A. insolens* west of the divide and the common ancestors of *A. lecontei* and *A. striata* east of it (Fig. 25).

Based on inferred associations of amphizoids with particular early and mid-Tertiary vegetation types and the known distributions of the latter and/or their descendant vegetation types during mid-Tertiary time (Leopold and MacGinitie 1972; Wolfe 1969, 1978), I suggest that the common ancestor of *A. striata* and *A. lecontei* occupied a broad geographical range—one that extended from the eastern flank of the Sierra-Cascade divide eastward to include at least parts

of the Rocky Mountain region—during late Miocene and/or early Pliocene time (Fig. 25). The northern extent of this range was probably limited by development of a much cooler, continental climate east of the Coast Mountain system in British Columbia.

Pliocene fossil assemblages from areas east of the Cascades reflect increasing aridity, probably due to the enhanced rain-shadow effect of the rising Cascade Range, and increased seasonality in the region (Wolfe 1969). Eventually, this trend resulted in isolation of the last (relict) broad-leaved deciduous remnants of early Tertiary floras on opposite sides of the Columbia Plateau and northern Great Basin (i.e., just east of the Cascades in central Oregon [Wolfe 1969] and on the western fringe of the Rocky Mountain system in central Idaho [Leopold and MacGinitie 1972]). This climatic change may have been the historical event that isolated respective ancestral stocks of *A. striata* (in the west) and *A. lecontei* (in the east) (Fig. 26) and led to their divergence and, ultimately, speciation. A vicariance relationship between these taxa is still apparent at present.

Quaternary history and development of the present amphizoid fauna

If the sequence and timing of vicariance and speciation events suggested above is correct, then extant amphizoid diversity was achieved prior to Quaternary time (Fig. 26). Pleistocene and Recent events appear to have played a relatively minor role in the evolution of the present amphizoid fauna. Nonetheless, available evidence suggests that important changes in geographical (Fig. 27) and habitat ranges of the Nearctic species and in structural, physiological, and behavioral characteristics of their members occurred during Quaternary time. Geologic, climatic, and biotic events of the Quaternary are relatively well known, and the reader is referred to Black, Goldthwait, and William (1973), Heusser (1960), Wright and Frey (1965), and references therein for pertinent information on the period.

***Amphizoa insolens* LeConte.** The ancestral stock of this species appears to have been isolated in the area west of the Cascade-Sierra divide in late Miocene time (Fig. 25). Subsequently, and probably in response to profound cooling (associated with local and regional glaciation) and the continued rise of the Cascade-Sierra and Coastal mountain systems during early Pleisto-

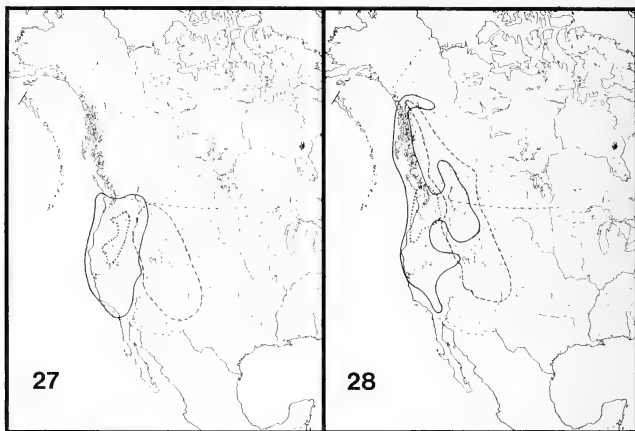
cene time, members of this species acquired several adaptations for life in cold, fast-flowing montane streams.

Adult structural changes apparently associated with adaptation to such streams included (1) modification in pronotal and elytral shape, which actually appears to have reduced streamlining, and (2) reduction in the size and extent of fringe setae on legs. Both of these changes may have accompanied a shift in locomotory behavior among members of this species from limited use of both swimming movements and passive transport with stream current to almost complete reliance on the latter locomotory mode. This locomotory strategy, common to all extant amphizoids, is most highly developed in *A. insolens* adults.

Reliance on passive transport with stream current in montane areas presents amphizoids with a high risk of drifting downstream into lowland areas of warmer climate where they cannot survive. To counteract downstream displacement, they may resort to either crawling back upstream on the substratum (in the water against the current, or out of water along stream banks) or flight. I have observed the former activity repeatedly, but this must result in very slow progress. Amphizoids have very large, thick-veined hindwings, and they appear to be capable of strong flight. The only record for amphizoid flight to date, however, is that of Darlington (1929).

Finally, increased cold-tolerance is also evident among *A. insolens* members, and this trait probably accounts for the success of this species in extending its geographical range so remarkably (Fig. 18). Eastward range expansion across the Great Basin and more northern Columbia and Central plateaus probably occurred during a major glacial (or pluvial in this area) period (Fig. 27). A general lack of evident differentiation among members of widely isolated populations over a large part of the Great Basin and western Rocky Mountain flank suggests that the present extent of range was achieved relatively recently, perhaps during the Wisconsinan. Similarly, members of populations in coastal Alaska and British Columbia are undifferentiated from those in populations to the south. Hence, occurrence of these populations in formerly glaciated areas probably represents postglacial range extension through dispersal from the south (Fig. 28).

***Amphizoa striata* Van Dyke.** Although they share several apotypic features with members of



FIGURES 27, 28. Figure 27. Hypothetical distribution of ancestral amphizoid stocks, mid-Pleistocene glacial period. Figure 28. Present distributions of Nearctic *Amphizoa* species. Limits of geographical distribution: *A. insolens* = solid line; *A. striata* = dotted line; *A. lecontei* = dashed line.

A. lecontei and no doubt represent the sister-group of that species, *A. striata* adults are surprisingly similar to the hypothetical common ancestor of Nearctic amphizoids in general form, structure, and habits. Their occurrence in relatively warm, slow-flowing streams is unique among extant amphizoids, but such streams probably represent the ancestral (plesiotypic) habitat. The present geographical distribution of this species (Fig. 19) suggests that its members are only marginally adapted to a continental climate.

I have proposed that the ancestral stock of this species first became isolated and differentiated on the eastern flank of the Cascade-Sierra divide, at the western limit of the Columbia Plateau and northern Great Basin, during Pliocene time (Fig. 26). This hypothesis requires that the present distribution pattern (Fig. 19) resulted from subsequent westward range extension over, around, or through the divide in Pliocene or Quaternary time. Several present lowland routes through or around the divide (e.g., through the lower Fraser and Columbia River valleys or across the low

area north and east of the Pit River in northernmost California) probably also existed through at least part of Pliocene and Pleistocene time. Populations of *A. striata*, members of which were marginally adapted to the regional climate of the Great Basin and Columbia Plateau, were apparently able to disperse westward along lowland routes and subsequently expand their range through the Willamette and Puget lowlands and into adjacent low mountains. Because potential dispersal routes were probably either filled with, or greatly restricted by, montane glaciers during major glaciations (Fig. 27), it is more likely that westward range extension coincided with some interglacial period. Nevertheless, an early post-glacial origin for the present pattern cannot be ruled out (Fig. 28).

***Amphizoa lecontei* Matthews.** Adaptation to a continental climate was probably well under way among western Rocky Mountain populations of the common ancestor of *A. lecontei* and *A. striata* (Fig. 25) even before the complete isolation of eastern and western descendant stocks (Fig. 26). The present geographical distribution of *A. le-*

contei (Fig. 20) suggests that members of this species now require such a climatic regime for survival.

At present, *Amphizoa lecontei* is widely distributed in the Rocky Mountain region. Many extant populations, especially at the southern limits of distribution, occupy mountain ranges that are now widely separated by warm, arid lowlands. There is considerable geographical variation in characters of form and structure among members of these disjunct populations, but the pattern of variation is highly discordant (see above). This suggests that the ancestral stock of this species became widely distributed throughout the central and southern Rocky Mountain regions during a major glacial period (probably the Illinoian) (Fig. 27). During a subsequent interglacial (e.g., the Sangamon), the formerly continuous geographical range became fragmented, and isolated populations differentiated to a limited degree. During one or more subsequent glacial periods (probably the Wisconsinan glaciations), ranges of previously isolated populations came in contact, and secondary intergradation occurred among several differentiated forms. Extant populations achieved their present geographical relationships (Fig. 20, 28), as disjunct isolates, in response to postglacial warming; the present pattern of discordance in geographical variation reflects a history of repeated episodes of isolation and dispersal among several evolving populations or groups of same.

Adults of *A. lecontei* are similar to those of *A. insolens* in their physiological and behavioral adaptations for life in cooler, relatively faster-flowing streams. Perhaps the most striking features of *A. lecontei* adults are the broad elytral carinae. The functional significance of these carinae is yet unknown, but their dorsal position suggests that they may somehow contribute to stability during passive transport in stream currents.

PROSPECTUS FOR FUTURE RESEARCH

Clearly, much remains to be learned about extant amphizoids and their evolutionary history. More information is needed about *Amphizoa davidi*—its geographical and habitat ranges, adult locomotory habits, and the form and structure of females. Because amphizoids are often difficult to find, even in areas where they are known to occur, it is yet uncertain whether or not other species occur in eastern Asia. Concerted field-

work in this region, carried out by individuals familiar with the habits of Nearctic amphizoids, is required to resolve this question.

Comparative morphological study of amphizoid larvae and those of other adephagan groups should provide valuable new data that can be used in tests of hypotheses of phylogenetic relationship among both amphizoid species and adephagan families. This potential source of data has gone largely untapped and much basic descriptive work on larvae is still lacking.

In order to learn more about the historical development of amphizoids in space and time, search must continue among fossil materials of Mesozoic as well as Cenozoic age. To the best of my knowledge, amphizoids are not represented anywhere in the known fossil record, even during Quaternary time. Organisms living in lotic environments are much less likely to be preserved as fossils than are their lentic equivalents, and this punctuates the notion that absence from the fossil record at any particular time does not preclude occurrence at that time. Clearly the search for additional fossil assemblages of appropriate age must be continued.

ACKNOWLEDGMENTS

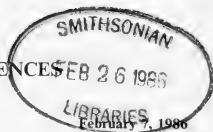
On different occasions, George E. Ball, Terry L. Erwin, Jean Menier, and Rob E. Roughley each tried to locate type-material for *A. davidi*. Lucas on my behalf in MNHP and/or in other European collections, and I thank them for their efforts in this regard. Both J. Gordon Edwards and Rob Roughley provided helpful comments and insights, based on their extensive personal experience with amphizoid beetles, during various phases of my study. The photograph of *Amphizoa davidi* was taken by Susan Middleton, and Mary Anne Tenorio took the scanning electron micrograph. Access to the PHYLIP program package was made possible through J. Russo (Office of Information Management, Smithsonian Institution). Alan Leviton provided access to the computer facility in the Department of Herpetology (CAS) and assisted me with use of the PHYLIP programs.

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ACANTHOGILIA, A NEW GENUS OF POLEMONIACEAE
FROM BAJA CALIFORNIA, MEXICO

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ABSTRACT: We propose the genus *Acanthogilia* for the spiny desert shrub first named *Gilia gloriosa* Brandege. The gametic chromosome number is nine, also the basic number for nine other genera and for the family.

Acanthogilia is unique among Polemoniaceae in its extreme leaf dimorphism, its persistent woody-spinose primary leaves, and its coarsely verrucate zonocolporate pollen grains. Though formerly placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, it differs further from all these genera in its persistent secondary leaf bases with deciduous blades, its numerous closely spaced corolla veins connected at several levels, and its winged seeds. It does share several unusual characters, such as the superficially adnate filaments, with species of *Gilia* sect. *Giliastrum*.

Acanthogilia seems closest to the Andean genus *Cantua*. *Cantua*, like *Acanthogilia*, is shrubby, with leaves dimorphic, on long shoots and axillary short shoots, with persistent leaf bases, with corolla veins connected at several levels, with winged seeds, with superficially adnate filaments (in some species), and with coarsely verrucate pollen grains (in one other species). *Cantua* differs in having the leaves broad and herbaceous, only weakly dimorphic, and neither woody-spinose nor with deciduous linear blades, the calyx entirely herbaceous, the pollen pantoporate, and the chromosome number hexaploid.

INTRODUCTION

Gilia gloriosa, of T. S. Brandege (1889), is a spiny but truly gloriose desert shrub of rather local occurrence on the Pacific drainage of north-central Baja California (Fig. 1-3). This plant is seldom seen and little known, and its best generic position has remained uncertain. Brand (1907) placed it in *Gilia* sect. *Leptodactylon*, and Wherry (1945) called it *Leptodactylon gloriosum*. Johnston (1924) informally listed it as *Loeselia gloriosa*. Current floras (Wiggins 1964, 1980) treat it as *Ipomopsis gloriosa*, following Alva Grant (in V. Grant 1956).

New information on the chromosome number, pollen grain type, and some other aspects shows that *Gilia gloriosa* differs from all de-

scribed genera of the family and has some unique characters. We therefore propose for it the following new monotypic genus.

SYSTEMATIC TREATMENT

Acanthogilia Day et Moran, genus novum mexicanum Polemoniacearum, ob folia valde dimorpha, primariis rigide spinosis persistentibus, granaque pollinis zonocolporata supraverrucata bene distinctum; Cantuae Juss. fortasse proximum, quae autem calyce toto herbaceo, aetate non rumpenti, pollinis granis pantoporatis, chromosomatumque numero polyploideo differt. Si vis descriptionem latine recipere, involucrum praeinscriptum praesolutumque mitte.

Stiff spiny shrub with dimorphic leaves, the



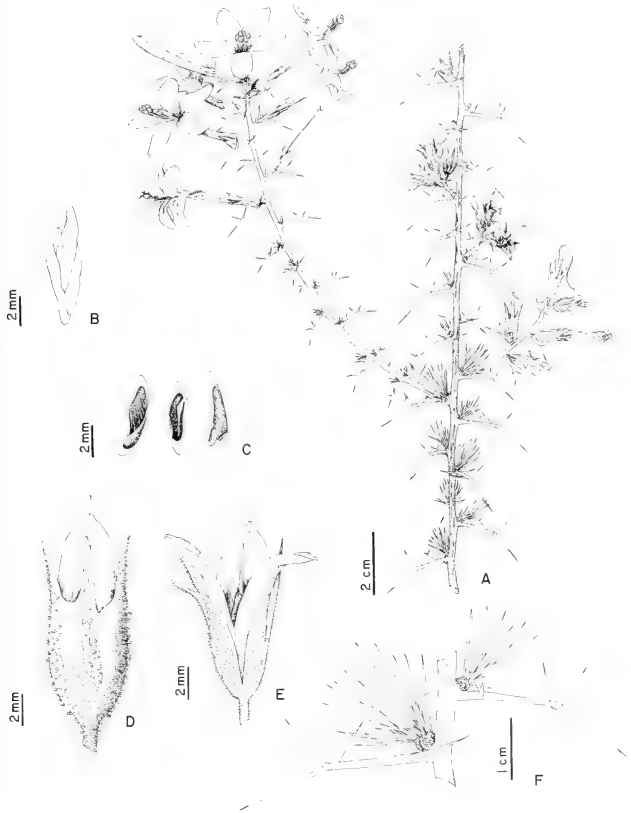


FIGURE 2. *Acanthogilia gloriosa* in flower and fruit. A. Flowering and fruiting branches on an older branch, with dehiscent capsules from previous season; B. Green, submature seeds, contents of a single locule; C. Dry seeds from dehiscent capsule; D. Calyx with mature, undeveloped capsule; E. Calyx with dehiscent capsule from previous season; F. Segment of branch with spinose primary leaves and fascicled herbaceous secondary leaves.

FIGURE 1. Inflorescence of *Acanthogilia gloriosa* (Brandg.) Day and Moran, El Colosal, Baja California, Mexico, 13 June 1976.

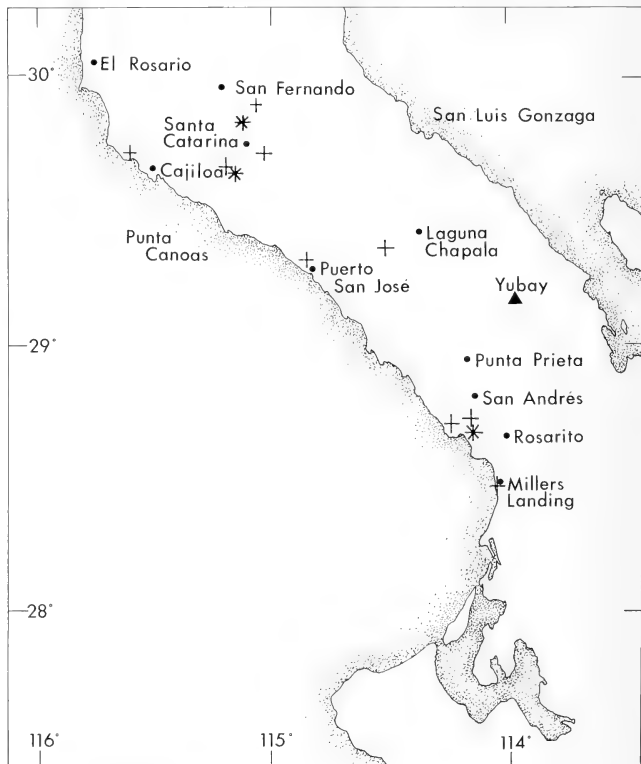


FIGURE 3. North-central Baja California, Mexico, showing distribution of *Acanthogilia gloriosa*. + = collection site, * = site of collection yielding chromosome count, ▲ = stated type locality.

primary alternate, woody-persistent, pinnate, with terete spinose divisions, the secondary fascicled on axillary short shoots, with persistent bases and deciduous, flat, linear, herbaceous blades. Calyx tubular, with equal spinose lobes and narrower scarious intervals that rupture in

fruit. Corolla regular, salverform. Stamens subequally adnate near middle of tube, superficially adnate below, subequal, well exerted. Pollen yellow, the grains zonocolporate, perreticulate, supraverrucate. Seeds elongate, flat, winged, mucilaginous when wet. Chromosomes: $x = 9$.

TYPE-SPECIES.—*Gilia gloriosa* Brandegee.

***Acanthogilia gloriosa* (Brandegee)**

Day and Moran, comb. nov.

Gilia gloriosa Brandegee, Proc. Calif. Acad. Sci. Ser. 2, 2:184, pl. 9. 1889. *Loeselia gloriosa* I. M. Johnston, Proc. Calif. Acad. Sci. Ser. 4, 12:962. 1924. *Leptodactylon gloriosum* Wherry, Am. Midl. Naturalist 34:383. 1945. *Ipomopsis gloriosa* A. Grant in V. Grant, Aliso 3:357. 1956.

TYPE.—Mexico, Baja California, Ubi, 8 May 1889, T. S. Brandegee s.n. (holotype, UC 101896); isotypes, DSI, GH). The type locality, Ubi, is the tinaja, or waterhole, of Yubay, near 29°11'N, 113°59'W, elevation ca. 650 m, ca. 9 km NE of the abandoned mine of Desengaño and ca. 52 km from the Pacific coast. Brandegee remarked that the plant appeared to be very local, having been observed only during an hour's journey and not again met with. He customarily gave bare locality names without direction or distance, and presumably he may have meant within half a day or so north or south of Yubay. His itinerary (Moran 1952) suggests south. Moran failed to find the plant about Yubay or along the old trail just to the south.

Stiff spiny shrub 1–3 m high and 1–5 m wide, much branched at base, the young parts glandular-pubescent and glutinous with two–many-celled trichomes mostly less than 0.5 mm long, each tipped with yellowish globule. Trunks to 6 cm thick, the bark light to dark gray, flaking in small plates; lower branches arching, sometimes rooting. Branching sympodial, the branches mostly flowering terminally the first year and so not elongating further, 1–125 cm long, 1–4 mm thick the first year, tan becoming gray, subterete, persistently spiny with old leaves; internodes averaging 5–8 mm, exceeded by leaves. Primary leaves subopposite to mostly alternate, 1–3 cm long, woody-spinose, rigidly divaricate and straight except terminal segment usually declined, green becoming tan and finally dark gray, persisting two to three (sometimes to six) years but weak after first or second year, the lowermost sometimes simple but most pinnate with narrowly linear rachis and one to two (sometimes to three) pairs of spreading spinose lobes to 9 mm long, the base 1.5–3.0 mm wide. Secondary leaves fasciated in axils, few and short the first season (on flowering branches), later to 25 per season, the bases whitish to tan, persistent, the blades herbaceous, mostly simple, rarely with one to two short lobes, linear-oblancheolate, spine-tipped, flattened, 5–20 mm long, to 1 mm wide, rather sparsely glandular, deciduous throughout plant all at about one time; first leaves of new shoot with enlarged semiglobular bases to 1.5 mm wide and blades sometimes less than 1 mm long. Short shoots producing leaves for

three to four (sometimes to six) years, to 8 mm long or some becoming long shoots. Inflorescence densely glandular-puberulent and glutinous, a thyse to 2 dm long on a new shoot, with terminal flower mostly opening first and with up to 30 short one–few-flowered branches below; or inflorescence reduced to short one–few-flowered shoot, though sometimes several such shoots borne on one older branch to form two-generational inflorescence. Flowers January to July, October, protandrous, open ca. four to five days and nights, odorless, visited by hummingbirds. Pedicels erect to spreading, 1–6 mm long, 0.5–1.0 mm thick. Calyx 10–16 mm long, 3.0–4.5 mm wide, cylindric, tapering to rounded at base, densely glandular and glutinous without, more sparsely so within, tubular in lower $\frac{2}{3}$; segments equal, erect or slightly outcurved, 3–8 mm long, triangular-lanceolate, pungent-acuminate, cartilaginous, with many crowded veins within, scarious-margined except near apex; sinuses V-shaped, the scarious intervals much narrower than ribs, distended at anthesis, folding inward as segments later converge, mostly rupturing in fruit. Corolla salverform, 3.0–4.5 cm long, glandular without, in bud pale yellow becoming orange; tube stout, slightly upcurved, 2.0–3.2 cm long, 2.5–3.5 mm wide below, gradually flaring to orifice 5–7 mm wide, dull orange-red to orange-brown, becoming paler and more purplish; throat yellow; limb 2–4 cm wide, white and mucilopapillose inside, rose-veined outside, the lobes in bud convolute, in anthesis widespread or somewhat reflexed, in age strongly reflexed, 8–20 mm long, 4–12 mm wide, obliquely oval to strap-shaped, obtuse to slightly emarginate, sometimes apiculate, with 30–50 close-spaced parallel veins per lobe. Filaments glabrous, 15–27 mm long, subequally attached at middle of tube or slightly above, superficially adnate below, with margins free throughout, subequally exerted 4–13 mm from throat; anthers oblong, sagittate, 4–5 mm long before anthesis, dehiscing as corolla begins to open. Pollen grains subsoblate to spheroidal (P 55–64 μ m, E 61–71 μ m). Nectary disk green, ca. 2 mm wide, shallowly cupped, the margin regularly undulate to form erect lobules opposite calyx segments and spreading ones between. Ovary three-celled, 4–5 mm long, ca. 1.5 mm thick; style 20–40 mm long, slightly shorter to slightly longer than filaments (consistent in each plant); stigma lobes acute, 1.5–2.0 mm long,

outcurved by third day. Ovules 14–24 per cell, ovoid, ca. 0.6 mm long, many aborting. Capsules 7–15 mm long, 4–5 mm thick, cylindric, beaked, crustaceous, yellowish brown, loculicidally dehiscent, the valves often recurving. Seeds overlapping, one to six per cell, narrowly oblong, flat, 6–7 mm long, 1.5 mm wide, the brownish body surrounded by elongated membranous wing, the body and wing swelling and mucilaginous when wet. Chromosomes: $n = 9$.

DISTRIBUTION.—Mexico, Baja California Norte: locally common on desert flats and hill-sides and in arroyo beds from 40 km SSE of El Rosario to Miller's Landing, a span of 200 km, and from the coast inland at least 45 km and to 525 m elevation (Fig. 3).

ADDITIONAL SPECIMENS EXAMINED.—San Fernando, 24 May 1894, *Anthony s.n.* (UC); Rosalia Bay, Jul.–Oct. 1896, *Anthony 92* (DS, UC); 2 km NW of Cajilloa, 29°41'N, 115°34½'W, Aug. 1980, *Binney s.n.* (SD); 2.9 m E of mouth of Arroyo San José, 29°12'N, 114°44'W, 28 Jun. 1969, *Bostic s.n.* (SD); 6.2 m S of Santa Catarina, 29°38'N, 115°10'W, 26 Aug. 1969, *Bostic s.n.* (SD); San Andreas Canyon above Santa Rosalillita, 20 Mar. 1984, *Breedlove 60808* (CAS); 2–3 km NE of Santa Rosalillita, 20 Mar. 1984, *Breedlove 60834* (CAS); 5–15 m N of Puerto Santa Catarina, road to San Agustín, 1 Mar. 1985, *Breedlove 62269* (CAS); 1 m NE of Rancho Santa Catarina, 20 Jun. 1979, *Clark 3167* (CAS); 10 m S of Punta Prieta, 9 Feb. 1947, *Constance 3125* (DS); 2 km W of La Ramona, 29°49'N, 115°07'W, 10 Jul. 1976, *Day and Moran 76-126* (CAS, SD); same data, *Day and Moran 76-129* (CAS, SD); 4.3 m S of El Colosal, 29°47'N, 115°06'W, 10 Jul. 1976, *Day and Moran 76-133* (CAS); Sierra Lino, 25 m S of Punta Prieta, 6 Mar. 1947, *Gentry 7345* (DS, SD, UC); S of Arroyo San Borja, 26 Mar. 1947, *Gentry 7617* (DS, UC); San Andreas, 26 Jul. 1941, *Harbison s.n.* (SD); Arroyo San José, 29°10'N, 114°45'W, 18 Oct. 1966, *Hastings and Turner 66-154* (DS, SD); Rancho La Ramona, Santa Catarina, 21 Jun. 1947, *Huey s.n.* (SD); 3 m S of Miller's Landing, 9 Jul. 1937, *Lindsay s.n.* (DS); Arroyo Santo Dominguito, 6.7 m S of San Andres, 28°42'N, 114°15'W, 28 May 1959, *Moran 7498* (DS, SD, UC); 1½ m N of Rancho Ramona, 29°50'N, 115°05'W, 25 Mar. 1970, *Moran 16896* (SD); 11 m N of Puerto Santa Catarina, 29°39'N, 115°12'W, 28 Mar. 1970, *Moran 17030* (SD); 3 m SE of Santa Rosalillita, 28°40'N, 114°13'W, 2 Jan. 1976 and ex hort. San Diego, 16 Jul. 1976, *Moran 22779*, (CAS, SD); 10 km S of El Aguila, 29°52½'N, 115°04½'W, 12 Jun. 1976, *Moran 23518* (SD); 2 km W of La Ramona, 29°49'N, 115°07'W, 12 Jun. 1976, *Moran 23519* (SD); 2 km W of La Luciana Mine, 29°42'N, 115°02'W, 13 Jun. 1976, *Moran 23521* (CAS, SD); 3 km NW of Santa Catarina, 29°44½'N, 115°06½'W, 13 Jun. 1976, *Moran 23522* (CAS, SD); coastal region near Rosario, 28°38'N, 114°05'W, 5 Oct. 1970, *Rauh 25416* (HEID, SD); 1 m NW of Santa Catarina, 29°44'N, 115°06'W, *Robinson s.n.* (SD); 23 m S of Punta Prieta, 1 Jun. 1931, *Wiggins 5731* (DS UC); 17 m S of Punta Prieta, 9 Apr. 1961, *Wiggins 16193*, (DS).

At Rancho Santa Catarina this plant was called "mala mujer" (bad woman). That name is used in Baja California and elsewhere in Mexico for

some other prickly plants, as well as for several stinging and poisonous plants (Martínez 1937).

FLORAL BIOLOGY.—Floral characters of *Acanthogilia* predominantly suggest outcrossing. The anthers dehisce as the flower opens, but stigmas do not open out until the third day. Styles usually exceed stamens, as in many Polemoniaceae that are insect- or hummingbird-pollinated. In some individuals, however, styles are consistently shorter, with stigmas opening just beneath the anthers, as in various autogamous flowers. This heteromorphism in the population may help ensure some seed production even if outcrossing fails. The floral characters strongly suggest adaptation to hummingbird pollination, and Moran has observed hummingbirds visiting the flowers. The flowers are open by day, odorless, with stamens and style well exerted. The corolla is robust, with a long and ample tube. Its color pattern is well marked, with glistening white lobes around a yellow orifice, and with an orange-red to orange-brown tube. Other hummingbird flowers in the family have similar characters. In *Cantua*, *Gilia*, *Ipomopsis*, *Loeselia*, and *Polemonium*, hummingbird flowers are diurnal and odorless, with long red or yellow corolla tubes and usually with exerted stamens and style (Grant and Grant 1965). Superficially, some hummingbird flowers of different genera look more like each other than like bee- or fly-pollinated flowers of their own genus.

COMPARISONS WITH OTHER POLEMONIACEAE

CHROMOSOME NUMBER.—The basic chromosome number of *Acanthogilia* is nine. We base it on counts from propionic-carmines squashes of anthers from three collections of *A. gloriosa* (mapped in Fig. 3): (1) *Moran 17030* from 18 km N of Puerto Santa Catarina; (2) *Moran 22779*, ex hort. San Diego, from 4.8 km SE of Santa Rosalillita; and (3) *Moran 23519*, from 2 km W of La Ramona. Meiotic counts from collection 1 showed $n = 9$; chromosome behavior was regular, with 9_{II} at M_1 (Fig. 4). From premeiotic sporogenous cells of collection 2 (Fig. 4) and from tapetal cells of collection 3, mitotic counts showed $2n = 18$.

Nine is the basic number for more than half the genera of the family (Table 1) and is regarded as the primitive basic number in the Polemoniaceae. The other genera have lower basic numbers apparently derived independently in different tribes by aneuploid reduction (Grant 1959).

Thus, *Acanthogilia* stands among the ten genera that still have the primitive number. These are a mixed lot, from all five tribes in the classification of Grant (1959). Hence chromosome number gives no clue to the tribal placement of *Acanthogilia*.

The basic number is mostly constant within genera of the family (Table I); where it is not (*Allophyllum*, *Gilia*), the number varies by only one chromosome pair ($x = 9, 8$). *Gilia gloriosa* was placed in *Ipomopsis* (A. Grant in V. Grant 1956) before its chromosome number was known. Since *Ipomopsis* has $x = 7$, a count of $n = 9$ for *I. gloriosa* showed us it was in the wrong genus. That was the starting point for this study.

POLLEN.—Pollen studies in the Polemoniaceae (Erdtman 1952; Stuchlik 1967; Taylor and Levin 1975) have not included *Acanthogilia*. We sent a pollen sample to Dr. Leon Stuchlik, who kindly prepared the following diagnosis, in 1980, with permission to include it here (see Fig. 5–8).

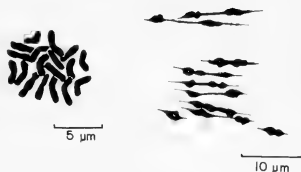


FIGURE 4. Chromosomes of *Acanthogilia gloriosa*. Left, mitosis; right, meiosis. Traced from micrographs.

Pollen grains 5–6 colpiate (zonocolporate), suboblate to spheroidal; diameter 55–64 $\mu\text{m} \times 61$ –71 μm . Colpi short, only slightly longer than pores are broad. Pores lalongate to circular; diameter 5–7 $\mu\text{m} \times 7$ –10 μm . Exine 2.4–2.9 μm thick; nexine 0.8–1.2 μm thick, thickened up to 1.7 μm in pore area, finely perreticulate. Lumina variable in shape and size; diameter less than 0.5 μm to 1 μm ; muri supported by simple bacula densely spaced,

TABLE I. COMPARISON OF THE GENERA OF POLEMONIACEAE. I, 9, 8 = intrageneric aneuploidy; 9/8 and 8/7 = dibasic polyploidy. II. Pollen groups 1–4 are the alliances of Taylor and Levin (1975), with *Acanthogilia* added. III. Pin = leaves pinnately veined, dissected, or lobed; PinC = leaves pinnately compound; Palm = leaves palmately lobed; * = true foliage leaves lacking. IV. N = seeds not winged; NW = seeds very narrowly winged; W = seeds broadly winged. V. A = filaments superficially adnate; M = filaments merged with corolla; I = filaments intermediate; merged below. VI. M = calyx membranous below sinuses; H = calyx herbaceous throughout. VII. A = veins connected at base of lobe and in upper lobe; B = veins connected only at base; C = veins connected only well above base; D = veins free; * = venation too simplified to classify.

| | I Basic chromosome number | II Pollen group | III Leaf form | IV Seed type | V Filaments | VI Calyx type | VII Venation of corolla lobe |
|----------------------|------------------------------------|-----------------------|------------------|-----------------|----------------|---------------------|------------------------------------|
| <i>Acanthogilia</i> | 9 | 1 | Pin | W | A | M | A |
| <i>Cantua</i> | 9 | 1 | Pin | W | A, M | H | A, B |
| | ($2n = 27_n$) | | | | | | |
| <i>Huthia</i> | ? | 1 | Pin | W | I | H | B |
| <i>Cobaea</i> | 9/8 | 2 | PinC | W | A | H | A |
| | ($2n = 26_n$) | | | | | | |
| <i>Phlox</i> | 7 | 2 | Pin | N | M | M | A, B |
| <i>Microsteris</i> | 7 | 2 | Pin | N | M | M | * |
| <i>Gymnosteris</i> | 6 | 2 | * | N | M | H | * |
| <i>Polemonium</i> | 9 | 3 | PinC | N | M, I | H | A, B |
| <i>Bonplandia</i> | 8/7? | 3 | Pin | N, NW | M | H | A |
| | ($2n = 15_n$)† | | | | | | |
| <i>Gilia</i> | 9, 8 | 4 | Pin | N | A, M, I | M | A, B, D |
| <i>Collomia</i> | 8 | 4 | Pin | N | M | H | B, C |
| <i>Eriastrum</i> | 7 | 4 | Pin | N | M, I | M | B |
| <i>Navarretia</i> | 9 | 4 | Pin | N | M | M | B, * |
| <i>Ipomopsis</i> | 7 | 4 | Pin | N | M, I | M | B, D |
| <i>Langloisia</i> | 7 | 4 | Pin | N | M, I | M | B, C |
| <i>Allophyllum</i> | 9, 8 | 4 | Pin | N | M | M | C |
| <i>Loeselia</i> | 9 | 4 | Pin | N, NW | M | M | C, D |
| <i>Leptodactylon</i> | 9 | 4 | Palm | N | M | M | D |
| <i>Linanthus</i> | 9 | 4 | Palm | N | M | M | D |

† *Bonplandia geminiflora* chromosome number, $2n = 15$ bivalents, determined from the following collections: Sinaloa, Mexico, D. E. Breedlove 44637; Chiapas, Mexico, D. E. Breedlove 56256. Vouchers deposited at CAS. Counted by A. Day.

sometimes merged 2–3 together. Diameter of bacula ca. 0.5 μ m. Reticulum supraverrucate. Verrucae on surface of exine very variable in shape and size, from very small and flat with diameter ca. 1 μ m to circular or oval with diameter to 10 μ m, in young pollen grains very densely spaced. Surface of verrucae ultra-finely striate or rugulate, as seen with scanning electron microscope at 7000 \times magnification.

This diagnosis is based on a single collection (Day and Moran 76133, CAS). Other collections show that the grains may be 7–8-colporate (Moran 7498, CAS) or the colpi may be longer (Fig. 6; Wiggins 5731, DS). Variation in the number and distribution of verrucae is seen by comparing Figures 5 and 6.

The most distinctive feature of *Acanthogilia* pollen grains is the coarsely verrucate exine (Fig. 5–8). Among other Polemoniaceae with zonocolporate grains, only *Eriastrum* and *Gilia* sect. *Giliastrum* have the exine verrucate, but there the verrucae are minute. Dr. Stuchlik (pers. comm. 1980) remarked that *Acanthogilia* has probably a new pollen type for the family.

Pollen grains with large verrucae do occur, however, in *Cantua*. In *C. buxifolia* Juss. ex Lam. (Fig. 9, 10) the exine appears much as in *Acanthogilia*. In both *C. buxifolia* and *Acanthogilia* the verrucae are diverse in size and shape, the larger ones supported by groups of bacula. Viewed with SEM (Fig. 9, 10), the verrucae of *C. buxifolia* differ from those of *Acanthogilia* only in being somewhat broader and flatter.

In the Cantueae (*Cantua* and *Huthia*) the exine is semitectate and, as illustrated (SEM) by Taylor and Levin (1975), generally consists of large, closely spaced areoles (Taylor and Levin's term) or insulae (Stuchlik 1967). However, *Cantua buxifolia* is exceptional in having areoles of such small diameter that they have been described as large verrucae (Erdtman 1952). This exine pattern may have evolved through reduction of larger areoles.

Despite the similarity in exine, the pollen grains of *Cantua buxifolia* differ from those of *Acanthogilia* in aperture type; for, as in other Cantueae, they are pantoporate, not zonocolporate. Since, however, both zonocolporate and pantoporate grains can occur within a single genus elsewhere (Collomia, Loeblich 1964, Chuang et al. 1978; *Gilia*, Stuchlik 1967), this difference between *Acanthogilia* and *Cantua* is not necessarily fundamental. In view of other notable shared

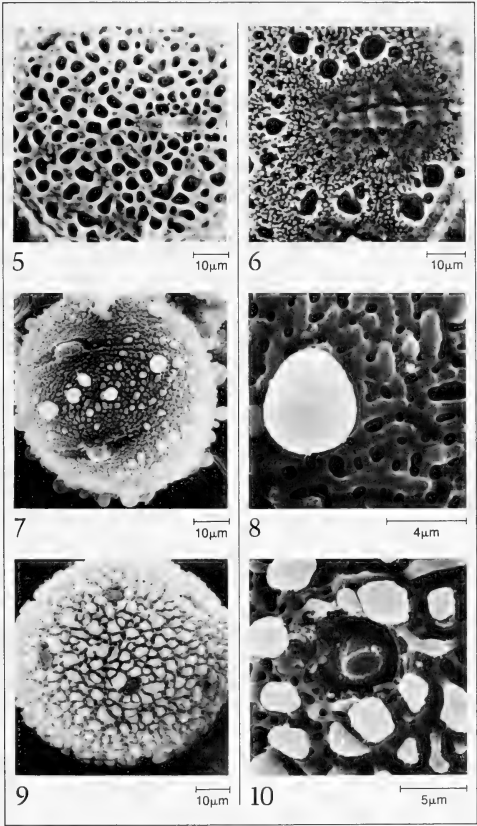
characters (Table 1), we interpret the similarity in exine as a mark of relationship.

On the basis of pollen morphology, Taylor and Levin (1975: fig. 1) grouped the genera of Polemoniaceae into four unnamed alliances (pollen groups 1–4 of our Table 1). One alliance included only *Cantua* and *Huthia*, but we would add *Acanthogilia*.

LEAVES.—In *Acanthogilia* the leaves of long shoots and axillary short shoots are markedly different, with no intermediates (Fig. 2F). The leaves of long shoots are woody-spinose and persistent, as in no other Polemoniaceae. Base and blade are scarcely delimited, and the blade is pinnately divided, with terete rachis and lobes. On the contrary, the fascicled axillary leaves are each clearly divided by a constriction into a persistent base and a deciduous blade (Fig. 11A). The broadened bases remain indefinitely in a compact spiral on the short shoot, but the blades fall at one time throughout the plant with drying of the season. These are smaller blades than those of the primary leaves, mostly simple, linear but flattened, herbaceous, and greener.

Cantua, *Huthia*, *Leptodactylon*, *Loeselia*, and some species of *Ipomopsis* also have leaves on long shoots and in axillary fascicles; but although the fascicled leaves may be smaller, all leaves are nearly alike. *Cantua* is somewhat exceptional: the primary leaves are large and more or less lobed and fall early, whereas the secondary, axillary leaves are more persistent and in most species are smaller and have entire margins (Infantes Vera 1962; Gibson 1967). In *C. buxifolia* grown in San Francisco, we note that, except for young shoots, leafy stems bear only the smaller secondary leaves. In various other Polemoniaceae, especially annuals, leaves are gradually different from base to apex, grading into bracts above. Only *Acanthogilia*, however, has markedly dimorphic leaves.

In most perennial Polemoniaceae the leaves wither persistent, though they may finally erode away. In several evergreen shrubs (*Cantua*, *Huthia*, *Loeselia mexicana* (Lam.) Brand, *L. purpusii* Brandege), however, leaf blades finally fall, leaving the persistent bases conspicuous (Fig. 11B). In *Cantua buxifolia* and *C. pyrifolia* Juss. ex Lam., both of which produce fascicled leaves, the short shoots and crowded leaf bases, with blades gone, somewhat resemble those of *Acanthogilia* (Fig. 11A, B).



FIGURES 5-10. Pollen grains of *Acanthogilia gloriosa* and *Cantua buxifolia* Juss. ex Lam.; Fig. 5, 6. (light microscope) *Acanthogilia*; Fig. 5. Day and Moran 76-133 (CAS); Fig. 6. Wiggins 5731 (DS); Fig. 7, 8. (SEM) *Acanthogilia*, Wiggins 5731 (DS); Fig. 9, 10. (SEM) *Cantua buxifolia*, cultivated, McClintock s.n., 15 Mar 1976 (CAS).

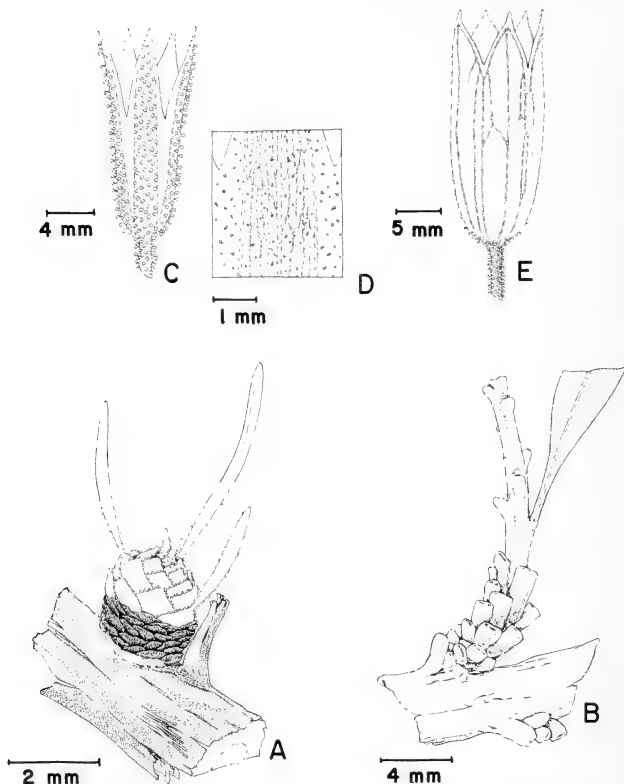


FIGURE 11. Short shoots and calyxes. A. Short shoot of *Acanthogilia gloriosa* with persistent leaf bases after most blades have fallen, the leaf bases from previous seasons compacted below, primary leaf mostly eroded away; B. Short shoot of *Cantua buxifolia* with crowded leaf bases, growing out into long shoot above; C. Calyx of *Acanthogilia gloriosa* at anthesis; D. Part of calyx, ventral side, showing venation in rib; E. Calyx of *Cantua buxifolia* at anthesis.

SEEDS.—The seed of *Acanthogilia* is flat and is bordered by a membranous wing 1–3 mm wide (Fig. 2C). In most Polemoniaceae, seeds are wingless, though in *Bonplandia* and *Loeselia* they

are sometimes very narrowly winged. Only in *Cantua*, *Cobaea*, and *Huthia* are the seeds likewise flat and broadly winged. In these genera, however, both seeds and wings are considerably

wider; and the wings, though thin, are opaque rather than membranous.

Acanthogilia has only 1–6 seeds per locule, whereas *Cantua*, *Cobaea*, and *Huthia* have many, in platelike layers. However, the ovary of *Acanthogilia* has 14–24 ovules per locule, suggesting that the ancestral capsule may have had many more seeds. A hint of layering in the capsules suggests that if more seeds were present they might form layers as in the other genera.

STAMENS.—The filaments of *Acanthogilia* are attached to the corolla tube about midway but are only superficially adnate below; they are well formed, with free margins, and are distinguishable to the base. Likewise in *Cobaea*, *Cantua* (*C. candelilla* Brand and *C. quercifolia* Juss. but not *C. buxifolia*), and *Gilia* sect. *Giliastrum* (*G. rigidula* Benth. and *G. ripleyi* Barneby but not *G. insignis* (Brand) Cory and Parks or *G. incisa* Benth.) the filaments are superficially adnate. This appears to be a rare and primitive condition in the family. In our sampling of other genera, the filaments are so merged with the corolla, at least basally and commonly to the point of insertion, that they are not distinguishable.

CALYX.—The calyx of *Acanthogilia* is narrowly membranous and veinless below the sinuses and has many veins crowded in the herbaceous ribs (Fig. 11C, D); it ruptures between ribs as the capsule grows. In eleven other genera (Table 1), including *Gilia* and most allies as well as *Phlox* and *Microsteris*, similarly, the calyx is narrowly to broadly membranous below the sinuses, with veins again confined to the ribs; it may or may not rupture in fruit. In all examples seen, veins are fewer and less crowded than in *Acanthogilia*. In all these genera, including *Acanthogilia*, lateral veins of adjacent ribs are connected only near the base of the calyx.

On the other hand, in *Boonplandia*, *Cantua* (Fig. 11E), *Cobaea*, *Collomia*, *Gymnosteris*, *Huthia*, and *Polemonium* the calyx is not alternately ribbed and membranous but is herbaceous or somewhat chartaceous throughout, and it enlarges without rupturing as the capsule grows. Venation is various but generally is spread out more than in the genera with membranous calyx. Lateral veins of adjacent sectors may be connected just below the sinuses (Fig. 11E) or much lower. They are connected in *Cantua quercifolia* near the base of the calyx but in *C. buxifolia* at various levels, even in the same calyx (Fig. 11E).

The herbaceous calyx type, found also in related families, presumably is primitive in the Polemoniaceae, the membranous calyx perhaps arising independently in more than one line in arid habitats. A division of the family by calyx types then would separate some related genera. Thus *Collomia* (herbaceous calyx) belongs with the *Gilia* group (otherwise membranous), and *Phlox* and *Microsteris* (membranous calyx) seem related to genera with herbaceous calyx (Table 1). Similarly, *Acanthogilia* appears related to *Cantua* despite the difference in calyx (Table 1).

COROLLA VENATION.—Surveying corolla venation in the family, Day has found patterns to link *Acanthogilia* with some genera and to separate it from others. Generally in the family, each sector of the corolla has a median vein and two laterals more or less parallel in the tube, with branches in the lobes and commonly with connections; positions of vein connections are characteristic for many taxa. Figures 12–14 show examples from 12 out of 19 genera—all traced from photographs of dissected corollas stained with safranin. The staminal veins, alternating with the corolla veins in the tube, are omitted.

Venation patterns fall mainly into four types (identified in Table 1 by letters A–D): A. *Cantua* type—veins connected near corolla orifice, curving and connected once or twice above in the lobe (Fig. 12G–H, 13K–O); B. *Gilia* type—veins connected near orifice but straighter above and without other connections (Fig. 12B–D); C. *Loeselia* type—veins often connected near middle or apex of lobe but not near orifice (Fig. 14P–R); and D. *Leptodactylon* type—veins free, not connected in orifice or lobes, even in large corollas with many veins; often each sector with only a single vein in basal half of tube (Fig. 12E–F, 14S–U). Some genera show only one venation type, some two, and one three (Table 1). In very small corollas (*Microsteris*, Fig. 13J; many *Navarretia* species, Fig. 12A; *Gymnosteris*; and occasional species in other genera) venation may be so simplified that it tells little of relationship.

In *Acanthogilia* the corolla veins are connected at several levels in the lobes (Fig. 12H), much as in *Cantua*, *Cobaea*, and *Phlox* (Fig. 13). *Acanthogilia* differs from them in having more closely spaced veins that are nearly parallel and less curved. Its pattern is perhaps most closely ap-

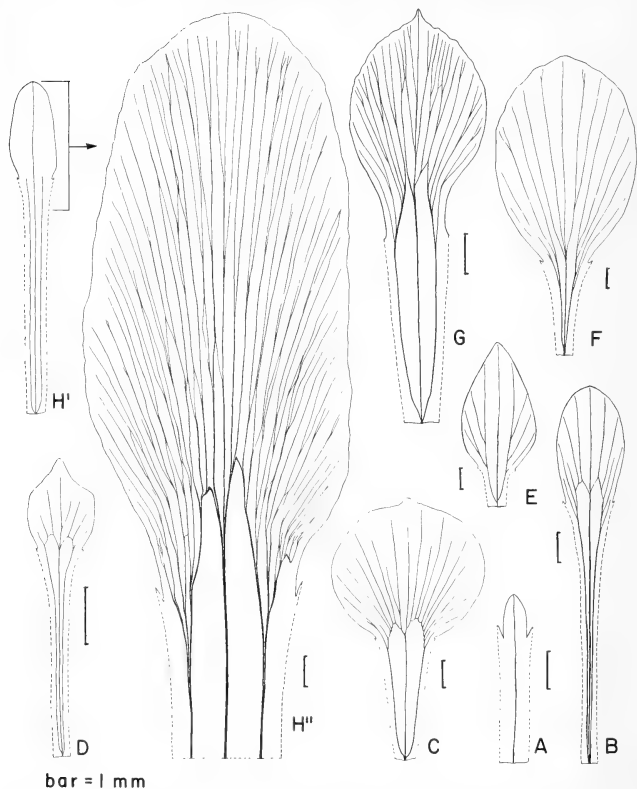


FIGURE 12. Corolla venation patterns in Polemoniaceae, each showing a sector from base of tube to apex of lobe. Dashed lines show where corolla tube cut. Stamens and staminal veins not shown. A. *Navarretia fossalis* Moran; B. *N. mitracarpa* Greene; C. *Gilia tricolor* Benth.; D. *G. leptomeria* Gray; E. *G. incisa* Benth.; F. *G. rigidula* Benth.; G. *G. ripleyi* Barneby; H', H''. *Acanthogilia gloriosa* Day and Moran.

proached in *Cantua candelilla* (Fig. 13M). On the other hand, despite more numerous veins with connections at several levels, the pattern of *Acanthogilia* resembles that of *Gilia* and allies

(Fig. 12B-D) in its straighter and closer-spaced veins. And although most species of *Gilia* sect. *Giliastrum* have free veins (Fig. 12E-F), the anomalous *G. ripleyi* (Fig. 12G) has connections

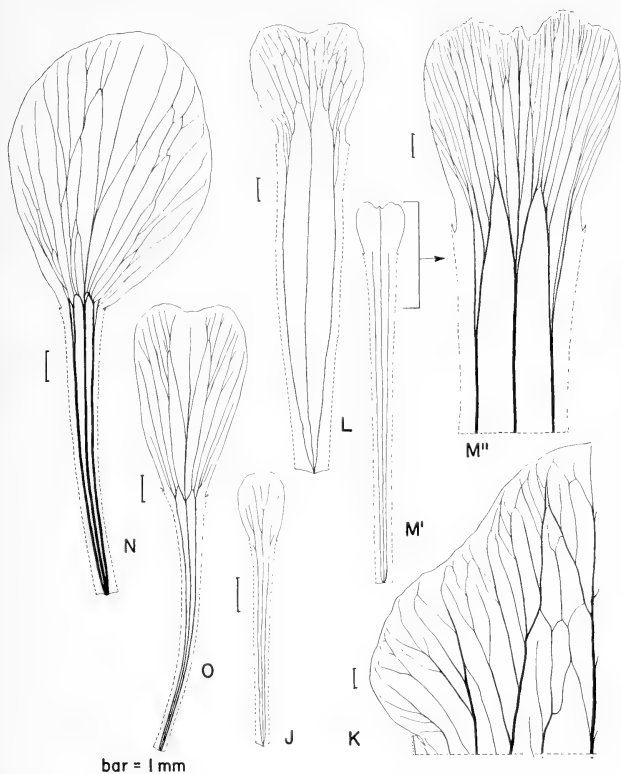


FIGURE 13. Corolla venation patterns, cont. J. *Microsteris gracilis* (Hook.) Greene; K. *Cobaea baurita* Standl.; L. *Cantua pyrifolia* Juss. ex Lam.; M', M''. *C. candelilla* Brand; N. *Phlox andicola* Nutt. ex Gray; O. *Bonplandia geminiflora* Cav.

at several levels, thus somewhat approaching *Acanthogilia*.

Although the species *gloriosa* has been placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, each of these genera has a venation pattern different from that of *Acanthogilia*. The distinc-

tive patterns of *Leptodactylon* and *Loeselia* especially seem to make close relationship with *Acanthogilia* unlikely.

WOOD ANATOMY.—Carlquist et al. (1984) studied the wood anatomy of the Polemoniaceae, comparing the relatively few woody species. Be-

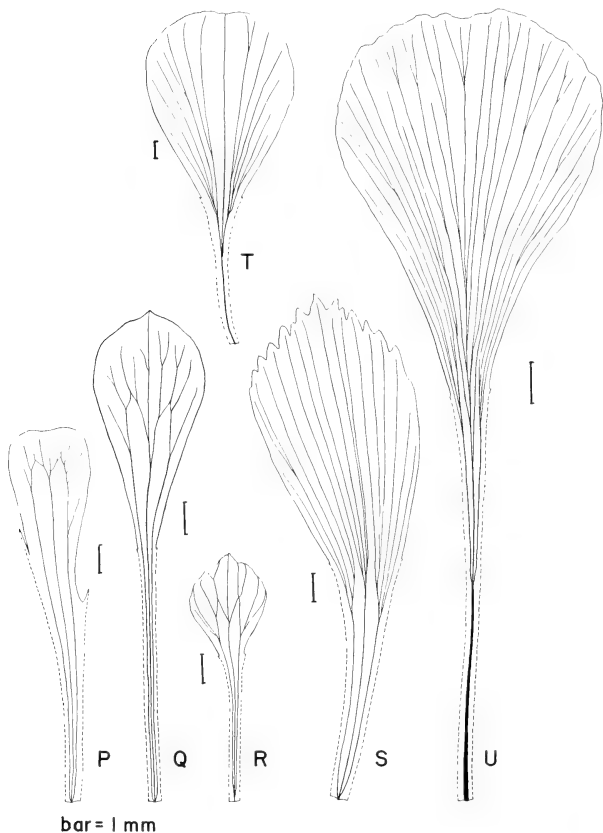


FIGURE 14. Corolla venation patterns, cont. P. *Loeselia greggii* S. Wats.; Q. *L. amplexens* (Hook. and Arn.) Benth.; R. *Allophyllum glutinosum* (Benth.) A. and V. Grant; S. *Linanthus dianthiflorus* (Benth.) Greene; T. *L. grandiflorus* (Benth.) Greene; U. *Leptodactylon pungens* (Torr.) Rydb.

sides *Acanthogilia*, these species fall in *Cantua* and *Huthia* (Cantueae), *Cobaea* (Cobaeae), and *Eriastrum*, *Ipomopsis*, and *Leptodactylon* (Gilieae). In general, they thought the wood anatomy probably more closely correlated with growth form as related to habitat, than with systematic relationships.

The authors noted that *Acanthogilia* and a species of *Ipomopsis* are alike in having banded axile parenchyma—unusual in the family but occurring also, in its most incipient form, in *Cantua*. Likewise, in the imperforate tracheary elements and in the vascular rays, *Acanthogilia* is similar to *Ipomopsis* on the one hand and to the Cantueae on the other. The coincidence in these characters among *Acanthogilia*, the Gilieae, and the Cantueae somewhat parallels other similarities we report here (Table 1) and would seem to be due to relationships rather than to environmental factors alone.

RELATIONSHIPS

Acanthogilia is unique among Polemoniaceae in its extreme leaf dimorphism, its persistent woody-spinose primary leaves, and its coarsely verrucate zonocolporate pollen grains. Although *A. gloriosa*, the sole species, has been placed in *Gilia*, *Ipomopsis*, *Leptodactylon*, and *Loeselia*, it differs further from all these genera in its persistent secondary leaf bases with deciduous blades, its numerous closely spaced corolla veins with interconnections at several levels, and its winged seeds, and from all these except for two species of *Gilia* in its superficially adnate filaments. It differs still further from *Gilia* and *Ipomopsis* in its large shrubby habit, from *Ipomopsis* in its basic chromosome number of nine, and from *Leptodactylon* in its pinnate leaves and its three corolla veins instead of one in each sector of the lower tube.

Among North American Polemoniaceae, *Acanthogilia* seems to have most in common with *Gilia* and allies, and especially with species of *Gilia* sect. *Giliastrum*. As in *Acanthogilia*, all *Gilia* species have the calyx membranous below the sinuses, and most, including sect. *Giliastrum*, have zonocolporate pollen and have the primitive $x = 9$. In this polymorphic genus of five sections, usually the pollen is blue and the exine reticulate to striate and not verrucate. In sect. *Giliastrum*, however, the pollen is yellow as in *Acanthogilia*, and the exine is somewhat similar,

being peritectate and minutely verrucate whereas in *Acanthogilia* it is perreticulate and coarsely verrucate. Although in most species of *Gilia* the filaments merge with the corolla below, in *G. ripleyi* and *G. rigidula*, of sect. *Giliastrum*, the filaments are superficially adnate, as in *Acanthogilia*. Most species of *Gilia* are annual and none are truly woody, but *G. ripleyi* is a suffrutescent perennial. Finally, although most species of sect. *Giliastrum* have free corolla veins, *G. ripleyi* is unique in *Gilia* and further resembles *Acanthogilia* in having the veins connected at several levels.

Acanthogilia is perhaps most closely related to the Andean genus *Cantua*. *Cantua*, like *Acanthogilia*, is shrubby, with leaves dimorphic, borne on long shoots and axillary short shoots, with crowded leaf bases remaining on the short shoots after the blades have fallen, with corolla veins connected at more than one level, with seeds flattened and broadly winged, with a basic chromosome number of nine, with superficially adnate filaments in *C. candelilla* and *C. quercifolia*, and with coarsely verrucate pollen in *C. buxifolia*. The lower branches of *C. buxifolia* (grown in San Francisco) take root, as do those of *Acanthogilia*. *Cantua* differs in that the leaves are broadly herbaceous and only slightly dimorphic, with primary leaves deciduous, not at all woody-persistent, and secondary leaves more persistent; the calyx herbaceous, not membranous below the sinuses, and not rupturing in age; the pollen pantoporate, not zonocolporate; the chromosome number hexaploid, not diploid. We suggest that *Acanthogilia* may be a specialized desert descendent of a diploid line also ancestral to *Cantua*. Since *Cantua* is hexaploid, however, and probably amphiploid, such divergent characters as the herbaceous calyx may perhaps derive from some other line.

Grant (1959) divided the Polemoniaceae into five tribes. *Acanthogilia* probably belongs to the Cantueae but apparently has some relationship also with the Gilieae. Much new evidence bearing on generic relationships has accumulated, especially from pollen studies, since Grant's classification, and the time seems ripe for a new tribal arrangement.

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Stuchlik of the Botanical Institute, Cracow, Poland, for his pollen diagnosis of *Acanthogilia* and observations concerning it; Jerry Morgan of University of California, San Francisco, for the SEM micrographs; the Gift Fund, Dudley Herbarium of Stanford University for support for the SEM work; Terry Bell for line drawings of *Acanthogilia*; Colleen Sudekum for the corolla venation tracings; Barbara Stewart for drawing the distribution map; and Dave and Dru Binney for sending two points for the map, from far, out-of-the-way places. We appreciate suggestions given by Dr. Robert Patterson on the pollen morphology section, by John Thomas Howell on the Latin diagnosis, and by Dr. Dennis Breedlove and Dr. Leslie Landrum on various points along the way. An early preview of the wood-anatomy manuscript was kindly offered by the senior author, Dr. Sherwin Carlquist. We thank Dr. Frank Almeida, Dr. Christopher Davidson, Dr. Verne Grant, and two unsigned reviewers for reading this manuscript and making many helpful comments. We appreciate the courtesies extended at the following herbaria: California Academy of Sciences (CAS), Dudley Herbarium of Stanford University (DS), San Diego Museum of Natural History (SD), and University of California, Berkeley (UC). Lastly, for making the color plate possible, we are most grateful to seventy-two colleagues and friends enlisted by Annetta Carter and Lincoln Constance as Los Amigos de *Acanthogilia*.

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THE DIATOM GENUS *THALASSIOSIRA*: SPECIES FROM
THE SAN FRANCISCO BAY SYSTEM

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ABSTRACT: Twenty species of the diatom genus *Thalassiosira*, including one previously undescribed species, were collected from diverse habitats of San Francisco Bay, California, extending from nearly freshwater in Suisun Bay to marine salinity near the Golden Gate. In this paper the morphology of these 20 species is elucidated by scanning electron microscopy (SEM) and light microscopy (LM). The species range from large taxa with linear areolae to small, lightly silicified forms with eccentrically arranged areolae. The basic form of the genus is seen as a moderately small diatom with rectangular outline in girdle view and a simple process pattern of one central and one marginal ring of strutted processes and a single labiate process.

The distribution of species is influenced by salinity. Major species show limited distributions: *T. visurgis* Husted, fresh to brackish water; *T. decipiens* (Grunow) Jørgensen, brackish water; *T. nodulolineata* (Hendey) Hasle and G. Fryxell, tidal marine to brackish; *T. hendeyi* Hasle and G. Fryxell, and *T. wongii* Mahood sp. nov., tidal marine water; *T. nordenskiöldii* Cleve and *T. pacifica* Gran and Angst, coastal marine. These distributions demonstrate the value of species as indicators of salinity patterns within the bay ecosystem.

INTRODUCTION

The San Francisco Bay system has been studied by many investigators since 1816, when the Russian ship *Rurik* anchored in the bay (Hedgepeth 1979). The bay estuarine system extends from the mouth of the Guadalupe River in the south to the lower reaches of the Sacramento-San Joaquin delta near the city of Pittsburg (Fig. 1) in the north. Early studies of the bay concentrated on hydrology, fisheries, and physical parameters of the system. Not until the early 1920s was a serious effort to study the bay's biota and

their interactions begun at the University of California, Berkeley (Hedgepeth 1979). The phytoplankton flora was not examined until 1939, when F. W. Whedon, using a Sedgewick-Rafter chamber, made a limited study of San Francisco Bay phytoplankton and presented a brief species list, including *Thalassiosira rotula* Meunier.

The flora of San Francisco Bay remained largely unstudied until 1958, when the Sanitary Engineering Research Laboratory (SERL) of the University of California, Berkeley, began a multidisciplinary study of the bay (Harris et al. 1961;

TABLE 1. KEY TO COLLECTION SITES, DATES OF COLLECTION, AND COLLECTORS.

| Date | Collector | Location |
|-------------------|--------------------------------|----------|
| 3 September 1980 | R. L. J. Wong | 1 |
| 16 October 1980 | R. L. J. Wong | 2 |
| 2 May 1971 | A. D. Mahood | 3 |
| 6 July 1981 | G. A. Fryxell/ A. D. Mahood | 3 |
| 6 June 1971 | A. D. Mahood | 4 |
| 20 February 1972 | C. A. McNeil | 4 |
| 6 July 1981 | A. D. Mahood | 5 |
| 24 April 1971 | A. Hauser | 6 |
| June 1972 | P. Wares | 6 |
| 1 November 1979 | L. L. Lack | 7 |
| 3 September 1980 | R. L. J. Wong | 8 |
| 13 November 1980 | R. L. J. Wong | 9 |
| 12 September 1979 | A. D. Mahood | 10 |
| 7 July 1981 | A. D. Mahood | 10 |

Storrs et al. 1966). Although the species list generated by SERL was established from raw material (i.e., not cleaned of organic material so that the siliceous parts can be clearly seen) and was thus of limited systematic value, it is one of the few comprehensive references to the San Francisco Bay diatoms available. Hasle (1978a, b) published the first careful taxonomic papers on *Thalassiosira* from the bay system. The most recent inventory of bay diatom species (Wong and Cloern 1981), though still in progress, offers a basis for future diatom floristics and phytoplankton ecology studies of the bay.

Thalassiosira Cleve, one of the dominant diatom genera in the bay's phytoplankton, has been frequently mentioned in species lists: *T. decipiens* (Grunow) Jørgensen; *T. eccentrica* (Ehrenberg) Cleve; *T. lacustris* (Grunow) Hasle (= *Coscinodiscus lacustris* Hustedt); *T. nordenskiöldii* Cleve; *T. punctigera* (Castracane) Hasle (= *T. angustii* (Gran) Makarova); and *T. rotula* Meunier. The diversity of species of the genus in the bay system is not surprising because the *Thalassiosira* probably evolved in a similar estuarine and coastal environment (Round and Sims 1981).

The species diversity of diatoms is limited by salinity variations within the bay system (pers. comm. Wong, United States Geological Survey, 1983). The use of the genus *Thalassiosira* as an indicator of marine influence in the bay system has been hindered by several conditions: the confusion with other centric genera (e.g., *Coscinodiscus*), difficulty in identification (especially in water mounts), problems connected with sample

preparation (including the need for mounting in a medium with a high refractive index for light microscopy), and widely scattered pertinent taxonomic literature.

In this paper we report on the distribution of *Thalassiosira* species in the bay and discuss morphology and its application to systematic problems within the bay.

METHODS AND MATERIALS

Samples were collected with a Kemmerer water bottle and net over a broad range of the navigable section of the San Francisco Bay estuarine system (Fig. 1). Net hauls are particularly useful in concentrating material for identification before quantitative work is attempted on water samples. Fixed samples were examined in Utermohl settling chambers using an Olympus IMT inverted microscope. Most often positive identification must be made from cleaned material, mounted in medium of high refractive index such as Hyrax (Hanna 1930). Material was cleaned using the Van der Werff (1955) hydrogen peroxide method. Strewn and arranged slides were prepared for light microscope (LM) from cleaned materials and mounted in Hyrax. Similar strewn and also arranged material (mounted by the senior author) was prepared on scanning electron microscope (SEM) stubs for examination and photography using Jeolco JSM-35, Texas A&M University Electron Microscopy Center. Texas A&M Department of Oceanography phytoplankton cultures F190, F206, F209, and F226 were isolated by T. P. Watkins from collections made about a mile north of the Golden Gate Bridge, 6 July 1981. They were maintained in the Department of Oceanography phytoplankton culture collection: F/2 medium, 30‰ salinity, 16 hours light and 8 hours dark cycle, in 16°C growth chambers. Terminology follows that of the working Party on Diatom Terminology (Anonymous 1975; Ross et al. 1979).

RESULTS AND DISCUSSION

Twenty species of *Thalassiosira* were recovered from 33 samples from San Francisco Bay: *T. anguste-lineata* (A. Schmidt) G. Fryxell and Hasle; *T. decipiens* (Grunow) Jørgensen; *T. eccentrica* (Ehrenberg) Cleve; *T. endoseriata* Hasle and G. Fryxell; *T. hendeyi* Hasle and G. Fryxell; *T. incerta* Makarova; *T. lacustris* (Grunow) Hasle; *T. lundiana* G. Fryxell; *T. minuscula*

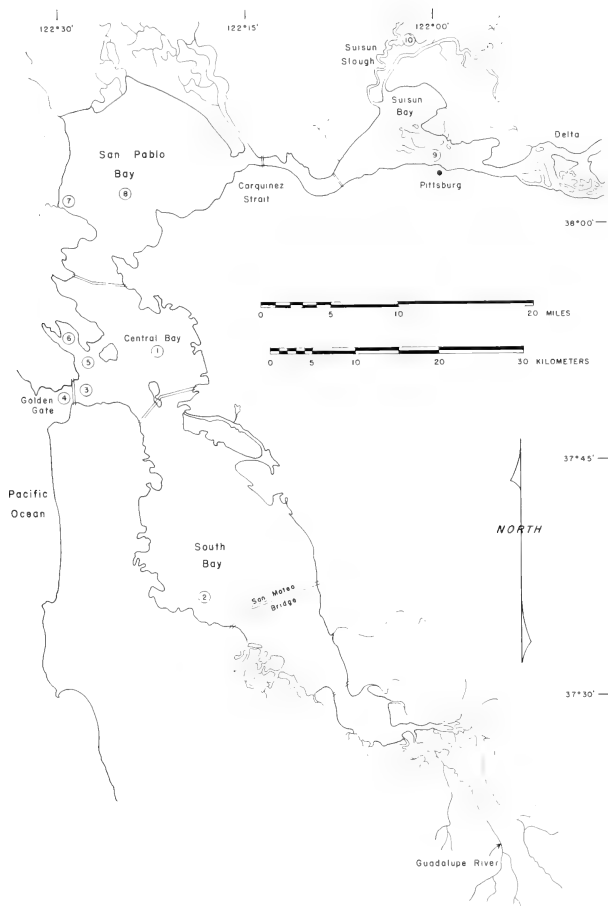


FIGURE 1. San Francisco Bay System.

Krasske; *T. nodulolineata* (Hendey) Hasle and G. Fryxell; *T. nordenskiöldii* Cleve; *T. oestrupii* var. *venrickae* G. Fryxell and Hasle; *T. pacifica* Gran and Angst; *T. punctigera* (Castracane) Hasle; *T. rotula* Meunier; *T. simonsenii* Hasle and G. Fryxell; *T. stellaris* Hasle and Guillard; *T. tenera* Proschkina-Lavrenko; *T. visurgis* Hustedt; and *T. wongii* Mahood sp. nov.

An understanding of the individual species, their similarities and differences, the habitats in which they occur, and their distributions within the bay system is essential to understanding the phytoplankton dynamics of the bay and the role of the *Thalassiosira* species in the bay ecosystem.

The genus is characterized by a number of morphological features: one to a few labiate processes (Fig. 16); many strutted processes (Fig. 11); none to many occluded processes (Fig. 38); eccentric, linear, or fasciculated patterns of the rows of areolae, in a basically radial pattern; and the placement of the areola cribrum on the internal side of the loculate areolae and the foramen on the external side (Fig. 14, 17). For this paper and to assist the light microscopist, we have stressed the characters particularly visible in LM: number and location of labiate processes; number and arrangement of the areolae; and location and number of strutted processes. Several species can be identified under LM, whereas others require SEM in order to resolve definitive characters.

Because our primary purpose includes gaining a greater understanding of San Francisco Bay, an essential goal is to distinguish between marker species with similar morphological characteristics but differing distributions, species which have been confused in earlier literature. For such comparisons, we have separated the *Thalassiosira* species in this paper into five morphological groups: 1) species with basic linear areola patterns, 2) species with eccentric areola patterns, 3) species with one central strutted process and one marginal ring of strutted processes, 4) species with no central strutted processes and modified rings of strutted processes, and 5) two otherwise dissimilar species that have radial areola patterns and multiple central strutted processes. These are form groupings only; they are not placed together to imply close taxonomic relationships.

GROUP 1.—*Thalassiosira* species with linear areola patterns.

Thalassiosira simonsenii Hasle and G. Fryxell, 1977

(Figures 2–5)

DETAILED DESCRIPTION. Hasle and Fryxell (1977).—Cell diameter 30–57 μm ; areolae 4–5.5 in 10 μm across the valve, 8–10 in 10 μm at mantle edge (Fig. 2, 4); one small central strutted process (Fig. 5); two rows of alternating strutted processes on margin, five to six in 10 μm (Fig. 3); two opposing labiate processes (Fig. 2); distinctive marginal ribs, eight in 10 μm ; large tubular occluded processes, one in 10 μm on margin above strutted processes (Fig. 4). Marginal ribs distinctive in SEM, but not always clear in LM.

DISTRIBUTION.—Marine, found only in central San Francisco Bay in association with other marine diatoms. Observed previously at 28°00'N, 112°17.5'W, Pacific (Hasle and Fryxell 1977).

Thalassiosira hendeyi Hasle and G. Fryxell, 1977

(Figures 6–11, 86)

DETAILED DESCRIPTION. Hasle and Fryxell (1977).—Cell diameter 38–120 μm ; areolae, regularly linear, five to six 10 μm ; prominent central strutted process (Fig. 6, 8) set to one side of central areola; two closely adjacent rings of marginal strutted processes (Fig. 9) alternating in orientation (Fig. 11, internal view), not easily resolved with LM (Fig. 86); wavy mantle ridge (Fig. 9, 86); two labiate processes (Fig. 6, external [arrow]; Fig. 10, internal); labiate process with two adjacent strutted processes (Fig. 7); valve slightly concentrically undulated (Fig. 6).

DISTRIBUTION.—Common but never abundant from San Pablo Bay to south San Francisco Bay. Previously found in warm coastal waters of West Africa (Hasle and Fryxell 1977), Uruguay and Brazil (Muller-Melchers 1953).

Thalassiosira nodulolineata (Hendey) Hasle and G. Fryxell, 1977

(Figures 12–17, 87, 90)

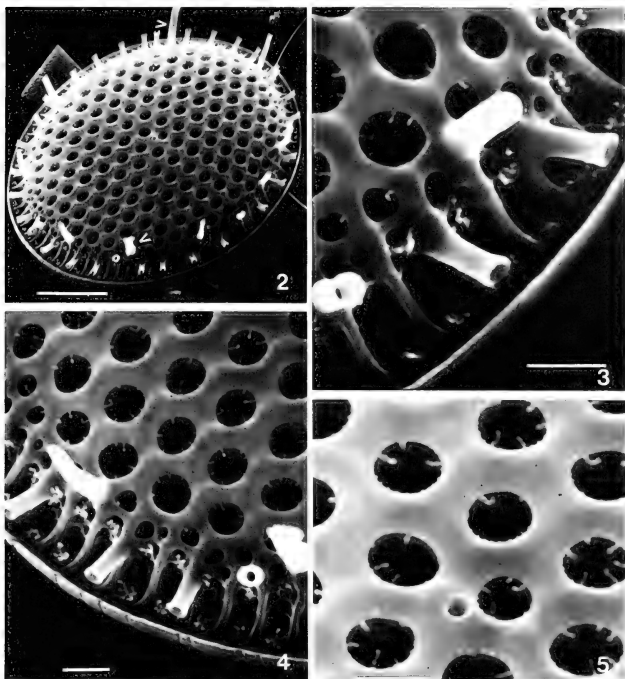
DETAILED DESCRIPTION. Hasle and Fryxell (1977).—Cell diameter 26–58 μm ; areolae linear, regular, 3.5 (one with 9.0) in 10 μm (Fig. 12); four strutted processes in 10 μm with spines (Fig. 12, 15) along the margin; five to six strutted processes inside the central areola (Fig. 14, external; Fig. 17, internal; Fig. 90); single labiate process at valve margin (Fig. 12, 16). In our samples, central areolae surrounded by six symmetrical areolae (Fig. 90), although central areolae surrounded by five areolae have been reported (Hasle and Fryxell 1977).

DISTRIBUTION.—Central San Francisco Bay, San Pablo Bay, and Suisun Slough; common but never in large numbers.

Thalassiosira tenera Proschkina-Lavrenko, 1961

(Figures 18–23, 103–104)

DETAILED DESCRIPTION. Hasle and Fryxell (1977).—Cell diameter 10–29 μm ; areolae 9–16 in 10 μm ; marginal strutted



FIGURES 2-5. *Thalassiosira simonsenii* Hasle and G. Fryxell. SEM. Figure 2. Scale = 5 μ m, external view of valve, two labiate processes across valve from each other (arrow). Figure 3. Scale = 2 μ m, two rows of alternating strutt processes on margin. Figure 4. Scale = 1 μ m, large tubular occluded process on margin above strutt processes. Figure 5. Scale = 1 μ m, view of central strutt process.

processes three to five in 10 μ m, one central strutt process (Fig. 18-20, 23); one labiate process (Fig. 20, 22, arrow); arrangement of areolae linear (Fig. 23, 103, 104) or fasciculated; marginal strutt processes often with siliceous overgrowths and flattened (Fig. 18, 21, 23).

DISTRIBUTION.—Restricted to coastal waters (Hasle and Fryxell 1977). Material examined from San Francisco Bay entirely prepared from

cultures from samples taken just north of the Golden Gate (6 July 1981).

DISCUSSION.—*T. hendeyi*, *T. simonsenii*, and *T. nodulolineata* have been confused in bay studies and erroneously reported as *Coscinodiscus lineatus* Ehrenberg (= *T. leptopus* [Grunow] Hasle and G. Fryxell). In our samples, *T. nodulolineata* specimens were most easily distinguished

from the other two by having a single labiate process and six symmetrical areolae surrounding the central areola (Fig. 14, 17). The five to six strutted processes inside the central areola further confirm the identification. Although *T. tenera* and *T. incerta* Makarova (to be discussed in Group 5) have a similar appearance to *T. nodulolineata*, the coarser areolae of *T. nodulolineata* distinguish it from the two with finer areolae. In addition, the marginal strutted processes of *T. tenera* often are in heavily silicified areas of the margin and are markedly distinct in LM, in contrast to other species.

Distinguishing specimens of *T. hendeyi* and *T. simonsenii* is extremely difficult under LM. Examination of SEM micrographs of the margin of *T. hendeyi* (Fig. 6) and the central area (Fig. 8) will assist the light microscopist in differentiating these two species. Both species have two labiate processes and similar central areas. For identification under the LM (Fig. 86), careful examination of the margin is necessary. Under the SEM (Fig. 6, 9), the margin of *T. hendeyi* is irregular and wavy, but with the light microscope a clean break can be noticed when focusing from the margin to the valve face. The valve face forms a rather sharp angle with the margin in *T. hendeyi*, while in *T. simonsenii* (Fig. 4) the transition from valve face to margin is smooth. Although the marginal strutted processes of *T. simonsenii* are more prominent than those of *T. hendeyi*, this characteristic is not easily resolved under LM.

In our samples the salinity ranges for *T. hendeyi* and *T. nodulolineata* overlap, and both are found from south San Francisco Bay to Suisun Bay, indicating a more brackish environment. *Thalassiosira simonsenii*, much less common than the others, was confined to the central San Francisco Bay and was associated with other marine diatoms. *Thalassiosira tenera* was collected near the Golden Gate Bridge in a marine habitat. *Thalassiosira tenera* is the only one of this group with strutted processes in the middle of the central areola.

GROUP 2.—*Thalassiosira* species with eccentric areola patterns.

***Thalassiosira wongii* Mahood, sp. nov.**

(Figures 24–29, 99–101)

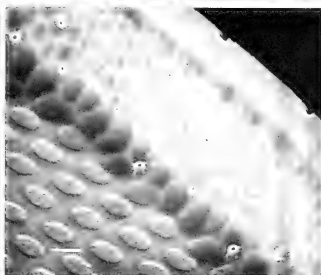
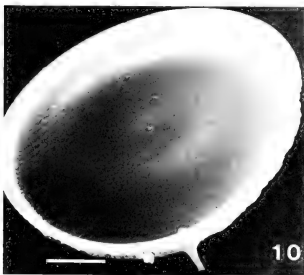
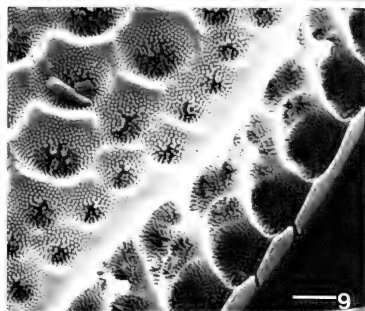
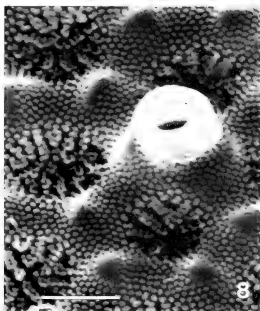
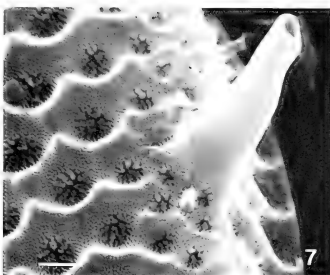
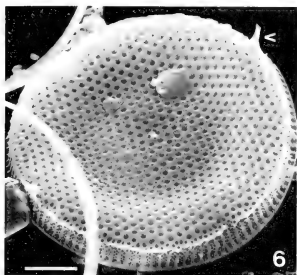
DETAILED DESCRIPTION. Mahood.—Diameter 27–51 μm ; areolae radial, fasciculated, 9–11 in 10 μm with areolar rows parallel to central areolar row of fascicle; strutted processes at margin three to five in 10 μm (Fig. 24–26, 29, 99–101); four to five strutted processes observed around central areola (Fig. 25, 26); strutted processes usually forming two irregular rings between central areola and margin (Fig. 26, 99, 100); one marginal ring of strutted processes near margin, four to five in 10 μm (Fig. 29); one labiate process set slightly inside marginal ring (Fig. 27, internal and external, Fig. 28, 99, 100); three spines in 10 μm around margin in same ring as labiate process (Fig. 24); small spines often above each strutted process on outside of valve (Fig. 27, internal and external; Fig. 29).

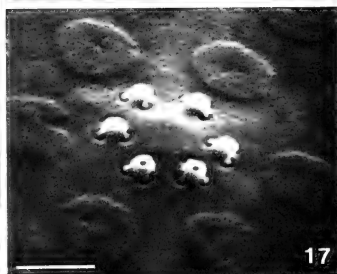
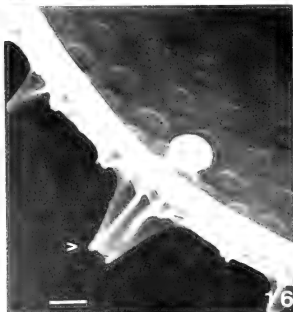
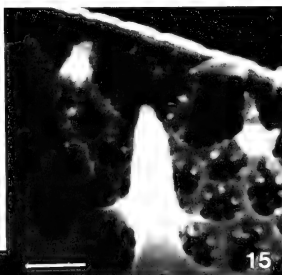
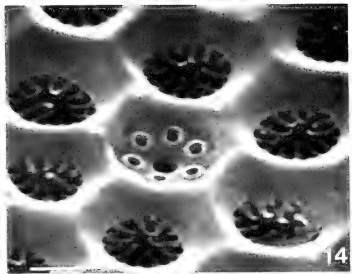
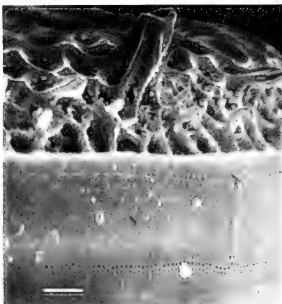
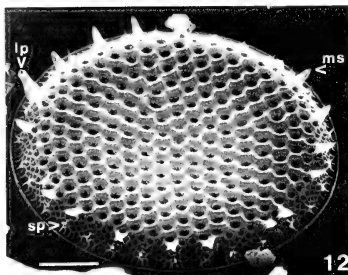
Diameter 27–51 μm ; areolae 9–11 in 10 μm ; fulcortortulae ad marginem, 3–5 in 10 μm ; 4–5 fulcortortulae circum areolam centralem visae; fulcortortulae plus minusve annulus duos irregulares formantes inter areolam centralem et marginem; annulus marginalis unicus fulcortortularum prope marginem 4–5

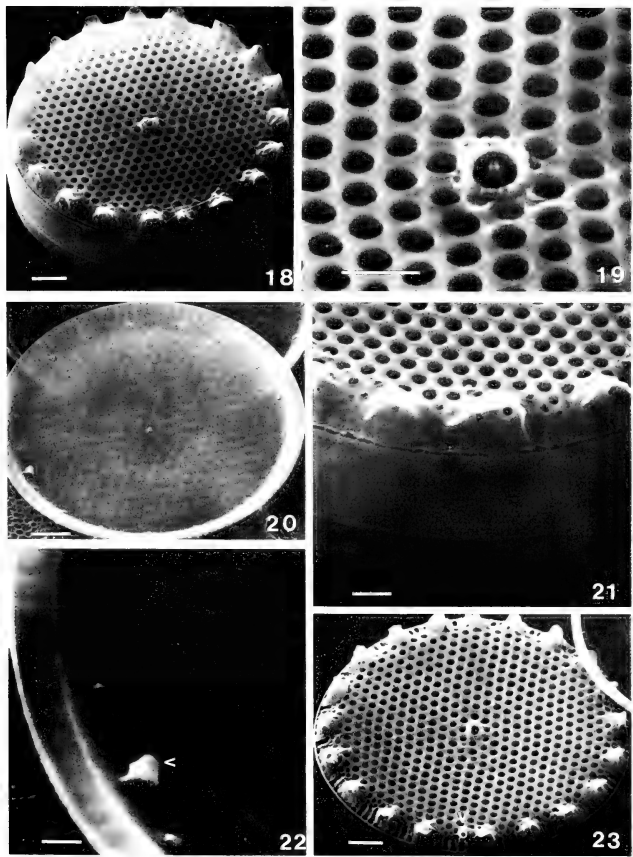
FIGURES 6–11. *Thalassiosira hendeyi* Hasle and G. Fryxell. SEM. Figure 6. Scale = 10 μm ; external view of valve; two labiate processes (arrow), valve slightly concentrically undulated, distinctive marginal ridge, linear areolae. Figure 7. Scale = 1 μm , labiate process with two adjacent processes. Figure 8. Scale = 1 μm , prominent central process. Figure 9. Scale = 1 μm , wavy marginal ridge, two closely adjacent rows of strutted processes. Figure 10. Scale = 10 μm , internal view of valve, alternating marginal strutted processes. Figure 11. Scale = 1 μm , internal view of valve, alternating marginal strutted processes.

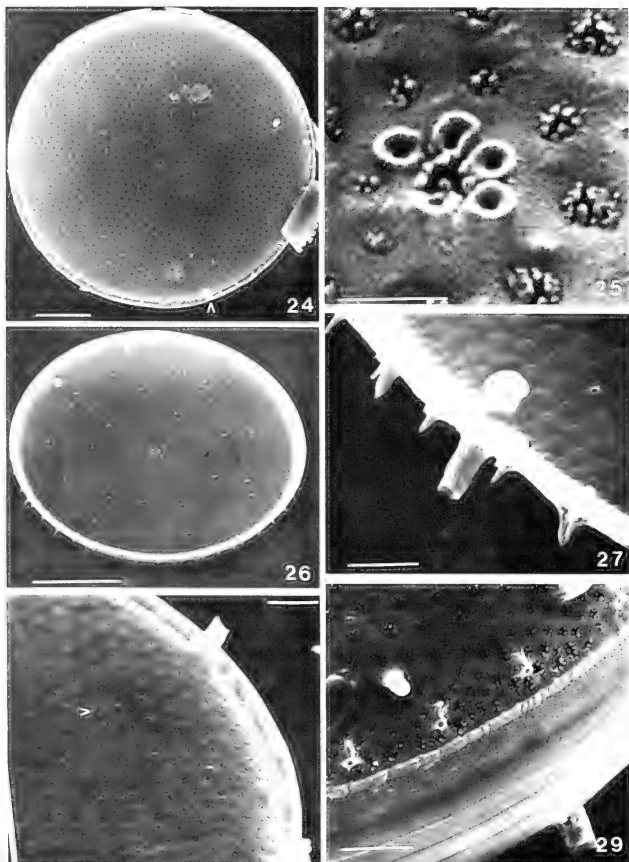
FIGURES 12–17. *Thalassiosira nodulolineata* (Hendey) Hasle and G. Fryxell. SEM. Figure 12. Scale = 5 μm ; external view of valve; linear areolae, marginal strutted processes (sp), marginal spines (ms), single labiate process (lp). Figure 13. Scale = 1 μm , single labiate process, bands. Figure 14. Scale = 1 μm ; strutted processes in the central areola, six symmetrical areolae surrounding central areola with radial threads. Figure 15. Scale = 0.5 μm , external marginal spine, strutted processes. Figure 16. Scale = 1 μm , internal view of valve, internal labia with external labiate process (arrow). Figure 17. Scale = 1 μm , internal view of central strutted processes.

FIGURES 18–23. *Thalassiosira tenera* Proschkina-Lavrenko. SEM. Figure 18. Scale = 2 μm ; external view of valve; marginal strutted processes, one central strutted process. Figure 19. Scale = 1 μm , distinctive central strutted process. Figure 20. Scale = 2 μm , internal view of valve, one central strutted process. Figure 21. Scale = 1 μm , external view of marginal strutted process with siliceous overgrowths. Figure 22. Scale = 0.5 μm , internal view of labia (arrow). Figure 23. Scale = 2 μm ; external view of valve; single external labiate process (arrow), marginal strutted processes with siliceous overgrowths.









FIGURES 24–29. *Thalassostira wongii* Mahood, sp. nov. SEM. Figure 24. Scale = 10 μ m; external view of valve; fasciculated areolae, small marginal spines, single labiate process (arrow). Figure 25. Scale = 1 μ m; external view of irregularly arranged processes surrounding the central areola. Figure 26. Scale = 10 μ m; internal view of valve; single labia, two irregular rings of strutted processes, marginal ring of strutted processes. Figure 27. Scale = 2 μ m; internal view of labia and external labiate

in 10 μm ; rimoportula unica annuli marginalis parum penitus posita, spinis 3 in 10 μm circum marginem in eodem annulo cum rimoportula; spinae parvae saepe supra fuloportulam omnem extus valvarum.

DISTRIBUTION.—South and central San Francisco Bay, associated with marine diatoms.

HOLOTYPE.—Slide, deposited at California Academy of Sciences, CAS 61243.

Thalassiosira oestrupii var. *venrickae*

G. Fryxell and Hasle, 1980

(Not figured)

DETAILED DESCRIPTION. Fryxell and Hasle (1980).—Cell diameter 5.5–39 μm ; areolae 6–9 in 10 μm in central area, 7–11 in 10 μm toward margin; one labiate process, usually located three areolae from center; one central strutted process, one to two in 10 μm , on margin. May be confused with *T. decipiens*, but marginal strutted processes internal rather than external. Dominant characteristics: labiate process away from margin and marginal strutted processes with internal projection seen in same plane of focus (Fryxell and Hasle 1980, fig. 15A, B, 17).

DISTRIBUTION.—Coastal, temperate waters. Central San Francisco Bay, rare.

Thalassiosira eccentrica (Ehrenberg) Cleve, 1904 (Figures 30–35, 102)

DETAILED DESCRIPTION. Fryxell and Hasle (1972).—Cell diameter 12–101; areolae 5–8 in 10 μm in central area, 7–10 in 10 μm toward margin (Fig. 102); scattered strutted processes across valve face (Fig. 32); irregular spines around margin, three to four in 10 μm ; central areola surrounded by seven areolae with single strutted process next to the central areola (Fig. 30, 33); two to three rings of strutted processes in 10 μm near margin (Fig. 31; Hasle 1979); one prominent labiate process (Fig. 34, internal; Fig. 35). Valve face relatively flat.

DISTRIBUTION.—Possibly brackish to definitely saline waters, common in central San Francisco Bay.

DISCUSSION.—The confusion within this group stems in part from the areola patterns of *T. eccentrica* (Fryxell and Hasle 1972), which varies from the classic eccentric pattern to a fasciculated arrangement. For example Cupp (1943), a primary reference source for Bay studies, does not clearly distinguish *T. decipiens* (to be discussed in Group 3) and *T. eccentrica* (= *Coscinodiscus eccentricus*). The overall eccentric pattern is representative of three species in this group.

Other morphological characteristics may be used to facilitate identification. *Thalassiosira oestrupii* var. *venrickae* lacks external labiate process tubes. Only *T. wongii* has multiple central processes, fasciculated valves, and spines above each strutted process. A single row of marginal strutted processes further distinguishes *T. wongii* from *T. eccentrica*. The spines above each strutted process of *T. wongii* are only seen under SEM.

GROUP 3.—*Thalassiosira* species with one central and one marginal ring of strutted processes and one labiate process near the margin.

Thalassiosira minuscula Krasske, 1941

(Figures 36, 37)

DETAILED DESCRIPTION. Hasle (1976).—Cell diameter 10–20 μm ; areolae small, 30 in 10 μm in rows parallel to radial row; one large radially oriented labiate process located in from margin (Fig. 36); strutted processes in ring on margin four to five in 10 μm near margin, one strutted process in center (Fig. 36), plus one adjacent to labiate process (Fig. 37). Distinguished from other fasciculated species of *Thalassiosira* in San Francisco Bay by the unique arrangement of a strutted process adjacent to the labiate process and by the finer areolae.

DISTRIBUTION.—Originally described from coastal plankton of Chile (Krasske 1941). Central San Francisco Bay, rare.

Thalassiosira lundiana G. Fryxell, 1975a

(Figures 36–41, 89)

DETAILED DESCRIPTION. Fryxell (1975a).—Cell diameter 7–43 μm ; areolae 24–30 in 10 μm , fasciculated; marginal striae; strutted processes in ring inside margin (Fig. 38), approximately 10 in 10 μm ; often irregularly arranged large occluded processes in ring farther from margin (Fig. 38, 39); one central strutted process (Fig. 40, arrow; Fig. 41, csp); one labiate process inside marginal ring (Fig. 41, arrow) in same ring as occluded processes; weakly silicified.

DISTRIBUTION.—Inshore euryhaline (Fryxell 1975a); found in our samples from central San Francisco Bay to Suisun Bay, indicating a broader freshwater range than previously proposed.

Thalassiosira punctigera (Castracane) Hasle, 1983 (= *T. angustii* (Gran) Makarova)

(Figures 42–48, 92)

DETAILED DESCRIPTION. Gran and Angst (1931), G. Fryxell (1978).—Cell diameter 43–145 μm ; areolae across valve face

← process, small spines above marginal strutted processes, Figure 28. Scale = 2 μm ; external view of margin at the single labiate process, valve strutted processes (arrow). Figure 29. Scale = 2 μm , marginal strutted processes with short spines, large spines back from edge of margin.

15 in 10 μ m; areolae fasciculated with areolae arranged parallel to center of fascicle (Fig. 45); strutted processes four to five in 10 μ m along margin (Fig. 44, 46, 92); single central process (Fig. 43, arrow); one labiate process (Fig. 46; Fig. 47, internal); large occluded processes irregularly arranged around margin (Fig. 42), although some specimens lack large occluded processes entirely (Fig. 48).

DISTRIBUTION.—Coastal, large population of *T. punctigera* reported in Richardson Bay (A. Hauser, pers. comm., 1976), which is constantly flushed by waters from the Golden Gate.

Thalassiosira nordenskiöldii Cleve, 1873

(Figure 106)

DETAILED DESCRIPTION. Hasle (1978b).—Cell diameter 10–50 μ m; areolae 14–18 in 10 μ m across valve face; marginal strutted processes three in 10 μ m; separated from margin by ca. 6–8 areolae. Single strutted process in center of valve (Fig. 106); one labiate process in same ring as marginal strutted processes but not in a constant position relative to a strutted process; marginal striae 18–20 in 10 μ m in mantle rim.

DISTRIBUTION.—Marine, cold water (Hasle 1978b); only in samples near the Golden Gate Bridge.

Thalassiosira pacific Gran and Angst, 1931

(Figures 49–55, 105)

DETAILED DESCRIPTION. Hasle (1978b).—Cell diameter 7–46 μ m; areolae 10–18 in 10 μ m in central area, 20 in 10 μ m at margin (Fig. 49); one labiate process (Fig. 54); pronounced, regular marginal strutted processes, four to seven in 10 μ m (Fig. 52); single central strutted process (Fig. 51, internal; Fig.

53, external; Fig. 105) adjacent to central areolae. Areolae usually in fasciculated rows with areolae parallel to radius.

DISTRIBUTION.—Marine, from central San Francisco Bay through Golden Gate to Gulf of Farallons.

Thalassiosira visurgis Hustedt, 1957

(Figures 56–61, 95, 96)

DETAILED DESCRIPTION. Hasle (1978a).—Cell diameter 9–18 μ m; areolae in central area 13–14 in 10 μ m, 18 in 10 μ m at the margin (Fig. 58); one central strutted process (Fig. 58, external; Fig. 60, internal [arrow]), and four to five strutted processes in 10 μ m in ring near margin (Fig. 56, external; Fig. 57); two labiate processes on opposing sides, each found between marginal strutted processes and slightly inside the ring of strutted processes (Fig. 56, 58–60, 95, 96). In our preparation, valves often convex or concave, suggesting heterovalvate cells with one convex and one concave valve. Granules on valve often extending onto processes (Fig. 57).

DISTRIBUTION.—Usually found surrounded with silt and clay, fresh to brackish water. *Thalassiosira visurgis* occasionally the dominant *Thalassiosira* in Suisun Slough, a brackish environment.

Thalassiosira decipiens (Grunow) Jørg., 1905

(Figures 62–67, 97, 98)

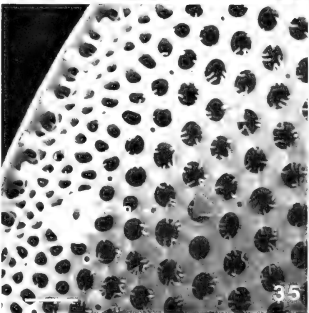
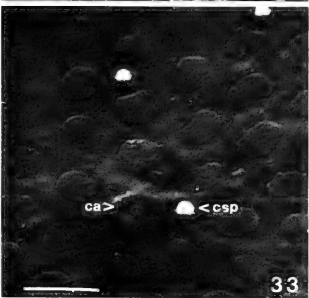
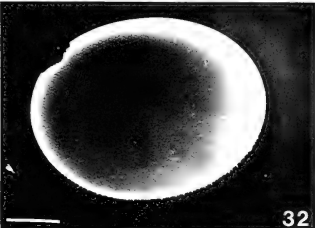
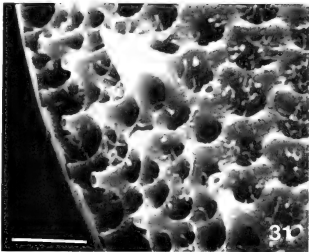
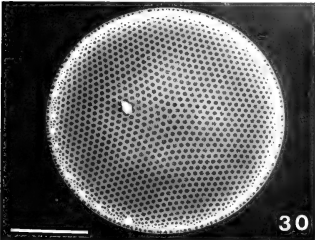
DETAILED DESCRIPTION. Hasle (1979).—Cell diameter 9–29 μ m; areolae across valve face 8–12 in 10 μ m, much smaller on mantle (Fig. 62); single ring of marginal strutted processes four to six in 10 μ m (Fig. 62, 64); one central strutted process (Fig. 63, arrow); labiate process located between two marginal strutted processes (Fig. 62, arrow; Fig. 97, arrow; Fig. 98), closer

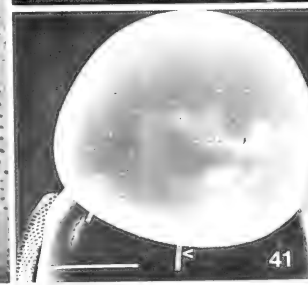
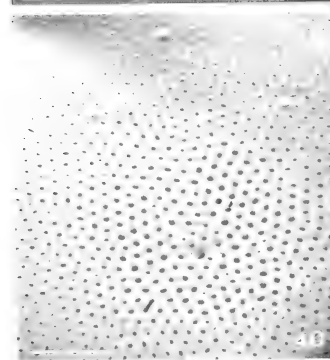
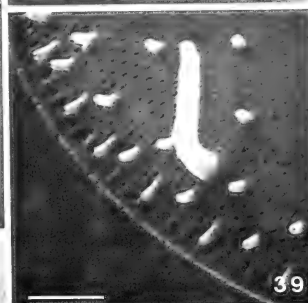
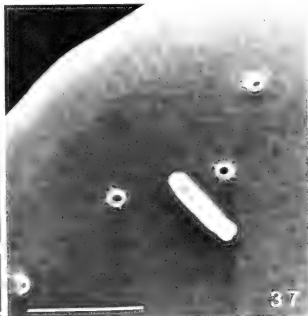
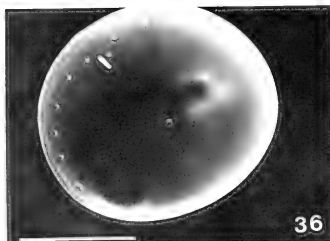
FIGURES 30–35. *Thalassiosira eccentrica* (Ehrenb.) Cleve. SEM. Figure 30. Scale = 20 μ m; external view of valve; eccentric areolar pattern, irregular spines. Figure 31. Scale = 2 μ m, large marginal spines, two rings of marginal strutted processes. Figure 32. Scale = 20 μ m, internal view of valve, scattered processes across valve. Figure 33. Scale = 3 μ m; internal view of central area, seven areolae with cribrum surrounding central areola (ca), central strutted process (csp) just off center. Figure 34. Scale = 2 μ m, internal view of labia, scattered strutted processes. Figure 35. Scale = 3 μ m; external view of valve; single labiate process (lp), scattered strutted processes, marginal strutted processes.

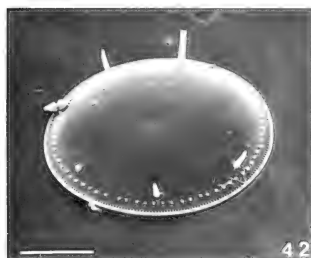
FIGURES 36, 37. *Thalassiosira minuscula* Krasske. SEM. Figure 36. Scale = 10 μ m; internal view of valve, single labia set back from margin, single row of marginal strutted processes, central strutted process. Figure 37. Scale = 2 μ m; same valve, internal view of marginal strutted processes, labia set back from margin.

FIGURES 38–41. *Thalassiosira lundiana* G. Fryxell. SEM. Figure 38. Scale = 10 μ m; external view of valve; irregular strutted processes ring valve, irregular occluded processes (arrow). Figure 39. Scale = 2 μ m; large occluded process, marginal strutted processes. Figure 40. Scale = 2 μ m; external view of central area (arrow), fasciculation. Figure 41. Scale = 10 μ m; internal view of valve; scattered valve strutted processes, single labiate process (arrow), single central strutted process (csp).

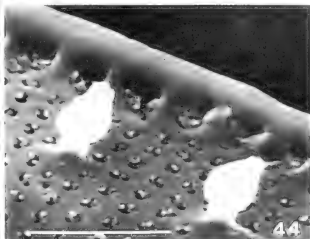
FIGURES 42–48. *Thalassiosira punctigera* (Castracane) Hasle. SEM. Figure 42. Scale = 20 μ m; external view of valve; marginal strutted processes, irregular large occluded processes. Figure 43. Scale = 2 μ m, single strutted process in central area. Figure 44. Scale = 2 μ m, marginal strutted processes. Figure 45. Scale = 20 μ m, internal view of fasciculated areolae, marginal strutted processes. Figure 46. Scale = 2 μ m, external view of labiate process, marginal strutted processes. Figure 47. Scale = 2 μ m, internal view of labia and external labiate process. Figure 48. Scale = 20 μ m, external view of valve lacking occluded processes.



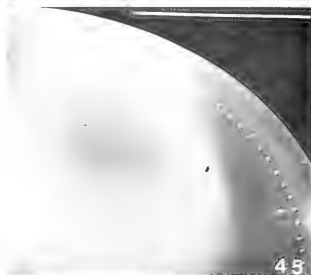




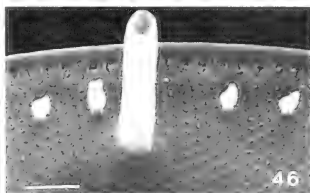
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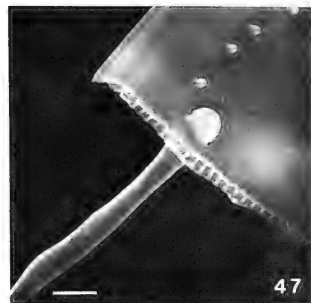
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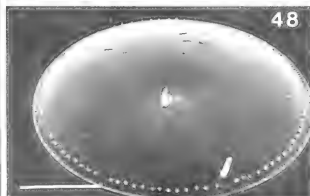
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to one than the other. Often found coated with sediment (Fig. 67).

DISTRIBUTION.—San Joaquin estuary, a brackish environment (Hasle 1979). Dominant *Thalassiosira* in the Suisun Bay area (Arthur and Ball 1980; Wong and Cloern 1981).

DISCUSSION.—Confusion of the species *T. punctigera* and *T. lundiana* may lead to misinterpretation of environmental conditions. *Thalassiosira punctigera* is the larger of the two species, although there is a slight overlap between the smaller diameters of *T. punctigera* and the larger diameters of *T. lundiana*. The larger diameter of *T. punctigera*, the more heavily silicified valve, and the prominent marginal strutted processes are the most important distinguishing features (Fig. 44, 46, 48, 92), with only a single strutted process in the center of the valve. *Thalassiosira lundiana* is fragile and weakly silicified making the fine areolar pattern more difficult to resolve, but strutted processes are scattered over the valve face (Fig. 89).

The differentiation of *T. decipiens* and *T. visurgis* has proven both difficult and interesting. In our samples these species commonly appear in large numbers in Suisun Slough, Suisun Bay, and the delta of the Sacramento and San Joaquin rivers. The presence of the two labiate processes clearly distinguishes *T. visurgis* (Fig. 56, 60, 95, 96) from *T. decipiens*. Confusion of the species is possible if one process is obscured by detritus (Fig. 67). The best distinguishing character in

both cleaned and uncleaned specimens is the arrangement of the areolae. In *T. decipiens* the number of areolae in 10 μm is constant across the valve face (Fig. 97, 98). On these small valves, the cell diameter, number of areolae, and the presence of the second labiate process may not be clear enough under the light microscope to differentiate the two species. A peculiar characteristic of *T. visurgis* is seen as the light microscope focuses through the valve: the central area areolae display a winking effect, optically separating the central area from the margin (Fig. 95, 96). Unless the material is cleaned and mounted in Hyrax or other suitable medium, however, we cannot differentiate these two species.

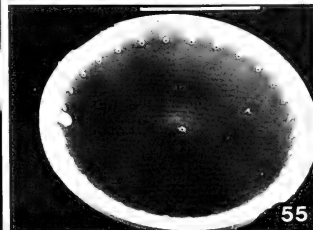
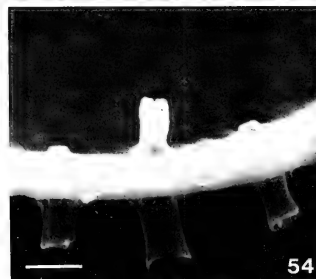
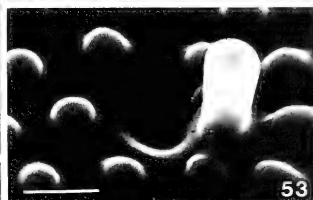
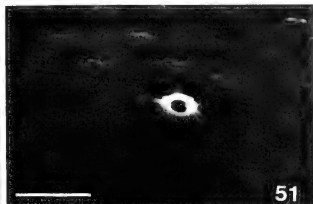
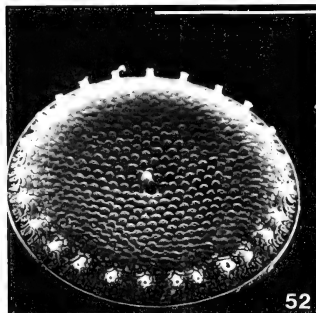
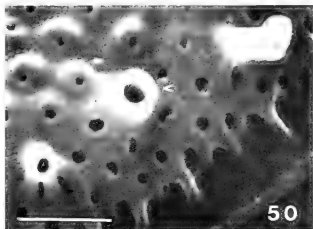
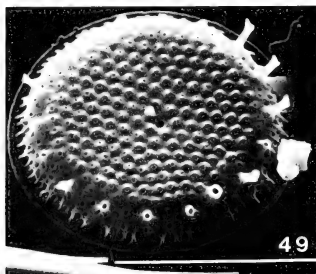
The overall eccentric pattern, overlap of cell diameter, and overlap of number of areolae in 10 μm make it difficult to differentiate *T. eccentrica* and *T. decipiens* in the 30 μm diameter range without reference to more recent works. Distinctive characteristics that aid their differentiation include pronounced, regular strutted processes seen on *T. decipiens* versus the irregular spines of *T. eccentrica* and the concave or convex valves of *T. decipiens* versus the relatively flat valve of *T. eccentrica*. *Thalassiosira eccentrica* is a coastal marine species, while viable *T. decipiens* cells in the bay system are usually restricted to the Suisun Bay-Delta, a brackish environment; non-viable cells may be flushed from Suisun Bay by tidal action.

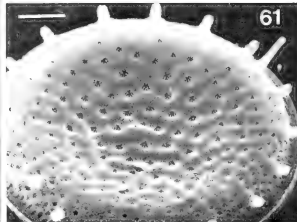
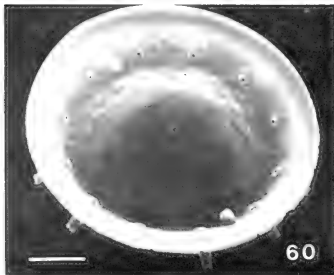
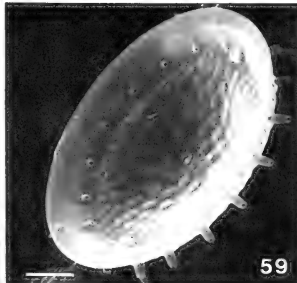
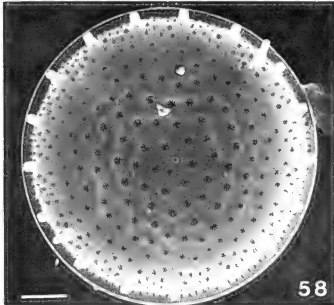
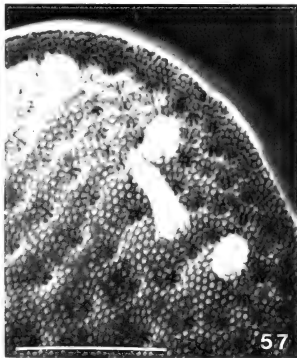
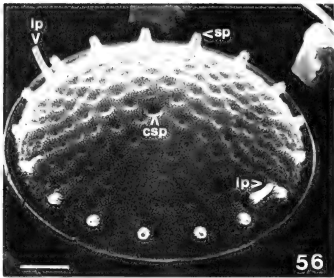
It is possible that *T. eccentrica* reported in eco-

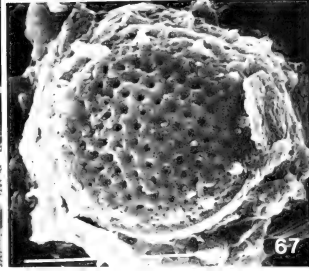
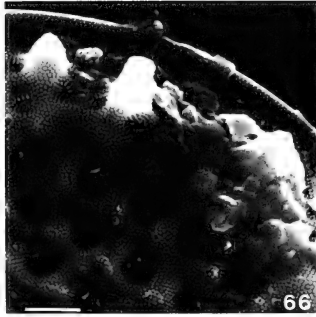
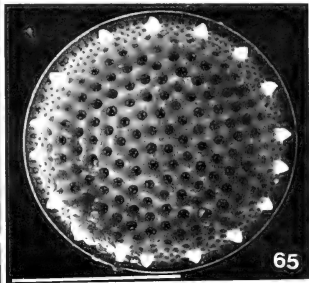
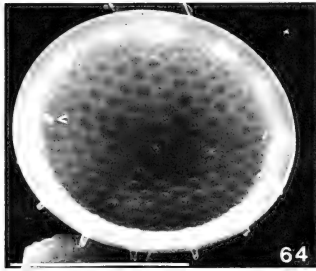
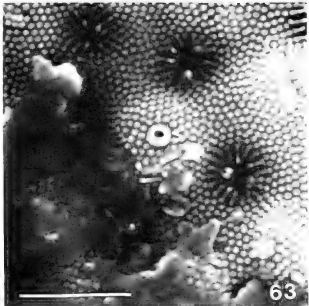
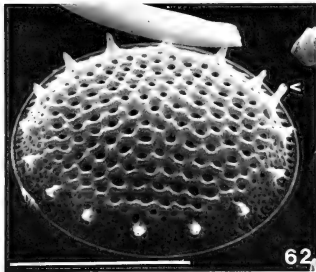
FIGURES 49–55. *Thalassiosira pacifica* Gran and Angst. SEM. Figure 49. Scale = 10 μm ; external view of valve; fasciculated areolae, single central strutted process, marginal strutted processes. Figure 50. Scale = 2 μm , single labiate process (arrow) on margin between strutted processes. Figure 51. Scale = 1 μm , internal view of single strutted process. Figure 52. Scale = 10 μm , regular marginal strutted processes. Figure 53. Scale = 1 μm , external details of central strutted process. Figure 54. Scale = 1 μm , internal view of labia and external labiate process. Figure 55. Scale = 10 μm ; internal view of valve; regular marginal strutted processes, single central strutted process, internal labia.

FIGURES 56–61. *Thalassiosira visurgis* Hustedt. SEM. Figure 56. Scale = 2 μm ; external view of valve; strutted processes (sp) at margin, two labiate processes (lp), single central strutted process (csp). Figure 57. Scale = 2 μm , labiate process between two strutted processes on margin. Figure 58. Scale = 2 μm , central areolae distinct from those toward margin. Figure 59. Scale = 2 μm , internal view of convex valve, regular marginal strutted processes. Figure 60. Scale = 2 μm , internal view of concave valve, two opposing labia. Figure 61. Scale = 2 μm , external view of concave valve.

FIGURES 62–67. *Thalassiosira decipiens* (Grunow) Jørgensen. SEM. Figure 62. Scale = 10 μm ; external view of valve; single labiate process (arrow), regular marginal strutted processes. Figure 63. Scale = 1 μm ; single central process (arrow), fine siliceous granulations on external side of valve. Figure 64. Scale = 10 μm ; internal view of valve; single labia (arrow), regular marginal strutted processes. Figure 65. Scale = 10 μm ; external view of valve; consistent areola pattern across valve, regular arrangement of marginal strutted processes. Figure 66. Scale = 1 μm , labiate process between two strutted processes. Figure 67. Scale = 10 μm , detritus accumulation surrounding cell.







logical studies of San Francisco Bay (Arthur and Ball 1980) is in reality a complex of *T. decipiens* and *T. visurgis*, two species usually found in the entrainment zone in Suisun Bay. Freshwater from the Sacramento and San Joaquin rivers flows westward to meet the tidal wedge moving eastward in Suisun Bay. This mixing area produces vertical and horizontal circulation that tends to concentrate populations of phytoplankton (Arthur and Ball 1980). The average salinity is low (0.1–5‰, Arthur and Ball 1980; Sitts and Knight 1979) and well within the range established for *T. decipiens*, *T. visurgis*, and *T. incerta*.

GROUP 4.—*Thalassiosira* species with no central strutted process but a modified ring of processes on the face of the valve.

***Thalassiosira stellaris* Hasle and Guillard, 1977**
(Not figured)

DETAILED DESCRIPTION. Fryxell and Hasle (1977).—Cell diameter 6–20 μ m; areolae elongate, fasciculated, 30 in 10 μ m; marginal strutted processes three to five (sometimes six) in 10 μ m; a ring of two to seven strutted processes $\frac{1}{2}$ the distance between the center and the margin.

DISTRIBUTION.—Marine (Fryxell and Hasle 1977), San Francisco Bay samples described from cultures (F226) developed at Texas A&M University and maintained at ca. 30‰ salinity.

***Thalassiosira lacustris* (Grunow) Hasle and Fryxell, 1977**

(Figures 68–73, 88)

DETAILED DESCRIPTION. As *Coscinodiscus lacustris*, Husted

(1930).—Cell diameter 20–75 μ m; areolae 10–14 in 10 μ m in central area; valve face tangentially undulated (Fig. 68, 88); areolae fine (Fig. 71), arranged in dichotomous branching radiating rows (Fig. 71); five to seven strutted processes in ring ca. $\frac{1}{2}$ radius from center of valve (Fig. 68, external; Fig. 69, internal); also ring on edge of mantle (Fig. 69). Labiate process large, with slit parallel to the margin (Fig. 72). This species marked by tangentially undulated structure of the valve face (Fig. 68, 69) and areolar pattern. Other tangentially undulated centric species usually in San Francisco Bay include members of the genus *Cyclotella*.

DISTRIBUTION.—Specimens in our samples from Suisun Slough indicate a brackish preference.

***Thalassiosira endoseriata* Hasle and G. Fryxell, 1977**

(Figure 91)

DETAILED DESCRIPTION. Hasle and Fryxell (1977).—Cell diameter 20–60 μ m; areolae 11–18 in 10 μ m; one labiate process, located $\frac{1}{4}$ distance from margin to center; marginal strutted process projecting internally 5–6 in 10 μ m; central irregular ring of 4–14 strutted processes. Areolae fasciculated with rows of areolae parallel to the radius (Fig. 91).

DISTRIBUTION.—The number of specimens from samples was too small to draw positive conclusion concerning the distribution of this species, but it apparently lives at ca. 20‰ salinity.

***Thalassiosira anguste-lineata* (A. Schmidt) G. Fryxell and Hasle, 1977**

(Figures 74–79, 93)

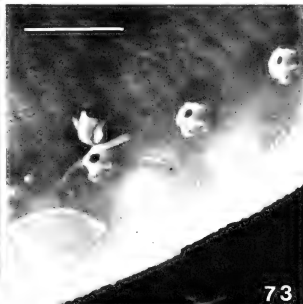
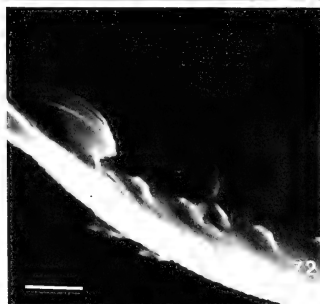
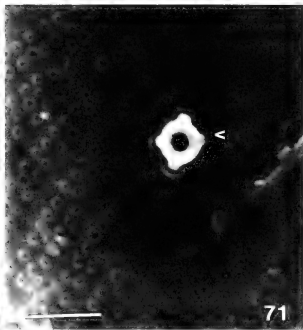
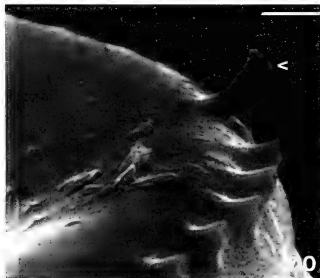
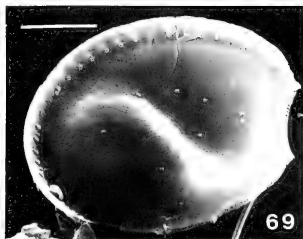
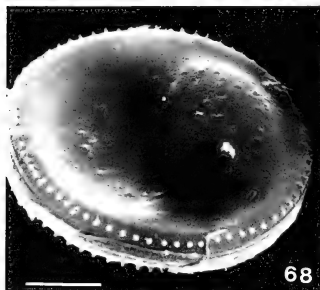
DETAILED DESCRIPTION. Fryxell and Hasle (1977).—Cell diameter 17–78 μ m; areolae fasciculated 8–18 in 10 μ m; one

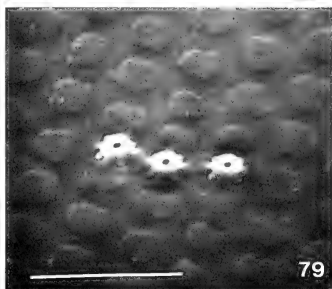
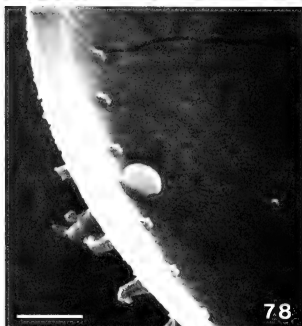
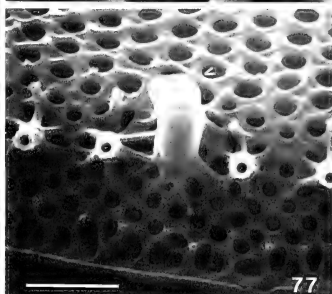
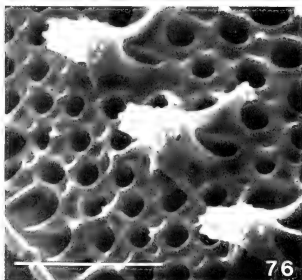
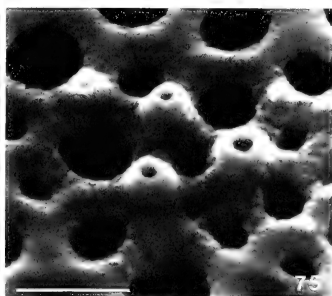
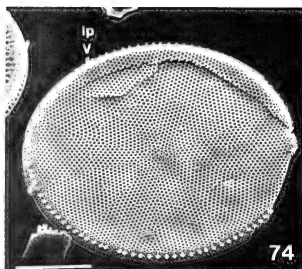
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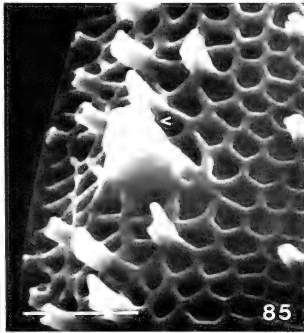
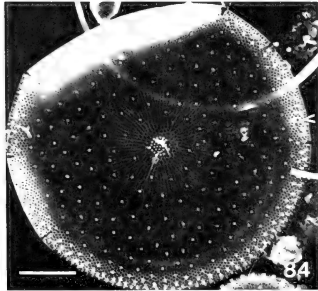
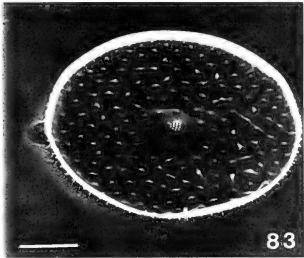
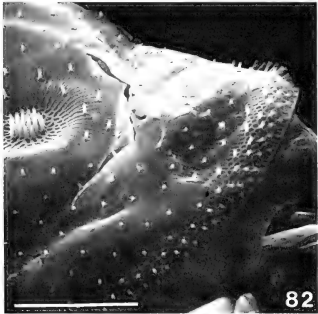
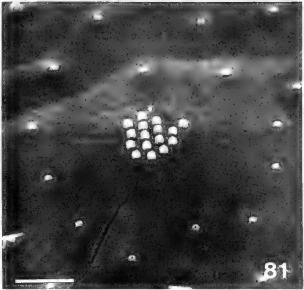
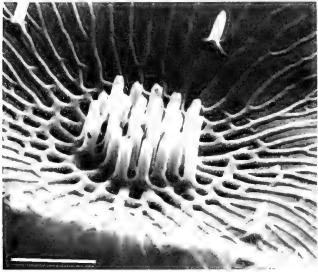
FIGURES 68–73. *Thalassiosira lacustris* (Grunow) Hasle. SEM. Figure 68. Scale = 10 μ m; external view of valve; tangentially undulated, marginal strutted processes. Figure 69. Scale = 1 μ m; internal view of valve; ring of valve strutted processes, pronounced tangential undulation. Figure 70. Scale = 1 μ m; external view of margin, labiate process (arrow) between marginal strutted processes. Figure 71 (arrow). Scale = 1 μ m; internal view of valve strutted process, areolae in dichotomous branching rows. Figure 72. Scale = 1 μ m, internal view of labia and marginal strutted process. Figure 73. Scale = 10 μ m; internal view of marginal strutted processes, dichotomous branching rows of areolae.

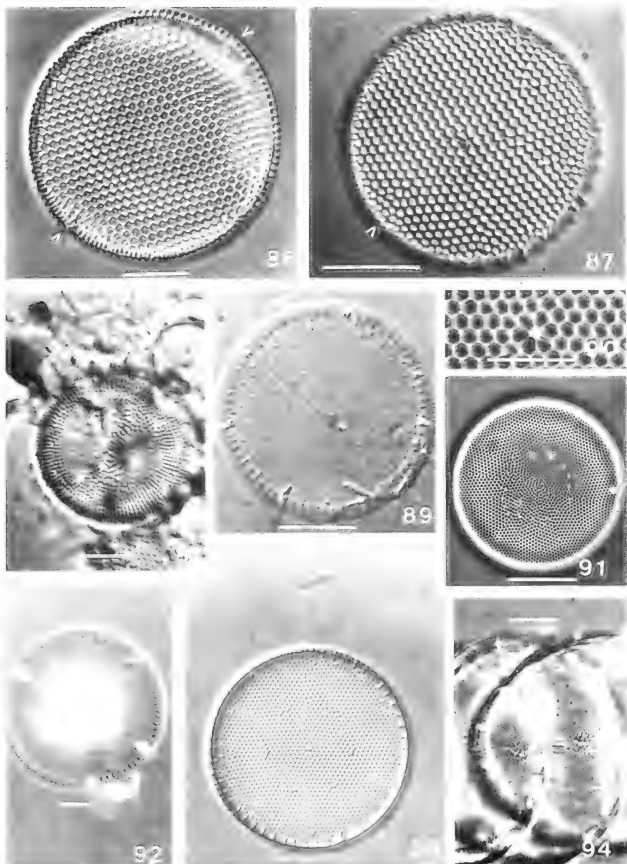
FIGURES 74–79. *Thalassiosira anguste-lineata* (A. Schmidt) G. Fryxell and Hasle. SEM. Figure 74. Scale = 20 μ m; external valve view; areolae fasciculated, regular marginal strutted processes, arc of valve strutted processes in each fascicle (arrow). Figure 75. Scale = 1 μ m, external view of valve strutted processes. Figure 76. Scale = 2 μ m, marginal strutted processes. Figure 77. Scale = 2 μ m; single labiate process (arrow) between two marginal strutted processes, small processes above each strutted process. Figure 78. Scale = 2 μ m, internal view of labia. Figure 79. Scale = 2 μ m, internal view of valve strutted processes.

FIGURES 80–85. *Thalassiosira rotula* Meunier. SEM. Figure 80. Scale = 2 μ m, external view of central area strutted processes. Figure 81. Scale = 2 μ m, internal view of central area strutted processes and scattered strutted processes on valve. Figure 82. Scale = 10 μ m; external view of center and margin; weakly silicified valve, many marginal and valve strutted processes. Figure 83. Scale = 10 μ m, internal view of valve, central and valve strutted processes. Figure 84. Scale = 10 μ m, external view of valve, single labiate process (arrow), radial arrangement of areolae. Figure 85. Scale = 2 μ m, external labiate process (arrow).









FIGURES 86-94. LM. Scale = 10 μ m. Figure 86. *Thalassiosira hendeyi* Hasle and G. Fryxell. Linear arranged areolae, two labiate processes (arrow), wavy margin. Figure 87. *T. nodulolineata* (Hendey) Hasle and G. Fryxell. Linear arranged areolae, six symmetrical areolae surrounding central area, marginal strutted processes, single labiate process (arrow). Figure 88. *T.*

labiate process (Fig. 77, arrow; Fig. 78); ring of strutted processes in small arcs (Fig. 74, 75, 79) in each fascicle located ca. $\frac{1}{2}$ the distance between the margin and the central areolae (Fig. 74). Characteristic arc-shaped grouping of strutted processes regularly arranged in each fascicle diagnostic for this species.

DISTRIBUTION.—Coastal, prefers cold to temperate waters, usually associated with other marine forms. Central San Francisco Bay to Golden Gate.

DISCUSSION.—*Thalassiosira stellaris*, a lightly silicified species, was found in culture from a sample taken north of Golden Gate Bridge. *Thalassiosira endoseriata* was found only once. As previously mentioned, *Thalassiosira lacustris* displays a tangentially undulated valve face (Fig. 68), an aid in identification. The largest concentration of viable cells of *T. lacustris* was found in the brackish waters of Suisun Slough (Mahood 1981). *Thalassiosira anguste-lineata*, with its fasciculated areolar pattern and distinguishing arrangement of strutted processes in each fascicle (Fig. 74, 79, 93) is easily distinguished from other fasciculated species seen within the Bay in cleaned material in permanent mounts. However, the strutted processes on the valve face are not always easily seen in an uncleaned sample, and lack of resolution may result in some confusion. When cells are united in chains, however, several threads can be seen to extend from one cell to the next, one from each cluster of strutted processes instead of the single central thread commonly seen in the genus.

GROUP 5.—*Thalassiosira*, otherwise dissimilar species that have radial areolae patterns and multiple central processes.

Thalassiosira rotula Meunier, 1910

(Figures 80–85, 94)

DETAILED DESCRIPTION. Fryxell (1975b); Syvertsen (1977).—Cell diameter 8–61 μm (40–61 μm , Gran and Angst 1931); areolae very fine, only clearly seen in the central area (Fig. 84); cluster of strutted processes in center (Fig. 80, external; Fig.

81, internal), with scattered processes across entire valve face (Fig. 83, 84); single labiate process (Fig. 84, arrow; Fig. 85, arrow); valve weakly silicified (Fig. 82). Usually observed in chains (Fig. 94).

DISTRIBUTION.—In our samples *T. rotula* restricted to the more saline portion of the central bay and Golden Gate with other marine forms.

Thalassiosira incerta Makarova, 1961

(Not figured)

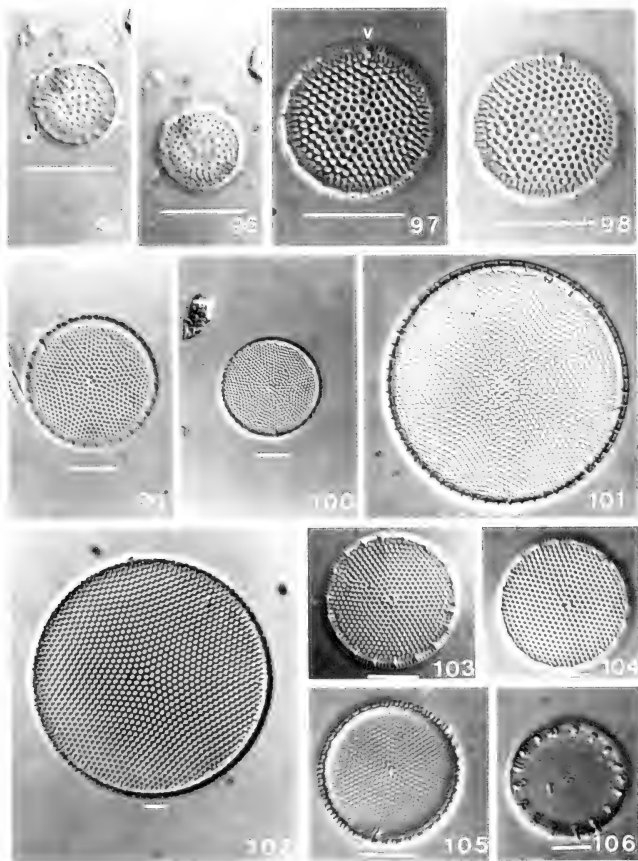
DETAILED DESCRIPTION. Hasle (1978a).—Cell diameter 13–38 μm ; areolae 8–16 in 10 μm ; three to four strutted processes in 10 μm at margin; four to six strutted processes surrounding central areolae.

DISTRIBUTION.—Fresh to brackish water, rare in our samples.

DISCUSSION.—Both brackish and marine members of this group show distinctive characteristics that clearly differentiate them from other *Thalassiosira* species of the bay. *Thalassiosira rotula*, first mentioned by Whedon (1939), is usually found in the central bay (Wong and Cloern 1981). This species has been reported from similar estuarine environments (Marshall 1980). Our experience has been to associate *T. rotula* with other coastal or marine forms. Its characteristic chain formation with coin-shaped cells connected by a thick central thread, narrow girdle bands, delicate structure, and scattered strutted processes on the valve face aid in the identification.

Thalassiosira incerta, *T. decipiens*, and *T. visurgis* are all characterized by small size, eccentric to linear areolar patterns, and an accumulation of detritus around the margin of the living cell. This group has proven to be the most difficult to differentiate by light microscopy. All three species have similar diameters and general characteristics (Table 2) and can only be differentiated after the sample has been cleaned of organic material. In cleaned material *T. incerta* possesses characteristics that distinguish it from

←
lacustris (Grunow) Hasle. Tangential undulations, radial arrangement of areolae. Figure 89. *T. hundsiana* G. Fryxell. Weakly silicified, large irregular occluded processes at margin, irregularly arranged strutted processes on valve. Figure 90. *T. nodulolineata* (Hendey) Hasle and G. Fryxell. Detail of central area, strutted processes in central areola. Figure 91. *T. endoseriata* Hasle and G. Fryxell. Fasciculated areolae, ring of strutted processes near center of valve. Figure 92. *T. punctigera* (Castracane) Hasle. Regular marginal strutted processes, weakly silicified. Figure 93. *T. anguste-lineata* (A. Schmidt) G. Fryxell and Hasle. Fasciculated, arc of strutted processes in each fascicle. Figure 94. *T. rotula* Meunier. Central strutted process, random valve strutted processes, forming chains.



FIGURES 95-106. LM. Scale = 10 μ m. Figure 95. *Thalassostira visurgis* Hustedt. Focused on center, two labiate processes (arrows), radial pattern of areolae. Figure 96. *T. visurgis* Hustedt. Same valve as Figure 95, focused on margin. Figure 97. *T. decipiens* (Grunow) Jorgensen. Focused on center, regular marginal strutted processes, one labiate process (arrow). Figure 98. *T. decipiens* (Grunow) Jorgensen. Same valve as Figure 97, focused on margin, uniform areolae across valve. Figures 99-101. *T. wongii* Mahood sp. nov. Fasciculated, two circles of strutted processes on valve, one labiate process (arrow), raised central

TABLE 2. *THALASSIOSIRA* SPECIES FROM SAN FRANCISCO BAY AREA. Measurements from the literature and our observations.

| Species | Diameter (μm) | Areolae in 10 μm | Labiate processes | Marginal strutted processes in 10 μm | Central strutted processes | Distinctive characteristics |
|--|---------------|------------------|-------------------|--------------------------------------|----------------------------|--|
| Group 1—Species with a linear areolar pattern | | | | | | |
| <i>T. hendeyi</i> | 38–120 | 5–6 | 2 | 5–6 | 1 | wavy margin |
| <i>T. nodulolineata</i> | 26–58 | 3.5–7.0(9.0) | 1 | 3–5 | 5–6 | strutted processes in central areola |
| <i>T. simonsenii</i> | 30–57 | 4.0–5.5 | 2 | 5–6 | 1 | two marginal rings of strutted processes |
| <i>T. tenera</i> | 10–29 | 9–16 | 1 | 3–5 | 1 | flattened marginal processes |
| Group 2—Species with eccentric patterns | | | | | | |
| <i>T. eccentrica</i> | 12–101 | 5–10 | 1 | irregular 10–20 | 1 | seven areolae around central areola |
| <i>T. oestrupii</i> var. <i>venrickae</i> | 5.5–39.0 | 6–9 | 1 | 1–2 | 1 | strutted processes project inward |
| <i>T. wongii</i> | 27–51 | 9–11 | 1 | 3–5 | 4–5 | fasciculated central ring of strutted processes |
| Group 3—Species with 1 central process and 1 marginal ring of strutted processes | | | | | | |
| <i>T. lundiana</i> | 7–43 | 24–30 | 1 | 5–10 | 1 | fasciculated, weakly silicified |
| <i>T. punctigera</i> | 43–145 | 15 | 1 | 4–5 | 1 | fasciculated, regular marginal strutted processes |
| <i>T. nordenskiöldii</i> | 10–50 | 14–18 | 1 | 3 | 1 | radial, marginal strutted processes back from margin |
| <i>T. pacifica</i> | 7–46 | 10–18 | 1 | 4–7 | 1 | fasciculated, raised central process |
| <i>T. minuscula</i> | 10–20 | 30 | 1 | 4–5 | | labiate process away from margin |
| <i>T. visurgis</i> | 9–18 | 13–14 | 2 | 4–5 | 1 | irregular radial pattern |
| <i>T. decipiens</i> | 9–29 | 8–12 | 1 | 4–6 | 1 | eccentric radial pattern |
| Group 4—Species with no central strutted processes but a modified ring of strutted processes | | | | | | |
| <i>T. stellaris</i> | 6–20 | 30 | 1 | 3–5 (6) | | 2–7 processes in ring, fasciculated |
| <i>T. lacustris</i> | 20–75 | 10–14 | 1 | 5–7 | | tangentially undulated |
| <i>T. endoseriata</i> | 20–60 | 11–18 | 1 | 5–6 | | 4–14 processes in ring, fasciculated |
| <i>T. anguste-lineata</i> | 17–78 | 8–18 | 1 | 3–4 | | ring of arcs on face of valve, fasciculated |
| Group 5—Dissimilar species with radial patterns | | | | | | |
| <i>T. rotula</i> | 8–61 | 20 | 1 | 4–7 | cluster | cluster of central strutted processes |
| <i>T. incerta</i> | 13–38 | 8–16 | 1 | 3–4 | 4–6 | central processes around central areola radial pattern |

T. decipiens and *T. visurgis*. The central areola of *T. incerta* is surrounded by five to six strutted processes similar to the arrangement seen in *T. nodulolineata* (Fig. 14). Unlike those in *T. nod-*

ulolineata, the central strutted processes in *T. incerta* are extremely small and are just visible under the light microscope. *Thalassiosira incerta* was rare in our collections and was only found

strutted process, pronounced and regular marginal strutted processes. Figure 102. *T. eccentrica* (Ehrenb.) Cleve. Eccentric areolar pattern, irregular marginal spines. Figures 103, 104. *T. tenera* Proschkina-Lavrenko. Linear arrangement of areolae, robust flattened marginal strutted processes, central area raised around the central areola. Figure 105. *T. pacifica* Gran and Angst. Fasciculated pronounced regular marginal strutted processes, distinctive central process. Figure 106. *T. nordenskiöldii* Cleve. Large marginal strutted processes set back from margin, raised central process.

from the Suisun Bay material. Hasle (1978a) has also reported *T. incerta* from waters of the San Joaquin delta.

CONCLUSIONS

The 20 species presented require additional study to delineate more clearly their ecological variables. Other than salinity, little is known of their habitat requirements. Of the species presented, *T. decipiens*, *T. nodulolineata*, *T. eccentrica*, *T. hendeyi*, and *T. wongii* appear to be best suited as indicators of salinity.

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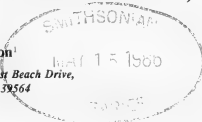
May 6, 1986

SYSTEMATIC RELATIONSHIPS AND ONTOGENY OF THE
SCULPINS *ARTEDIUS*, *CLINOCOTTUS*, AND
OLIGOCOTTUS (COTTIDAE: SCORPAENIFORMES)

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ABSTRACT: Using the methods of phylogenetic analysis proposed by Hennig (1966), characters of the larvae of 13 species of *Artedius*, *Clinocottus*, *Oligocottus* are examined in terms of synapomorphic states. Number and pattern of preopercular spines, gut diverticula, body shape, and a bubble of skin at the nape are identified as synapomorphic characters useful in systematic analysis of this group.

The synapomorphic character, multiple preopercular spines, provides strong evidence that *Clinocottus acuticeps*, *C. analis*, *C. embryum*, *C. globiceps*, *C. recalvus*, *Oligocottus maculosus*, *O. snyderi*, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* form a monophyletic group within the Cottidae. Within this group, the species of *Clinocottus* and *Oligocottus* are very closely related; each genus, however, appears to be monophyletic. Larvae of all species of *Clinocottus* possess the synapomorphy, auxiliary preopercular spines. Larval *Oligocottus maculosus* and *O. snyderi* share two derived characters, dorsal gut bumps and a bubble of skin at the nape. *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* also form a monophyletic group closely related to *Clinocottus* and *Oligocottus* on the basis of a unique multiple preopercular spine pattern.

Synapomorphic characters of the larvae provide strong evidence that *A. creaseri* and *A. meanyi* are more closely related to *Icelinus* than to species of *Clinocottus*, *Oligocottus maculosus*, *O. snyderi*, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*. Characters of the larvae strongly indicate that the genus *Artedius* as defined by Bolin (1934, 1947) is not monophyletic and that *A. creaseri* and *A. meanyi* should be placed separately from the other species of *Artedius*. Clarification of the exact position of these two species in relation to the *Artedius-Clinocottus-Oligocottus* group and other cottids must await reexamination of characters of adults.

Complete, identified, developmental series of larval cottids *Artedius fenestralis*, *A. creaseri*, *A. meanyi*, *Oligocottus snyderi*, *Clinocottus embryum*, and *C. globiceps* are described for the first time. Partial developmental series of two species, *Artedius Type 3* and *Clinocottus analis*, are also described and illustrated for the first time. In addition, four species, *Artedius harringtoni*, *A. lateralis*, *Oligocottus maculosus*, and *Clinocottus acuticeps* are redescribed providing new and comparative information on larval development.

INTRODUCTION

The Cottidae are a large, morphologically diverse family of fishes composed of nearly 67 gen-

era and 300 species (Nelson 1976). Most of these species are marine and generally distributed in coastal waters of all oceans except the Indian Ocean. Cottids are most speciose in the North Pacific where 90 species distributed in 40 genera are reported to occur between Baja, California and the Aleutian Islands, Alaska. Sixteen of these species belonging to the genera *Artedius*, *Cli-*

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cottus, and *Oligocottus* are common intertidal and subtidal inhabitants of the northeast Pacific coast (Table 1). Despite their abundance the systematic status and early life history of members of *Artedius*, *Clinocottus*, and *Oligocottus* have received little study.

The few systematic studies that have addressed these genera have yielded contradictory results. Most workers have placed members of *Artedius*, *Clinocottus*, and *Oligocottus* in the family Cottidae (Jordan and Evermann 1898; Regan 1913; Bolin 1934, 1944, 1947; Berg 1940; Taranets 1941; Howe and Richardson 1978; Jordan (1923), however, placed the genus *Artedius* in the family Icelidae. Bolin (1934, 1947), in a review of marine cottids of California, proposed that *Artedius*, *Clinocottus*, and *Oligocottus* were closely related genera that evolved from an evolutionary line of cottids tending towards a reduction of gills, pelvic fin rays, preopercular spines, and squamation. In contrast, Taranets (1941) separated members of these genera into two subfamilies. He placed *Clinocottus*, *Oligocottus*, and five species of *Artedius* in the subfamily Oligocottinae, and placed *Artedius creaseri* and *A. meanyi* in the Icelinae. Howe and Richardson (1978) suggested that *Artedius*, *Clinocottus*, and *Oligocottus* form a closely related group, *Oligocottus* and *Clinocottus* being most closely related. However, they did not discuss characters that led to their proposal.

Much of the confusion in the systematic treatment of these genera is due to the use of primitive and reductive characters in classifications, and the failure of past workers to define the genera on the basis of unique, derived characters. Characters used in past studies have not been exclusive to this group and are present in other cottid genera.

The usefulness of characters of larvae and juveniles in elucidating systematic relationships has been demonstrated in several groups (Bertelsen 1951; Moser and Ahlstrom 1970, 1972, 1974; Johnson 1974; Okiyama 1974; Kendall 1979; Richardson 1981; and Moser et al. 1984). Results of these studies have indicated that ontogenetic characters provide an independent set of characters with which to evaluate phylogenetic relationships. Characters of larvae have been particularly helpful in groups in which characters of adults have been reductive or generalized (Moser and Ahlstrom 1972, 1974).

Although larvae of most species of *Artedius*,

Clinocottus, and *Oligocottus* are frequently collected in nearshore plankton samples in the northeast Pacific, until recently larvae of few species have been described. Of the 16 nominal species, developmental series of identified larvae have only been described for *A. harringtoni*, *A. lateralis*, *C. acuticeps*, *C. recalvus*, and *O. maculosus*. Other forms that belong to this group based on larval morphology, but not identified to species, were described by Richardson and Washington (1980) as *Artedius* Type 2, Cottidae Type 1, Type 2, and Type 3. Previous descriptions of *A. lateralis* and *O. maculosus* are inadequate for specific identification. Descriptions by Richardson and Washington (1980) were based on incomplete developmental series and too few specimens for specific and/or generic identification.

The objectives of this study were: 1) to evaluate phylogenetic relationships of *Artedius*, *Clinocottus*, and *Oligocottus* within the Cottidae following the phylogenetic methodology of Hennig (1966) and 2) to describe the ontogeny of larvae and juveniles of as many species of *Artedius*, *Clinocottus*, and *Oligocottus* as possible.

METHODS AND MATERIALS

Systematic Procedures

The investigation of systematic relationships in this study follows the phylogenetic approach first put forth by Hennig (1966) and modified and debated by Brundin (1966, 1968), Cracraft (1974), Sneath and Sokal (1973), Ashlock (1974), Mayr (1974), and others.

This methodology is considered best suited to the objectives of this study because the methodology is a phylogenetic approach, and is well defined in regard to character evolution. Other approaches currently used are not as well suited to the purpose of this study. Numerical taxonomy, best described by Sneath and Sokal (1973), is a phenetic approach in which taxa are clustered by overall similarity. Evolutionary systematics described by Mayr (1969) and Simpson (1961) combines both phyletic and phenetic information; however, a well-defined, repeatable methodology has not been incorporated into this approach.

The basic tenet of Hennig's approach is that the shared possession of derived character states is the only valid criterion for establishing phylogenetic relationships. Hennig (1966) defines a

TABLE 1. SPECIES OF *ARTEDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* AND THEIR MERISTICS.¹ (Mode is indicated in parentheses.)

| | Dorsal fin spines | Dorsal fin rays | Anal fin rays | Pectoral fin rays | Pelvic fin rays | Principal caudal rays | Total vertebrae ² | Branchio- stegeal rays |
|---|----------------------|--------------------|------------------|----------------------|--------------------|--------------------------|------------------------------|---------------------------|
| ³ <i>Artedius corallinus</i> | VIII-IX (IX) | 15-16 (16) | 12-13 (13) | 14-16 (16) | 3 | 6 + 6 | 31-33 (32, 33) | 6 |
| * <i>Artedius creaseri</i> | IX-X (X) | 12-14 (13) | 9-11 (10) | 15-17 (16) | 3 | 6 + 6 | 30-31 (31) | 6 |
| * <i>Artedius fenestratis</i> | VIII-IX (IX) | 16-18 (17) | 12-14 (12, 13) | 14-16 (15) | 3 | 6 + 6 | 32-35 (35) | 6 |
| * <i>Artedius harringtoni</i> | VIII-X (IX) | 15-18 (17) | 10-14 (13) | 13-15 (14) | 3 | 6 + 6 | 32-34 (33, 34) | 7 |
| * <i>Artedius lateralis</i> | VIII-X (IX) | 15-17 (16) | 12-14 (13) | 14-16 (15) | 3 | 6 + 6 | 32-34 (33) | 6 |
| * <i>Artedius meanyi</i> | IX-X (X) | 14-17 (16) | 10-12 (12) | 14-16 (15) | 2-3 (2) | 6 + 6 | 33-35 (34) | 6 |
| ³ <i>Artedius notospilotus</i> | IX-X (IX) | 14-16 (15) | 11-13 (12) | 14-17 (16) | 3 | 6 + 6 | 32-34 (32) | 6 |
| * <i>Clinocottus aculeiceps</i> | VII-IX (VIII) | 13-17 (15, 16) | 9-13 (12) | 13-15 (14) | 3 | 6 + 6 | 31-33 (32, 33) | 6 |
| * <i>Clinocottus analis</i> | IX-X (IX) | 14-18 (16, 17) | 11-14 (12, 14) | 14-15 (15) | 3 | 6 + 6 | 31-35 (32) | 6 |
| * <i>Clinocottus embryum</i> | VIII-X (IX) | 14-17 (15) | 9-12 (10) | 12-15 (14) | 3 | 6 + 6 | 33-35 (33, 34) | 6 |
| * <i>Clinocottus globiceps</i> | VIII-X (IX) | 13-17 (16) | 11-12 (11) | 13-15 (14) | 3 | 6 + 6 | 32-33 (33) | 6 |
| * <i>Clinocottus recalcus</i> | VIII-IX (IX) | 14-16 (16) | 9-13 (12) | 13-15 (14) | 3 | 6 + 6 | 33-34 (33) | 6 |
| * <i>Oligocottus maculosus</i> | VIII-IX (VIII) | 15-18 (17) | 12-14 (13) | 12-15 (14) | 3 | 6 + 6 | 34-37 (36) | 6 |
| <i>Oligocottus rimensis</i> | VIII-X (IX) | 16-19 (18) | 13-15 (14) | 13-15 (14) | 3 | 6 + 6 | 32-35 (33) | 6 |
| <i>Oligocottus rubellio</i> | VIII-IX (VIII) | 15-17 (16) | 12-14 (13) | 13-15 (14) | 3 | 6 + 6 | 34-37 (34, 35) | 6 |
| * <i>Oligocottus snyderi</i> | VII-IX (VIII) | 17-20 (19) | 12-15 (14) | 12-15 (14) | 3 | 6 + 6 | | |

¹ From original counts and from compilation of Howe and Richardson (1978).

² Includes hypural.

³ *Artedius* Type 3 larvae are either *A. corallinus* or *A. notospilotus*; see text for explanation.

⁴ Larvae described by Morris (1951).

* Species for which larvae are described in this study.

monophyletic group as a group in which all members are descended from a single stem. The common possession of one or more derived characters is the only conclusive evidence that a group is monophyletic. Shared, plesiomorphic characters are not used because primitive character states inherited from an ancestral taxon may remain unchanged in various divergent lineages and may not be evidence of close relationship. Monophyletic groups that arose from a common stem by the same splitting process are called sister groups. Every monophyletic group, together with its sister group, constitutes a monophyletic group of higher taxonomic rank.

Since only derived character states are used in determining phylogenetic relationships, the polarity of character states was determined through outgroup comparisons. The outgroup taxa examined in this study included larvae of seven different cottid genera: *Scorpaenichthys marmoratus*, *Hemilepidotus spinosus*, *Leptocottus armatus*, *Enophrys bison*, *Myoxocephalus* sp., *Icelinus* sp., and *Radulinus asprellus*. Members of these genera are quite varied and represent several divergent lineages within the Cottidae (Bolin 1934, 1947; Taranets 1941; Howe and Richardson 1978). Larvae of several other scorpaeniform families also were examined for outgroup comparisons. These taxa included: *Sebastes flavidus* (Scorpaenidae); *Hexagrammos* sp. (Hexagrammidae), Cyclopteridae Type 1 (Cyclopteridae), and *Stellerina xyosterna* (Agonidae).

SELECTION OF CHARACTERS FOR ANALYSES.—A variety of characters were examined in *Arteidius*, *Clinocottus*, and *Oligocottus* larvae including meristics, morphology, pigmentation, spination, and developmental osteology. However, of the 50 characters initially examined, many were deleted from final analysis. The criteria used in deleting characters are as follows:

- (1) Characters that exhibit a large amount of variability were deleted from analysis. Highly variable characters are poor indicators of phylogenetic relationships (Bolin 1947; Simpson 1961; Mayr 1969). Examples of variable characters are head pigmentation and number of posttemporal-supracleithral spines.
- (2) Derived character states found in only one species were deleted. Again characters of this nature are of no value in determining intra-

group relationships. Hindgut diverticula of *Clinocottus acuticeps* are an example of a specific character.

- (3) Characters in which the sequence of change or the primitive and derived states could not be identified were deleted from the analysis. Many of the morphometric and pigmentation characters fell into this category.

Taxonomic Procedures

Larval descriptions are based on both laboratory-reared larvae and field-collected specimens. Egg masses were spawned from ripe *Clinocottus globiceps*, *Oligocottus maculosus*, and *O. snyderi* collected from tidepools along the central Oregon coast during winter-spring 1979 and 1980. Larvae were maintained at 12–13°C. In addition to reared specimens, developmental series were put together with larvae obtained with 70 cm bongo nets and neuston nets off the coast of Oregon between 1969 and 1978. Samples were taken in all months of the year from an area concentrated along an east-west transect off Newport, Oregon (lat. 44°39.1'N). Specimens were also obtained from estuarine and coastal collections of the Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service; Scripps Institution of Oceanography; Los Angeles County Museum of Natural History; Marine Ecological Consultants; California Academy of Sciences; Humboldt State University; Northwest Fisheries Center, Seattle Laboratory, National Marine Fisheries Service; and University of Washington. Reared specimens of *Arteidius lateralis* from College of Fisheries, University of British Columbia and *Oligocottus maculosus* and *Clinocottus acuticeps* from Vancouver Public Aquarium were also utilized. Transforming and juvenile specimens were collected monthly from 1977 to 1980 from tidepools along the central Oregon coast.

All specimens were preserved in 5 or 10% buffered formalin and some material was subsequently transferred to 36 or 40% isopropyl alcohol.

Developmental series of larvae and juveniles were assembled for 12 of the 16 species of *Arteidius*, *Clinocottus*, and *Oligocottus*. The number of specimens examined in each series varies from 11–38 according to availability of material. Developmental series were formed utilizing field-caught larvae, except as noted below, because of

the large amounts of variation in morphology and pigmentation in laboratory-reared larvae. Newly hatched, reared larvae are included in series of *Artedius fenestralis*, *A. lateralis*, *Clinocottus acuticeps*, *C. globiceps*, *Oligocottus maculosus*, and *O. snyderi*. In addition, reared larvae were used to supplement incomplete developmental series of field-caught larvae of *Clinocottus globiceps* and *Oligocottus maculosus*. Marked differences between developmental series based on field specimens and laboratory-reared specimens are noted in the descriptions.

Developmental stages follow the terminology of Ahlstrom et al. (1976), except that the transitional period between the larval and juvenile stages is marked by an increase in pigmentation particularly over the head and in saddles along the dorsum, a reduction in the size and number of preopercular spines, an ossification of the pelvic fin spine and rays, and the formation of scales. Specimens are referred to as juveniles when they settle from the plankton and assume a benthic existence.

MORPHOMETRICS.—Measurements of selected body parts were made to the nearest 0.1 or 0.01 mm using an ocular micrometer in a stereomicroscope. Measurements were made following the definitions of Richardson and Laroche (1979) except as follows: body depth at anus = vertical distance from the dorsal to ventral body margin at the anus, snout to pelvic fin origin = horizontal distance from the tip of the snout to a vertical through the origin of the pelvic fin, and origin of pelvic fin to anus = horizontal distance from a vertical through the origin of the pelvic fin to the anus. Head length is abbreviated as HL. Detailed tables documenting the development of meristic elements for larvae of *Artedius*, *Clinocottus*, and *Oligocottus* are presented by Washington (1981).

All body lengths given in this study refer to either notochord length (NL), which is defined as snout tip to notochord tip preceding development of the caudal fin; standard length (SL), which is defined as snout tip to the posterior margin of the hypural plates; or total length (TL), which is defined as snout tip to the posteriormost margin of the caudal fin. Unless otherwise indicated, all lengths given are standard length.

MERISTICS.—Following the methods of Dingerkus and Uhler (1977), several larvae were cleared and stained with Alcian Blue and Alizarin Red S for each species when specimens were available in sufficient numbers. Counts were

made of dorsal fin spines and rays, anal fin rays, pelvic fin spines and rays, principal caudal rays, branchiostegal rays, preopercular spines, and vertebrae. Vertebral counts always included the urostyle. All meristic elements were counted if they absorbed Alizarin stain. Principal caudal rays are defined as the number of caudal fin rays that articulate with the upper and lower hypural plates.

Counts of meristic elements were also made on unstained larvae from the developmental series used in the morphometric examination. All fin rays and spines, branchiostegal rays, preopercular spines, and myomeres were counted when visible under magnification. In this study, all fin rays and spines were counted, regardless of whether they arose from the same pterygiophore. (For detailed meristic and spination tables of developmental series of known *Artedius*, *Clinocottus*, and *Oligocottus* larvae see Washington 1981).

SPINATION.—Spine terminology generally follows Richardson and Washington (1980) in which spines are named for the bones from which they originate.

TAXONOMIC TERMINOLOGY.—Results of this study do not agree with previously recognized limits of the genus *Artedius*. In order to avoid confusion, species in this group are designated as *Artedius* Group A including *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* (either *A. corallinus* or *A. notospilotus*) or *Artedius* Group B including *A. creaseri* and *A. meanyi*. Larvae referred to as *Artedius* Type 3 are either *A. corallinus* or *A. notospilotus*. Positive identification is not possible at this time because of the lack of late-stage larval specimens. (See descriptions for discussion of identification.)

RESULTS

Description of Characters Considered

PREOPERCULAR SPINATION.—The number of preopercular spines is a relatively stable, conservative character in larval cottids. Most cottid larvae (22 of 28 known genera) possess four approximately equal-sized spines situated along the posterior margin of the preopercle. Generally the dorsalmost spine increases in size with development while the lower three spines are reduced or lost.

A modification of this basic preopercular pattern is found in larvae of several species of *Ice-*

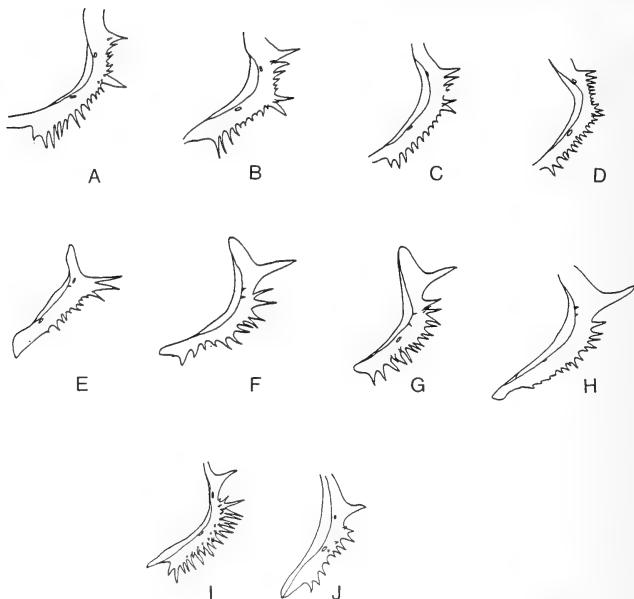


FIGURE 1. Multiple preopercular spines in larval *Artedius*, *Clinocottus*, and *Oligocottus*. A) *Artedius harringtoni*, B) *A. fenestralis*, C) *A. lateralis*, D) *A. Type 3*, E) *Clinocottus acuticeps*, F) *C. embryum*, G) *C. globiceps*, H) *C. analis*, I) *Oligocottus snyderi*, J) *O. maculosus*.

linus and *Myoxocephalus*. These larvae possess an additional small, auxiliary spine situated on the inner shelf of the preopercle anterior to the bases of the four principal preopercular spines.

A third pattern of preopercular spination is found in larvae of *Clinocottus*, *Oligocottus*, and *Artedius* Group A (Fig. 1). These larvae possess 5–24 small spines situated along the posterior margin of the preopercle. Two basic patterns of multiple preopercular spines occur in larvae of this group. In four species of *Artedius* (Group A), the dorsalmost, middle, and ventralmost spines become enlarged relative to the other preopercular spines. During transformation, the dorsal-

most spine continues to increase in size, while the middle spines (7–9), midventral spines (11–14), and ventralmost spines each fuse together, forming three large bumps on the preopercular margin. The other preopercular spines gradually disappear.

In larvae of *Clinocottus* and *Oligocottus* the dorsalmost spine increases in size relative to the other preopercular spines. During transformation the lower spines regress and disappear while the dorsalmost spine remains prominent.

Outgroup comparisons with larvae of closely related Scorpaeniformes indicate the presence of five or fewer approximately equal-sized pre-



FIGURE 2. Preopercular spines of larval *Artedius meanyi* and *A. creaseri*.

opercular spines. *Sebastes* and *Stellerina* larvae possess five and four spines, respectively; hexagrammid larvae possess five to six, three, or no spines, and cyclopterid larvae have lost all preopercular spines. The cottid taxa that possess four equal-sized preopercular spines also tend to have many other primitive character states. The presence of four equal-sized spines is considered the plesiomorphic state for preopercular spines in cottid larvae.

The modified pattern of spines found in larval *Icelinus* and *Myoxocephalus* could easily be derived from the basic pattern of four preopercular spines. In fact, larvae of several species of *Icelinus* and *Myoxocephalus* possess only four preopercular spines. The presence of an auxiliary spine on the preopercle probably represents an intermediate character state leading toward multiple preopercular spines.

The multiple preopercular spines of larvae of *Artedius* (Group A), *Clinocottus*, and *Oligocottus* are unique to this group. Multiple preopercular spines are not present in any other known cottid or scorpaeniform larvae. Multiple preopercular spines are derived character states indicative of the monophyletic origin of this group.

BASAL PREOPERCULAR SPINE.—Larvae of *Artedius meanyi* and *creaseri*, larvae of at least two species of *Icelinus*, and larvae of *Myoxocephalus* possess small projections or spines on the base of each of the four main preopercular spines (Fig. 2). These basal spines project out at 90° angles to the axis of the main preopercular spines. The basal spines are most pronounced in early postflexion larvae. With development, four bony

ridges form on the inner shelf of the preopercle, parallel to each basal spine. These bony ridges grow toward the basal spines and gradually fuse with them, forming bony arches over the forming lateral line canal of the preopercle. These basal spines are not present in other cottid or scorpaeniform larvae examined and probably are a derived character state.

INNER SHELF PREOPERCULAR SPINES.—Larval *Clinocottus* possess one or two tiny spines on the inner shelf margin of the preopercle. *Clinocottus acuticeps* larvae have only one inner shelf spine. All other *Clinocottus* larvae examined have two. These spines are transient features which form in postflexion larvae and are lost before transformation. They appear to be unique to this group and, as such, to be derived character states.

NAPE BUBBLE.—Larvae of *Oligocottus maculosus* and *O. snyderi* possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal fin (Fig. 3). This bubble is present at hatching and persists for two or three weeks (to about the beginning of flexion of the notochord). No other known cottid larvae possess a bubble of skin at the nape; accordingly, this bubble is probably a derived character unique to these two species. (Larvae of *O. rimensis* and *O. rubellio* are unidentified and it is not known if they also possess this character.)

GUT DIVERTICULA.—Long protrusions or diverticula extend dorsolaterally from either side of the abdominal cavity in larvae of *Artedius fenestralis*, *A. lateralis*, and *A. Type 3* (Fig. 4). These diverticula are present at hatching and persist throughout larval development. Newly

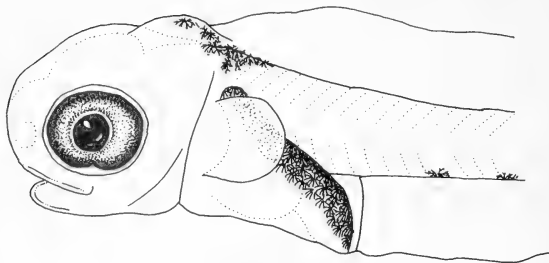


FIGURE 3. Nape bubble of larval *Oligocottus snyderi*.

hatched larvae of *Oligocottus maculosus* and *O. snyderi* possess similar but less pronounced bumps or protrusions on either side of the dorsal surface of the abdominal cavity. These bumps are present at hatching, but they disappear after two to three weeks at about the onset of notochord flexion. The diverticula of *Artedius fenestralis*, *lateralis*, and Type 3 and the smaller protrusions of *Oligocottus* appear to be homologous structures, with the smaller bumps constituting an intermediate form. These diverticula are unique, derived characters not known in other cottid larvae.

Larvae of *C. acuticeps* also possess long diverticula which extend posteriorly on either side of the anus. Larvae of *C. globiceps*, *C. embryum*, and *C. analis* have bulges on either side of the anus. Although these bulges appear to form an intermediate state in the evolution of hindgut diverticula, histological sections of the guts of larval *Clinocottus* yielded inconclusive results. Larval *C. analis*, *C. embryum*, and *C. globiceps* possess an enlarged coelom on either side of the hindgut, but no distinct diverticula. Hindgut diverticula appear to be unique to *C. acuticeps*.

PARIETAL AND NUCHAL SPINES.—Most larval cottids develop two spines, a large anterior parietal and a smaller posterior nuchal spine at the posterior edge of the parietal bones. The anterior parietal spine develops first, followed by a smaller nuchal spine that forms just posterior to it. These spines are generally transient structures that form late in larval development and are reduced or lost during transformation. In many

species of cottids, the spines appear to fuse together enclosing a small canal between the bases of the two spines. This canal eventually becomes part of the cranial lateral line system. In other species, the spines decrease in size without fusing together. Concurrently, sheets of bone extend anteriorly and posteriorly from the spines and eventually fuse together, forming an incipient cranial arch.

Similar parietal and nuchal spines occur in larvae of most other scorpaeniform families and appear to be homologous to those of cottid larvae. The presence of a parietal and nuchal spine is probably the primitive or ancestral condition in the Cottidae.

Parietal and nuchal spines have undergone modification and elaboration in larvae of most of the species of *Clinocottus* and *Oligocottus*, and in *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*. Two species (*Artedius harringtoni* and *Clinocottus acuticeps*) have lost these spines completely. Three species (*Clinocottus analis*, *C. embryum*, and *C. recalvus*) have retained the primitive condition of possessing a parietal and nuchal spine. The remaining species (*A. fenestralis*, *A. lateralis*, *O. maculosus*, *O. snyderi*, and *C. globiceps*) have tended toward an elaboration and increase in number of parietal spines. Generally, these larvae develop a cluster of three to six spines, which are situated in two transverse rows at the posterior margin of the parietal region. During transformation, these clusters of spines decrease in size and disappear. At the same time, sheets of bone extend ante-

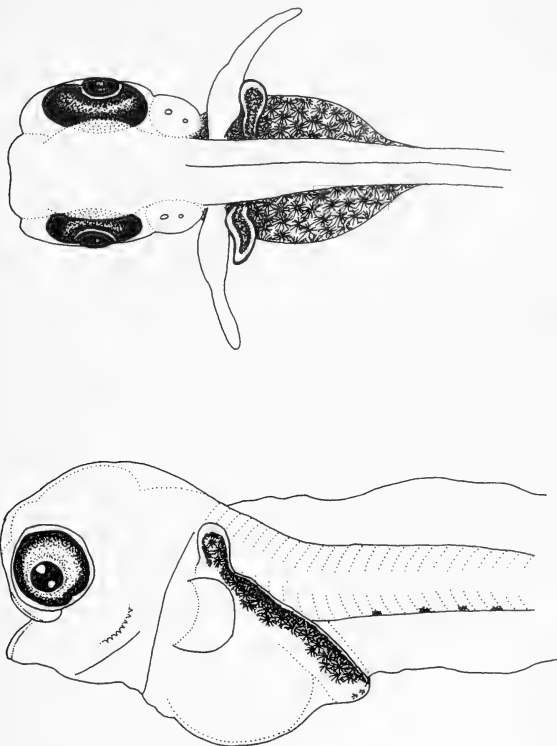


FIGURE 4. Dorsal gut diverticula in larval *Artedius fenestralis*.

riorly and posteriorly from the bases of the two rows of spines and eventually fuse together. This bony arch becomes a part of the cranial lateral line system in juveniles.

The absence of parietal spines in *A. harringtoni* and *C. acuticeps* is probably a secondary loss and, as such, represents a derived condition. The

elaboration of spines into clusters is apparently unique to larvae of *Artedius*, *Clinocottus*, and *Oligocottus* and is also a derived state.

PIGMENTATION.—Melanistic pigmentation varies greatly among cottid larvae ranging from relatively unpigmented forms to heavily pigmented ones. Larvae of *Artedius*, *Clinocottus*, and

Oligocottus are all lightly pigmented and possess numerous, intense melanophores over the dorsolateral surface of the gut and in a row posterior to the anus. The shape and number of midline melanophores varies between species. Larvae of all but one species, *A. creaseri*, possess several melanophores in the nape region. The presence of head pigment and anteroventral gut melanophores varies among the species of *Artedius*, *Clinocottus*, and *Oligocottus*.

Although pigment patterns are diagnostic at the specific level, they are difficult to evaluate for use in systematic analysis. Many fish larvae in distantly related families, and even orders, are similarly pigmented. Several cottid genera other than *Artedius*, *Clinocottus*, and *Oligocottus* also possess similar pigment patterns. Hence, it is difficult, if not impossible, to determine which pigment patterns are primitive and which are derived.

Nevertheless, trends in certain areas of pigmentation can be discerned. Among known cottid larvae, a discrete nape pigment patch is found only in members of *Artedius*, *Clinocottus*, *Oligocottus*, *Enophrys*, *Myoxocephalus*, and *Gymnocranthus*. Nape pigment is probably derived in cottid larvae. The number of ventral midline melanophores situated posterior to the anus ranges from 2 to 33 in larvae of *Artedius*, *Clinocottus*, and *Oligocottus*. In addition, the shape and spacing of these melanophores varies from small dots to long slashes extending onto the ventral finfold to large pigment blotches. *Artedius creaseri* and *A. meanyi* both possess irregularly shaped blotches of pigment along the ventral midline. *Artedius fenestralis*, *A. harringtoni*, and *A. lateralis* all possess distinctive pigment slashes. *Oligocottus* and *Clinocottus* larvae possess small, round melanophores. Although these pigment patterns bind certain species together, it is difficult to determine ancestral versus derived states. Both pigment blotches and distinctive midline slashes are found in larval *Icelinus*. Pigment, as well as other characters, indicates that *Icelinus* shares close affinities with *Artedius*; however, the direction of the evolution of pigment patterns cannot be determined.

MORPHOMETRICS.—Cottid larvae exhibit a diversity of body forms. Body shape ranges from short and stubby (*Artedius* [Group A] and *Enophrys*) to long and slender (*Radulinus* and *Icelus*) to globose (*Malacocottus*). Larval *Artedius* (Group

A), *Clinocottus*, and *Oligocottus* have short, stubby bodies with blunt, rounded snouts. Gut length is moderately long and the posterior portion of the hindgut trails well below the rest of the body.

Measurements of body parts frequently overlap in larval *Artedius* (Group A), *Clinocottus*, and *Oligocottus* because of their similarity in body shape. These similarities make it difficult to determine discrete character states or transformation series. In addition, many body parts change markedly during larval development, frequently exhibiting allometry. Because of the extreme diversity of forms found in larval cottids, it is difficult to evaluate morphometric characters for systematic analysis. Trends can be observed in only a few body parts.

Larvae of *Artedius creaseri* and *A. meanyi* have long, pointed snouts. They develop relatively long ascending processes on the premaxillary. The underlying ethmoid cartilage is relatively large, causing a pointed, humped appearance of the snout. Larval *Icelinus* exhibit pointed snouts similar to that of *A. meanyi* and *A. creaseri*.

In contrast, all other larval *Artedius*, *Clinocottus*, and *Oligocottus* have blunt, rounded snouts. The ascending processes of their premaxillaries are relatively short, and the ethmoid cartilage forms late in development.

Snout length is variable in the outgroup taxa. *Sebastes* larvae have a somewhat long, pointed snout, but the hexagrammid, cyclopterid, and agonid larvae examined have shorter, rounded snouts. Within the cottids, *Enophrys*, *Leptocottus*, *Hemilepidotus*, and *Scorpaenichthys* larvae all have blunt, rounded snouts. This condition is probably the primitive condition relative to larvae of *Artedius*, *Clinocottus*, and *Oligocottus* because it is widespread in several divergent genera of cottids and scorpaeniforms. The pointed snout appears to be a derived condition.

Although gut length varies greatly among cottid larvae (Richardson and Washington 1980), larval *Artedius* (Group A), *Clinocottus*, and *Oligocottus* possess distinctive guts with the hindgut coiled very loosely and extending posteriorly. The tip of the hindgut extends ventrally well below the rest of the body and posteriorly to the origin of the anal fin. This condition is most pronounced in *Clinocottus* larvae. Larval *C. acuticeps* and *C. embryum* have especially long, trailing hindguts which extend posteroventrally past

the anal fin origin. A trailing gut is unique to larvae of *Artedius* (excepting *A. meanyi* and *A. creaseri*), *Clinocottus*, and *Oligocottus*, and is assumed to be a derived condition.

PELVIC FIN RAYS.—The number of pelvic fin rays in cottids ranges from one spine and five rays to no spines or rays.

Pelvic fin rays are generally considered to be undergoing reduction in the cottids. The primitive state is 1,5 fin rays as in other Scorpaeniformes. Reduction in number of rays is a derived state.

Larvae of *Artedius*, *Clinocottus*, and *Oligocottus* all possess 1,3 pelvic fin rays, except for *A. meanyi*. *Artedius meanyi* usually possesses 1,2 pelvic fin rays. The outermost of these fin rays is markedly long and thickened, and the tips of this ray are separated. *Icelinus* also possesses 1,2 pelvic fin rays; however, both rays are relatively short and fine. The thickened outer ray of *A. meanyi* may have evolved through the fusion of two fin rays. If so, this condition may constitute an intermediate state between the three pelvic fin rays of *Artedius*, *Clinocottus*, and *Oligocottus* and the two pelvic fin rays of *Icelinus*.

BRANCHIOSTEGAL RAYS.—The scorpaenids, considered to be the most generalized scorpaeniform (Bolin 1947; Quast 1965), possess seven branchiostegals. The hexagrammids and the zaniolepidids, which occupy an intermediate position between the scorpaenids and cottids (Quast 1965), both possess six branchiostegals. Most cottids possess six branchiostegal rays; however, the psychrolutids and some freshwater *Cottus* species have seven branchiostegals. The psychrolutids are a distinct group which possess many derived characters and have apparently diverged from other cottids. Similarly, members of *Cottus* also possess many derived characters that apparently reflect adaptation to a freshwater habitat. Cottids that are generally considered to be primitive because they retain many primitive features all possess six branchiostegal rays.

Although the possession of seven branchiostegal rays is probably the primitive condition in the scorpaeniforms, possession of six branchiostegals appears to be the primitive state within the cottids. Cottid genera such as *Icelinus* and *Hemilepidotus*, which Bolin (1947) considered to have evolved from the evolutionary line leading to *Artedius*, *Clinocottus*, and *Oligocottus*, all possess six branchiostegal rays. Six branchioste-

gals is probably also the primitive state relative to *Artedius*, *Clinocottus*, and *Oligocottus*. Because those cottids generally considered to be from the same evolutionary lineage as *Artedius* (Bolin 1934, 1947) all have six branchiostegals, it is assumed that the seven branchiostegals found in *Artedius harringtoni* and in some *Clinocottus globiceps* are secondarily derived.

POSTTEMPORAL-SUPRACLEITHRAL SPINES.—Larvae of most known scorpaeniforms (including most known cottids) develop three spines in the posttemporal-supracleithral region of the head. Generally, two spines form first on the ventral portion of the posttemporal bone, and one spine forms midway along the posterior margin of the supracleithrum. These spines persist during transformation at which time the surrounding portions of the posttemporal and supracleithral bones undergo modification and canals form in these bones between the spines. This entire complex then develops into the junction point of the cephalic lateral line system and the lateral line system. This pattern of spines probably represents the plesiomorphic condition in larval cottids.

In larvae of *Artedius*, *Clinocottus*, and *Oligocottus* the posttemporal-supracleithral spines are frequently modified. The modifications appear to be correlated with those of the parietal and nuchal spines. Larvae that have lost parietal spines do not develop posttemporal-supracleithral spines, and larvae that have evolved complex clusters of parietal spines also develop clusters of posttemporal-supracleithral spines. Neither *A. harringtoni* nor *C. acuticeps* larvae develop any spines in the posttemporal-supracleithral region. Larvae of *A. creaseri*, *A. meanyi*, *C. embryum*, and *C. recalvus* possess two posttemporal and one supracleithral spine. *Artedius fenestralis*, *A. lateralis*, *O. maculosus*, *O. snyderi*, and *C. globiceps* all develop more than three posttemporal-supracleithral spines.

As described for parietal and nuchal spines, the posttemporal-supracleithral spines vary among species of *Artedius*, *Clinocottus*, and *Oligocottus*. This variability among closely related species suggests that these spines may be undergoing rapid modification in this group and loss of spines or possession of clusters of spines may represent convergent or parallel evolution.

As with the parietal and nuchal spines, the absence of posttemporal-supracleithral spines in

TABLE 2. CHARACTER STATES USED IN SYSTEMATIC ANALYSIS AND THEIR DISTRIBUTION AMONG LARVAL *ARTEDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* AND THE OUTGROUP TAXA.

| | Preopercular spine pattern | | | Basal preopercular spine | | Auxiliary preopercular spines | | | Bubble of skin at nape | |
|------------------------------------|----------------------------|----|----------------------|--------------------------------------|---------|-------------------------------|-----|-----|------------------------|--------|
| | No. of preopercular spines | | Dorsal spine largest | Dorsal, mid, & ventral spine largest | Present | Absent | One | Two | Present | Absent |
| | ≤5 | >5 | | | | | | | | |
| <i>Artedius fenestralis</i> | | X | | X | X | | | | | X |
| <i>Artedius harringtoni</i> | | X | | X | X | | | | | X |
| <i>Artedius lateralis</i> | | X | | X | X | | | | | X |
| <i>Artedius</i> Type 3 | | X | | X | X | | | | | X |
| <i>Oligocottus maculosus</i> | | X | X | | X | | | | | X |
| <i>Oligocottus snyderi</i> | | X | X | | X | | | | | X |
| <i>Clinocottus acuticeps</i> | | X | X | | X | | X | | | X |
| <i>Clinocottus analis</i> | | X | X | | X | | | X | | X |
| <i>Clinocottus embryum</i> | | X | X | | X | | | X | | X |
| <i>Clinocottus globiceps</i> | | X | X | | X | | | X | | X |
| <i>Clinocottus recalvus</i> | | X | X | | X | | | X | | X |
| <i>Artedius creaseri</i> | X | | X | | | X | X | | | X |
| <i>Artedius meanyi</i> | X | | X | | | X | X | | | X |
| <i>Scorpaenichthys marmoratus</i> | X | | X | | X | | X | | | X |
| <i>Hemulepidotus hemulepidotus</i> | X | | X | | X | | X | | | X |
| <i>Leptocottus armatus</i> | X | | X | | X | | X | | | X |
| <i>Enophrys bison</i> | X | | X | | X | | X | | | X |
| <i>Myoxocephalus</i> sp. | X | | X | | | X | X | | | X |
| <i>Icelinus</i> sp. | X | | X | | | X | X | | | X |
| <i>Radulinus asprellus</i> | X | | X | | | | X | | | X |
| <i>Sebastes flavidus</i> | X | | X | | | | X | | | X |
| <i>Hexagrammos</i> sp. | * | | * | | * | | X | | | X |
| <i>Cyclopteridae</i> Type 1 | * | | * | | * | | X | | | X |
| <i>Stellerina xyosterna</i> | X | | X | | X | | X | | | X |

* Character absent.

A. harringtoni and *C. acuticeps* is probably a secondary loss and hence a derived state. The trend toward an elaboration of these spines is found only in members of *Artedius*, *Clinocottus*, and *Oligocottus* and is also considered a derived state.

CHARACTERS SELECTED FOR SYSTEMATIC ANALYSIS.—Of the 50 characters examined, 10 characters were selected for use in the phylogenetic analysis (Table 2). These 10 best fit the

criteria for character selection listed in the methods.

Character 1: Number of preopercular spines.

- A) 5
- B) 0
- C) 4
- D) >5

Character 2: Preopercular spine pattern.

- A) preopercular spines equal-sized

TABLE 2. CONTINUED.

| Dorsal gut diverticula | | | Parietal spines | | No. pelvic fin rays | | | Snout shape | | Hindgut shape | | |
|------------------------|-------|-------|-----------------|----------|---------------------|---|---|-------------|---------|---------------|-----------------|----------------|
| Absent | Small | Large | Two | Modified | >3 | 3 | 2 | Rounded | Pointed | Compact | Trails slightly | Trails greatly |
| | | X | | X | | X | | X | | | X | |
| X | | | | X | | X | | X | | | X | |
| | | X | | X | | X | | X | | | X | |
| | | X | | X | | X | | X | | | X | |
| | X | | | X | | X | | X | | | X | |
| | X | | | X | | X | | X | | | X | |
| X | | | | X | | X | | X | | | | X |
| X | | | | X | | X | | X | | | X | |
| X | | | | X | | X | | X | | | | X |
| X | | | | X | | X | | X | | | X | |
| X | | | X | | | X | | X | | X | | |
| X | | | X | | | | X | | X | X | | |
| X | | | | X | X | | | X | | X | | |
| X | | | X | | X | | | X | | X | | |
| X | | | | | | | | X | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | X | | | X | | | | X | | |
| X | | | | X | X | | | X | | X | | |
| X | | | | X | * | | | X | | X | | |
| X | | | X | | | | X | X | | X | | |

B) dorsalmost spine largest

C) dorsal, middle, and ventral spines largest

Character 3: Basal preopercular spines.

A) absent

B) present

Character 4: Auxiliary preopercular spines.

A) absent

B) 1

C) 2

Character 5: Bubble of skin at nape.

A) absent

B) present

Character 6: Diverticula on dorsal surface of gut.

A) absent

B) small bumps

C) long diverticula

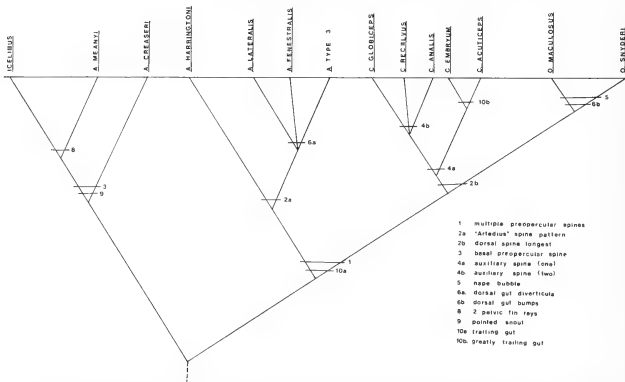


FIGURE 5. Cladogram of systematic relationships between *Artedius*, *Clinocottus*, and *Oligocottus*. Characters numbered on cladogram indicate synapomorphies.

Character 7: Parietal spines.

- A) 2
- B) modified: clusters of spines
- C) modified: absent

Character 8: Number of pelvic fin rays.

- A) >3
- B) 3
- C) 2

Character 9: Snout shape.

- A) rounded
- B) pointed

Character 10: Hindgut shape.

- A) compact; not trailing below body; ending anterior to anal fin origin
- B) hindgut trailing slightly below body; extending to origin of anal fin
- C) hindgut trailing well below body; extending posterior to anal fin origin

PHYLOGENETIC RELATIONSHIPS

A hypothesis of evolutionary relationships among species in the cottid genera *Artedius*, *Clinocottus*, and *Oligocottus* is presented in Figure 5. Two main lineages or sister groups of *Artedius*, *Clinocottus*, and *Oligocottus* larvae are repre-

sented in the resulting cladogram based on shared derived characters of the larvae. Species with larvae possessing the synapomorphic characters, multiple preopercular spines and trailing guts, form one major group. In addition to the possession of shared, derived characters, larvae of this group are extremely similar in pigmentation and body shape. The second major evolutionary line consists of species sharing two derived characters, basal preopercular spines and pointed snouts. This line includes *Artedius creaseri*, *A. meanyi*, and *Icelinus*.

The two main evolutionary lines or groups of *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus* correspond to Taranets's (1941) classification of these species. Taranets (1941) placed *Artedius meanyi* and *A. creaseri* in the subfamily Icelinae, along with members of *Icelinus* and *Chitonotus*. He based this decision on the following characters: the upper preopercular spine larger than the lower spines; two rows of bony plates on the body—one along the lateral line, the other at the base of the dorsal fins; and scales usually present on other parts of the body. All of these characters are undergoing reduction and are present in several different genera of cottids. As such, they have

low systematic value. Taranets (1941) combined *Clinocottus*, *Oligocottus*, *Arteidius corallinus*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. notospilotus* in the subfamily Oligocottinae. This subfamily was characterized by the absence of spines or ridges projecting through the skin on the head, weakly developed preopercular spines, body naked or with bony plates reduced, and "... other characters." Unfortunately, Taranets did not mention which other characters he examined.

In contrast, other investigators have placed *Arteidius manyi* and *A. creaseri* in the genus *Arteidius* along with the five other species of *Arteidius* discussed above. Howe and Richardson (1978) and Bolin (1947) proposed that although *Arteidius* shared close affinities with *Icelinus*, it was more closely related to *Clinocottus* and *Oligocottus*. Jordan (1923), however, stated that *Arteidius* was most closely related to *Icelinus* because of the common possession of bony plates on either side of the dorsal fins.

The evolutionary lineage (Fig. 5) containing larvae with multiple preopercular spines includes three distinct groups of species. One of these groups includes all the species of the genus *Clinocottus*. Larvae of this group share one synapomorphic character, inner-shelf preopercular spines. Larvae of *Clinocottus* possess one or two auxiliary spines on the inner preopercular shelf. These spines appear to be a derived character unique to members of this genus and provide evidence that the genus is monophyletic. This genus has been previously recognized and defined on the basis of adult characters, e.g., loss of scales, an advanced anus, and possession of a heavy, blunt penis (Hubbs 1926; Bolin 1934, 1944, 1947; Taranets 1941; Howe and Richardson 1978). None of these characters is unique to members of *Clinocottus*. Several different lineages of cottids exhibit reduction in squamation, advanced anuses, and penes.

Within the genus *Clinocottus*, *C. embryum* and *C. acuticeps* are grouped together on the basis of a synapomorphic character, a trailing hindgut which extends posterior to the origin of the anal fin. *Clinocottus acuticeps* larvae are unique in their possession of the autapomorphy, distinct hindgut diverticula. *Clinocottus embryum* and *C. acuticeps* larvae also are similar in possessing moderately pointed snouts relative to the blunt, rounded snouts of other *Clinocottus* larvae, a

loose bubble of skin in the head region, and light pigmentation.

Synapomorphic characters for clarifying interspecific relationships among *C. analis*, *C. recalvus*, and *C. globiceps* were not identified. Nevertheless, several pigmentation and morphological characters, for which direction of evolution is not known, do suggest possible relationships among these species. Both *Clinocottus globiceps* and *C. recalvus* larvae have intense pigmentation over the snout, head, and nape. Both have very blunt, globose heads, large bulging guts, and relatively deep bodies. Juveniles of the two species are nearly inseparable based on external morphology. These characters suggest that *C. globiceps* and *C. recalvus* may be a very closely related species pair. Postflexion larvae of *C. analis* differ from all other postflexion *Clinocottus* larvae in possessing an intense band of melanistic pigment over the lateral surface of the body. Unfortunately, the polarity (direction of evolution) of many of the transformation series of morphometric and pigment characters could not be determined; hence, these characters could not be used in the phylogenetic analysis. Pigmentation and morphometric characters have been useful in several systematic studies based on larvae and have frequently been correlated with other derived characters (Johnson 1974; Moser and Ahlstrom 1974; Okiyama 1974; Richardson 1981). Clarification of relationships among the species of *Clinocottus* must await identification of derived characters or a better understanding of the evolution of pigmentation and body shape within cottid larvae.

The relationships among species of *Clinocottus* postulated by Bolin (1947) are in close agreement with relationships suggested by larval characters. Bolin placed *C. acuticeps* in its own subgenus because of its unique possession of a modified penis with a tri-lobed tip, and a membrane connecting the innermost pelvic fin ray with the abdomen. Bolin also placed *C. analis* in its own subgenus because of the retention of minute prickles covering the body. All other members of the genus are scaleless. *Clinocottus embryum*, *C. globiceps*, and *C. recalvus* were placed in the same subgenus because of their large, rounded heads and the retention of a pore behind the last gill. The latter character is plesiomorphic and, hence, of little value for evaluating relationships. Bolin (1947:163) described *C. recalvus* and *C.*

globiceps as "two extremely closely related species" because of their hemispherical head shape, an increased number of cirri on the head, and a pair of lateral knobs near the tip of the penis.

Another group of species within the lineage having multiple preopercular spines consists of *Oligocottus maculosus* and *O. snyderi*. They share two synapomorphies—a bubble of skin at the nape, and dorsal gut bumps. Larval *O. rimensis* and *O. rubellio* are not yet identified and, therefore, it is not known if these larvae also possess the synapomorphic characters binding *O. snyderi* and *O. maculosus* together.

Bolin (1934, 1947) defined the genus *Oligocottus* on the basis of the following adult characters: absence of scales; presence of a long, slender, simple penis; and modification of the anterior anal fin rays in males. Only the last character appears to be unique to members of this genus. As mentioned above, evolution of penes and loss of scales have occurred in several diverse cottid genera. Bolin placed *O. maculosus*, *O. snyderi*, and *O. rubellio* in the same subgenus because of the greatly modified anal fin in males, a permanently external penis, and loss of all but lateral line scales. He further speculated that *O. maculosus* was the least specialized member of the subgenus and *O. rubellio* was the most specialized.

Larval *O. snyderi* possess the derived, autapomorphic characters of multiple prickles covering the parietal and posttemporal regions of the head. In addition, larval *O. snyderi* possess an accessory spine at the anterior base of most of the main spines on the posterior margin of the preopercle. Both of these conditions are unique specializations of larval *O. snyderi*. Clarification of relationships of other *Oligocottus* species must await identification of larval *O. rimensis* and *O. rubellio*.

Larval characters indicate that while *Oligocottus* and *Clinocottus* are each a monophyletic group, they are closely related. Larvae of both genera are linked together into a higher-level monophyletic unit by the possession of a distinctive preopercular spine pattern.

Taranets (1941) also concluded that *Oligocottus* and *Clinocottus* are closely related. He placed both genera in the supragenus *Oligocottini* because of the presence of a penis and the absence of bony plates in both groups.

Artedius fenestralis, *A. harringtoni*, *A. lateralis*, and *A. Type 3* form the third group of larvae with multiple preopercular spines. These larvae share one synapomorphy, an *Artedius*-type preopercular spine pattern. In addition, larvae of this group possess distinctive pigment slashes on the ventral midline posterior to the anus and a strongly humped appearance in the nape region. Known larvae of *Oligocottus* and *Clinocottus* do not possess either of these characters; however, larvae of several species of *Icelinus* and *Myoxocephalus* do possess similar pigment slashes on the ventral midline. Although these characters are not unique to *Artedius* species, they provide additional support for the cohesiveness of this group.

Within the *Artedius* group, *A. fenestralis*, *A. lateralis*, and *A. Type 3* form a distinct subgroup. Larvae of these species share one synapomorphic character, dorsal gut diverticula. Characters identified in this study do not define relationships among these three species. *Artedius harringtoni* is probably less specialized than the three species possessing gut diverticula. *Artedius harringtoni* is further distinguished from other *Artedius* larvae by the possession of seven branchiostegal rays. All other cottid larvae examined in this study possess six branchiostegal rays except several laboratory-reared *Clinocottus globiceps*. Although seven rays are probably a primitive character in scorpaeniforms, *A. harringtoni* appears to have secondarily derived this condition, since none of the outgroup cottids have seven branchiostegals.

This grouping of *Artedius* larvae with multiple preopercular spines corresponds to Taranets's (1941) classification. He placed *Artedius coralinus*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. notospirotus* together in the supragenus *Artediini* in the subfamily *Oligocottinae*.

Other workers have placed all species of *Artedius* in the same subfamily and genus (Hubbs 1926; Bolin 1934, 1947; Rosenblatt and Wilkie 1963; Howe and Richardson 1978). Bolin (1947: 161) included *A. creaseri* in *Artedius* because of the retention of hemilepidotid-like scales "in various degrees of reduction," large head, an unadvanced anus, and "normal structure of the pelvic fins."

Artedius meanyi was not reported to occur off California at the time of Bolin's work. Hence, he did not include this species in his classification.

Rosenblatt and Wilkie (1963) described *A. meanyi* as being extremely similar to *A. creaseri* and placed it in Bolin's subgenus *Ruscariops* along with *A. creaseri*.

Reduction in squamation and number of pelvic fin rays is found in many different cottid genera and appears to have evolved separately several times. *Icelinus*, *Chitonotus*, and *Orthonopias* also possess hemilepidotid-like scales in various degrees of reduction. Several species of *Icelinus*, *Orthonopias*, and *Chitonotus* possess large heads and unadvanced anuses.

Characters of the larvae indicate that *Artedius creaseri* and *A. meanyi* form a distinct grouping separate from the other species of *Artedius*. Two synapomorphic characters, a pointed snout and basal preopercular spines provide strong evidence that *A. creaseri*, *A. meanyi*, and *Icelinus* form a monophyletic group. In addition, *A. meanyi*, *A. creaseri*, and *Icelinus* larvae are very similar in other pigmentation, morphometric, and spination characters, giving further support for the cohesiveness of this group. In a phenetic study of larval cottids, Richardson (1981) also placed *A. meanyi* in a group with *Chitonotus*, *Paricelinus*, *Triglops*, and *Icelus*. (*A. meanyi* was misidentified as *Icelinus* spp. in Richardson's study. See literature section of *A. meanyi* description.) Although her study was based on similarities of the larvae and not synapomorphies, it supports the grouping of *A. meanyi* and *A. creaseri* with *Icelinus*.

Both phenetic and synapomorphic characters of the larvae provide strong evidence that the genus *Artedius* (as defined by Bolin 1934, 1947) is not monophyletic and that *A. creaseri* and *A. meanyi* should be placed separately. *Artedius meanyi* and *A. creaseri* appear to be more closely related to species of *Icelinus* and other members of Richardson's Group 2 than to other species of *Artedius*. Clarification of relationships among *A. meanyi* and *A. creaseri* must await a reexamination of characters of adult *Artedius*.

Although larvae of the *A. meanyi-creaseri* group and the *Artedius-Clinocottus-Oligocottus* group are distinct from one another, they share certain similarities in comparison to other cottid larvae. Both groups have similar pigment patterns, morphology, and meristics, suggesting that species of these two groups share a common ancestor. Bolin (1947:159) also speculated that *Icelinus*, *Chitonotus*, *Artedius*, *Clinocottus*, and

Oligocottus constitute a single evolutionary line within the Cottidae. He suggested that "certain details of the more primitive members, particularly the scales, indicate that while these forms undoubtedly did not spring from the modern genus *Hemilepidotus*, they shared a common and not particularly remote ancestor with the fishes of that genus." Although characters of the larvae do not exclude the possibility of a hemilepidotid-type ancestor, they do indicate that it would be a relatively distant ancestor. Larval *Hemilepidotus* differ markedly from larvae of *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus* in many characters including meristics, morphometrics, osteology, spination, and pigmentation. It is much more likely that the ancestor of this group possessed characteristics similar to both the *Artedius-Icelinus* group and the *Artedius-Clinocottus-Oligocottus* group. Larvae of at least one species of *Icelinus* and several species of *Myoxocephalus* possess a fifth or sixth accessory preopercular spine. Larvae of *Myoxocephalus* also possess two distinct patterns of pigment: one type is lightly pigmented similar to the two *Artedius* groups, whereas the other has intense bands of lateral pigmentation. An ancestor similar to *Icelinus* or *Myoxocephalus* may well have given rise to *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus*. This hypothesis is supported by the presence of one or two accessory preopercular spines in *Myoxocephalus* larvae. This preopercular spine condition appears to be intermediate between the primitive pattern of four preopercular spines and the derived pattern of multiple preopercular spines. Hence, larvae of the ancestor of *Artedius*, *Clinocottus*, and *Oligocottus* were probably relatively lightly pigmented with melanophores present on the head, nape, dorsal surface of the gut, and along the ventral midline posterior to the anus. In addition, the ancestral larvae probably possessed four large preopercular spines with one accessory spine on the inner preopercular shelf, two parietal spines, and three posttemporal-supracleithral spines.

In summary, the hypotheses of relationships between *Artedius*, *Clinocottus*, and *Oligocottus* based on larvae characters is in general agreement with previous classifications based on adult characters. Synapomorphic characters of the larvae provide strong evidence that *Clinocottus*, *Oligocottus maculosus*, *O. snyderi*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* form

a monophyletic group within the cottids. Within this group, the genera *Clinocottus* and *Oligocottus* are very closely related; however, each genus appears to be monophyletic. *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* also form a monophyletic species group closely related to *Clinocottus* and *Oligocottus*. However, synapomorphic characters of the larvae provide strong evidence that *A. creaseri* and *A. meanyi* are more closely related to *Icelinus* than to species of *Clinocottus*, *Oligocottus*, and other *Artedius*. The genus *Artedius* as defined by Bolin (1934, 1947) does not appear to be monophyletic; *A. meanyi* and *A. creaseri* should be placed separately. Clarification of the exact position of these two species in relation to *Icelinus* and *Myoxocephalus* and the *Artedius-Clinocottus-Oligocottus* group must await identification and examination of larvae of additional species of cottids and reexamination of adult characters.

TAXONOMIC DESCRIPTIONS

Larvae of *Artedius*, *Clinocottus*, and *Oligocottus* have been difficult to identify at both the specific and generic levels because of their striking similarities. Previous descriptions of larvae of this group have been inadequate to separate larvae at both the specific and generic levels because of inaccuracies or insufficient detail. Many of the diagnostic characters useful in separating these larvae are transient features which are present during only a part of larval development (e.g., head spines, nape bubble). Hence, frequently a combination of several characters is necessary for identification of the larvae. Therefore, to facilitate identification, larval descriptions are arranged in species groups formed by the shared presence of diagnostic characters (Table 3). This matrix table is based on a set of characters that will allow identification of the early life history stages of 13 species of *Artedius*, *Clinocottus*, and *Oligocottus*.

Larvae of *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, *A. Type 3*, *Oligocottus maculosus*, *O. snyderi*, *Clinocottus acuticeps*, *C. analis*, *C. embryum*, *C. globiceps*, and *C. recalvus* (Groups A, B, and C) are very similar in morphology, pigmentation, and spination. They are all relatively lightly pigmented with melanophores present on the nape, dorsolateral surface of the gut, and in a series on the ventral midline of the tail.

Presence and amount of head pigmentation varies within the group. All of these larvae possess blunt, rounded snouts, stubby bodies, and a bulging gut which trails somewhat below the rest of the body. These larvae are readily distinguished from all other known cottid larvae by the presence of multiple preopercular spines (> 5).

Larvae in Group A, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*, all have a distinctively stubby shape, a rounded snout, and a humped appearance in the nape region. They are further distinguished by a series of ventral midline melanophores posterior to the anus that extend onto the ventral finfold as characteristic pigment slashes in flexion and postflexion larvae. These *Artedius* larvae possess distinctive preopercular spination; postflexion larvae have a relatively high number (≥ 14) of preopercular spines. The dorsalmost, middle, and ventralmost spines are larger than the other spines creating the "*Artedius*" spine pattern unique to larvae of this group. Characters such as number of preopercular spines, number of ventral midline melanophores, size at formation of head pigmentation, presence of gut diverticula, and number of branchiostegal rays distinguish larvae of each species of *Artedius*.

Larvae in Group B are *Oligocottus maculosus* and *O. snyderi*. These larvae can be distinguished by the presence of a distinctive bubble of skin situated just anterior to the origin of the dorsal finfold in preflexion and early flexion larvae. Larvae of both species are more slender than larvae in Groups A and C and have a relatively short, compact gut. In contrast to larvae of Group A, the dorsalmost preopercular spine becomes larger than other spines in flexion and postflexion larvae. Characters useful in distinguishing larvae of the two species of *Oligocottus* are number and position of ventral midline melanophores, number of preopercular spines, number of parietal spines or prickles, and presence of melanophores on the nape bubble.

Group C includes *Clinocottus acuticeps*, *C. analis*, *C. embryum*, and *C. globiceps*. Larvae of *C. recalvus*, described by Morris (1951), also belong to Group C based on morphology. This is the least cohesive group in that larvae vary more in morphology and pigmentation than in the other groups. In general, larvae have a long gut, the posteriormost portion of which trails below the rest of the body. Larvae of all species except *C.*

TABLE 3. GROUPINGS OF *ARTEDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* LARVAE BASED ON CERTAIN DIAGNOSTIC CHARACTERS.

| Taxa | Preopercular spines* | "Arctidus" spine pat-tern† | "Clinocottus" spine pat-tern‡ | Ventral midline melano-phores | Branchio-stegals | Gut diver-ticulae | Nape bubble | Hindgut diver-tic-ulae | Head pigment | | Nape pig-ment | Fin-fold pig-ment | Lat-eral pigment# |
|---------------------------------|----------------------|----------------------------|-------------------------------|-------------------------------|------------------|-------------------|-------------|------------------------|--------------|--------------|---------------|-------------------|-------------------|
| | | | | | | | | | Pre-flexion | Post-flexion | | | |
| A. <i>Artedius fenestratis</i> | 18-22 | + | - | 21-23 | 7 | - | - | - | - | - | + | - | - |
| <i>Artedius harringtoni</i> | 18-22 | + | - | 13-19 | 6 | + | - | - | - | - | + | - | - |
| <i>Artedius lateralis</i> | 14-16 | + | - | 22-31 | 6 | + | - | - | + | + | + | - | - |
| <i>Artedius</i> Type 3 | 22-24 | + | - | 9-13 | 6 | + | - | - | - | - | + | - | - |
| B. <i>Oligocottus maculatus</i> | 9-11 | - | + | 16-36§ | 6 | - | + | - | + | + | + | - | - |
| <i>Oligocottus snyderi</i> | 18-22 | - | + | 3-7 | 6 | - | + | - | +/~ | +/~ | + | - | - |
| C. <i>Clinocottus acuticeps</i> | 11-13 | - | + | 2-10 | 6 | - | - | + | + | + | + | - | - |
| <i>Clinocottus analis</i> | 9-11 | - | + | 16-22 | 6 | - | - | + | + | + | + | - | + |
| <i>Clinocottus embryum</i> | 13-14 | - | + | 15-21 | 6 | - | - | - | - | + | + | - | - |
| <i>Clinocottus globiceps</i> | 16-19 | - | + | 4-8 | 6 or 7 | - | - | - | + | + | + | - | - |
| <i>Clinocottus recalvus</i> | 5-12 | - | + | 14-24 | 6 | - | - | - | + | + | + | - | - |
| D. <i>Artedius creaseri</i> | 4 | - | - | 7-11 | 6 | - | - | - | - | + | - | - | - |
| <i>Artedius meanyi</i> | 4 | - | - | 8-13 | 6 | - | - | - | - | + | + | + | - |

* Number at height of development.

† Upper, middle, and lower preopercular spines largest.

‡ Upper preopercular spine largest.

§ Reared larvae from California and Oregon have 14-20 melanophores; reared larvae from British Columbia have 26-36 melanophores.

|| Based partially on Morris 1951.

In postflexion larvae.

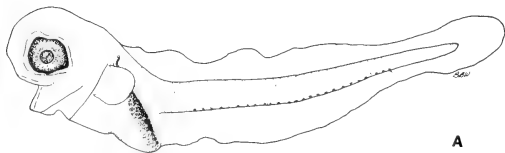
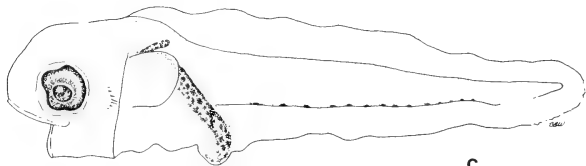
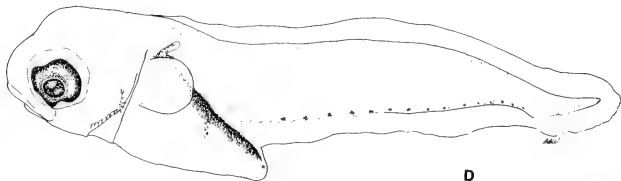
**A****B****C****D**

FIGURE 6. Larvae of *Artedius fenestralis*: A) 3.0 mm NL, B) 3.0 mm NL, C) 4.7 mm NL, D) 6.0 mm NL (from Richardson and Washington 1980).

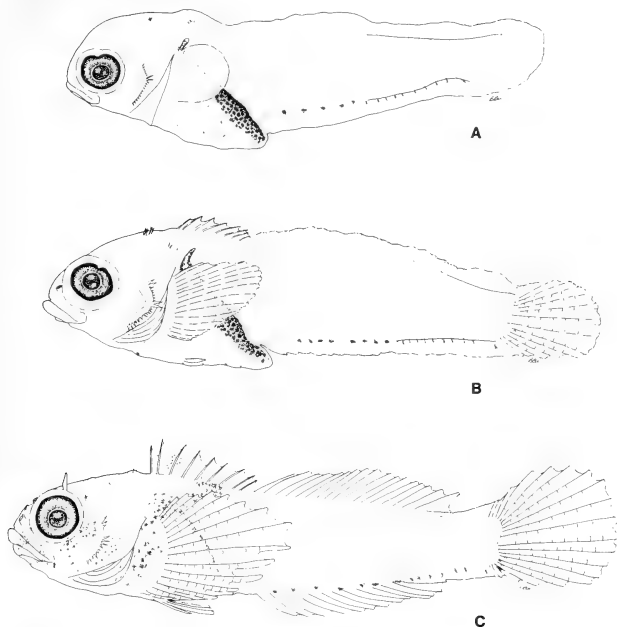


FIGURE 7. Larvae of *Artedius fenestralis*: A) 7.2 mm SL, B) 9.9 mm SL, C) 11.8 mm SL (from Richardson and Washington 1980).

embryum have melanistic pigmentation on the head and nape. The dorsalmost preopercular spine is larger than other preopercular spines in postflexion larvae. Characters such as number of preopercular spines, number and spacing of ventral midline melanophores posterior to the anus, and presence of hindgut diverticula or bulges are useful in separating larvae of each of these *Clinocottus* species.

Group D consists of *Artedius creaseri* and *A. meanyi*. These larvae differ from all other larvae of *Artedius*, *Clinocottus*, and *Oligocottus* species listed above in morphology, pigmentation, and spination. They have pointed snouts and large

heads, light pigmentation, and four preopercular spines. These characters bind them more closely with *Icelinus* larvae. In addition, *A. creaseri* and *A. meanyi* larvae are further distinguished by large blotch-like melanophores situated along the ventral midline posterior to the anus. Snout to anus length, meristics, finfold pigmentation, and nape pigmentation are useful characters in separating larvae of the two species.

Artedius fenestralis

(Figures 6–8; Table 4)

LITERATURE.—Blackburn (1973) illustrated an 8.5 mm SL larva similar to *Artedius fenestralis*,

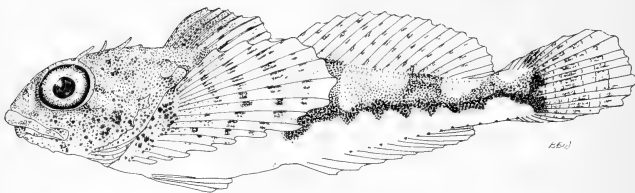


FIGURE 8. Juvenile of *Artedius fenestralis*, 19.1 mm SL.

which he described as Cottid 4. Eldridge (1970) and White (1977) briefly described and illustrated 3.2 mm and 3.9 mm larvae, respectively, which are similar to *A. fenestralis*. These illustrations also closely resemble *A. lateralis* larvae. Richardson and Percy (1977) listed these larvae as *Artedius* sp. 2. Richardson and Washington (1980) described and illustrated specimens 3.0, 4.7, 6.0, 7.2, 9.9, and 11.8 mm long as *Artedius* Type 2.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: high dorsal fin ray counts, absence of nasal and preorbital cirri, and the presence of scales on the head under the entire orbit and in a dense patch on the caudal peduncle. The developmental series was linked together primarily by pigmentation, body shape, gut diverticula, and preopercular and parietal spination. Identification of larvae was further confirmed through comparison with larvae reared from known eggs. Postflexion and transforming larvae were linked with juveniles using pigmentation, cirri patterns, spination, and meristics.

DISTINGUISHING FEATURES.—A combination of characters is useful in distinguishing preflexion *A. fenestralis* larvae including prominent gut diverticula protruding from the dorsal surface of the abdominal cavity, melanistic nape pigmentation, lack of head melanophores, and a series of 13–19 ventral midline melanophores posterior to the anus.

Late flexion and postflexion larvae are further distinguished by the presence of 18–22 preopercular spines with the dorsalmost, middle, and ventralmost spines being larger than the others. Postflexion larvae also have a cluster of 5 or 6

spines situated on the posterior margin of each parietal bone.

Juveniles of *A. fenestralis* are distinguished by meristics, dark pigmentation over the dorsolateral surface of the body, and 13–16 ventral midline melanophores posterior to the anus. Other useful characters include the absence of a nasal and preorbital cirrus, the presence of one or two small cirri on the eyeball, and two frontoparietal cirri.

PIGMENTATION.—Newly hatched larval *Artedius fenestralis* reared in the laboratory have no melanistic pigmentation on the head or nape. Intense melanophores are scattered over the dorsolateral surface of the gut. These lateral gut melanophores are frequently faded and difficult to see in field-collected larvae. Posterior to the anus, a series of 13–19 melanophores originates under the third or fourth postanal myomere and extends posteriorly along the ventral body midline. An additional 1 or 2 melanophores extend onto the ventral finfold near the notochord tip. These ventral midline melanophores are evenly spaced approximately one every other myomere.

During larval development, the head region remains unpigmented. Two to four melanophores are added on the nape in larvae 3.4 mm long and become embedded in musculature over the notochord by ~7 mm. By that size the posterior half of the series of ventral midline melanophores appear as distinctive slashes that extend onto the ventral finfold.

During transformation (planktonic specimens ~12–14 mm long) juvenile pigmentation begins to develop. Melanophores are added on the dorsal surface of the head, on the tip of the lower jaw, and on the pectoral fin base. Gradually, me-

TABLE 4. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *ARTEDIUS FENESTRALIS*, *A. HARRINGTONI*, *A. LATERALIS*, AND *A. TYPE 3*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

| Item | <i>Artedius fenestralis</i> | <i>Artedius harringtoni</i> | <i>Artedius lateralis</i> | <i>Artedius Type 3</i> |
|--|-----------------------------|-----------------------------|---------------------------|-------------------------|
| Head length/SL: | | | | |
| Preflexion | 22.2 ± 1.41 (21.1–25.0) | 20.9 ± 2.30 (18.7–22.3) | 20.2 ± 2.68 (16.4–22.9) | 21.8 ± 0.92 (20.7–23.2) |
| Flexion | 22.1 ± 1.22 (20.3–23.3) | 23.1 ± 3.86 (24.9–27.0) | 23.6 ± 1.92 (19.9–26.1) | 24.6 ± 1.71 (23.3–27.1) |
| Postflexion | 26.1 ± 2.85 (20.8–29.4) | 29.0 ± 0.50 (22.4–34.1) | 26.9 ± 1.89 (24.3–30.8) | 29.0* |
| Juvenile | 33.9 ± 2.08 (32.0–34.9) | 33.6 ± 3.46 (30.4–36.5) | 22.7 ± 3.21 (19.1–25.3) | – |
| Snout length/HL: | | | | |
| Preflexion | 15.1 ± 3.77 (10.5–20.0) | 18.9 ± 5.52 (9.9–25.1) | 28.0 ± 1.83 (25.8–30.1) | 19.8 ± 3.85 (15.4–24.6) |
| Flexion | 20.4 ± 5.96 (12.3–26.6) | 23.7 ± 6.14 (18.3–19.1) | 25.2 ± 1.91 (22.9–29.4) | 23.2 ± 3.51 (19.2–26.7) |
| Postflexion | 21.8 ± 3.57 (17.5–24.5) | 24.2 ± 4.19 (15.8–31.4) | 24.7 ± 3.77 (19.4–30.6) | 29.4* |
| Juvenile | 21.6 ± 2.08 (19.8–23.2) | 23.1 ± 1.00 (22.3–24.3) | 23.0 ± 1.73 (18.9–24.7) | – |
| Eye diameter/HL: | | | | |
| Preflexion | 39.7 ± 4.32 (33.7–46.9) | 44.7 ± 4.57 (39.7–50.1) | 44.7 ± 2.87 (40.8–47.1) | 46.7 ± 6.53 (39.0–57.6) |
| Flexion | 41.2 ± 3.42 (37.4–46.5) | 40.4 ± 7.33 (38.4–43.2) | 40.4 ± 2.88 (37.4–45.5) | 37.1 ± 2.16 (35.3–40.2) |
| Postflexion | 36.9 ± 7.10 (27.3–52.1) | 32.6 ± 4.09 (23.2–39.8) | 36.6 ± 4.06 (37.9–44.6) | 37.9* |
| Juvenile | 29.1 ± 1.00 (24.6–27.3) | 31.2 ± 5.77 (29.8–31.2) | 35.3 ± 5.03 (22.1–24.8) | – |
| Snout to anus length/SL: | | | | |
| Preflexion | 45.3 ± 3.59 (41.2–50.8) | 42.0 ± 3.21 (38.2–48.2) | 40.4 ± 4.83 (33.3–45.6) | 44.8 ± 2.76 (41.4–49.8) |
| Flexion | 45.9 ± 2.49 (44.5–50.1) | 47.3 ± 8.30 (36.5–55.9) | 42.7 ± 3.65 (38.2–47.9) | 45.1 ± 2.63 (43.2–48.1) |
| Postflexion | 48.4 ± 2.26 (42.7–51.4) | 49.9 ± 2.67 (45.9–55.4) | 48.4 ± 2.18 (44.4–50.9) | 50.2* |
| Juvenile | 49.1 ± 2.00 (47.0–51.5) | 47.4 ± 3.21 (43.1–49.2) | 48.7 ± 4.04 (44.1–51.2) | – |
| Snout to pelvic fin origin/SL: | | | | |
| Preflexion | – | – | – | – |
| Flexion | 25.6 ± 3.21 (20.2–29.8) | – | – | 25.3 ± 4.24 (21.9–27.6) |
| Postflexion | 26.1 ± 3.21 (20.2–29.8) | 27.8 ± 1.72 (24.5–30.8) | 28.1 ± 3.11 (24.9–34.1) | 29.3* |
| Juvenile | 30.4 ± 3.51 (26.5–30.1) | 27.4 ± 2.65 (24.1–29.4) | 27.0 ± 3.61 (23.8–31.0) | – |
| Pelvic fin origin to anus/SL: | | | | |
| Preflexion | – | – | – | – |
| Flexion | 22.2 ± 5.35 (16.1–27.0) | – | – | 23.1 ± 4.95 (19.1–26.1) |
| Postflexion | 26.1 ± 3.21 (20.2–29.8) | 22.8 ± 4.68 (17.2–34.8) | 20.1 ± 4.20 (14.4–26.7) | 20.9* |
| Juvenile | 18.9 ± 1.15 (18.2–20.2) | 19.9 ± 1.15 (18.9–21.3) | 22.3 ± 2.08 (20.3–24.1) | – |
| Body depth at pectoral fin base/SL: | | | | |
| Preflexion | 21.7 ± 1.81 (19.0–23.8) | 23.7 ± 2.99 (20.9–29.7) | 23.0 ± 3.16 (17.9–26.3) | 25.9 ± 1.77 (23.4–28.2) |
| Flexion | 28.5 ± 2.70 (24.9–30.1) | 28.1 ± 2.45 (28.0–31.2) | 26.6 ± 2.33 (24.2–27.1) | 28.2 ± 1.76 (26.3–30.1) |
| Postflexion | 28.2 ± 1.82 (24.2–32.1) | 30.5 ± 2.74 (23.4–34.1) | 28.1 ± 2.29 (24.1–32.2) | 30.0* |
| Juvenile | 25.8 ± 1.53 (24.4–26.8) | 22.3 ± 4.15 (24.6–25.2) | 19.7 ± 3.06 (21.9–25.0) | – |
| Body depth at anus/SL: | | | | |
| Preflexion | 19.0 ± 2.49 (14.8–22.2) | 27.8 ± 2.45 (17.2–27.6) | 20.4 ± 2.51 (15.8–21.8) | 22.9 ± 3.28 (18.2–27.2) |
| Flexion | 24.1 ± 2.59 (23.6–27.1) | 30.4 ± 3.32 (28.1–34.7) | 26.3 ± 2.29 (24.5–31.3) | 29.1 ± 2.06 (26.1–31.3) |
| Postflexion | 27.9 ± 2.79 (21.4–32.8) | 20.9 ± 5.77 (23.9–34.8) | 26.3 ± 2.82 (22.4–33.0) | 30.3* |
| Juvenile | 21.6 ± 2.65 (18.9–24.4) | 28.0 ± 1.72 (20.8–21.9) | 30.3 ± 3.51 (17.4–22.8) | – |
| Pectoral fin length/SL: | | | | |
| Preflexion | 9.1 ± 0.98 (8.2–10.9) | 7.4 ± 2.34 (4.4–11.1) | 11.0 ± 1.08 (9.6–12.2) | 10.4 ± 2.91 (7.1–13.3) |
| Flexion | 9.4 ± 0.71 (8.4–10.4) | 12.1 ± 3.54 (9.9–15.4) | 12.3 ± 1.98 (9.6–15.9) | 11.2 ± 3.50 (7.4–15.1) |
| Postflexion | 22.6 ± 6.21 (9.7–29.7) | 24.6 ± 7.59 (10.3–34.6) | 19.8 ± 4.66 (13.3–27.6) | 21.0* |
| Juvenile | 26.2 ± 1.53 (27.1–28.4) | 34.1 ± 3.61 (29.9–36.6) | 30.3 ± 3.51 (26.8–34.2) | – |

– = Not present at this stage.

* = Only one specimen available in this stage.

lanophores develop on the anteriormost portion of the spinous dorsal fin, then extend ventrally as a band of pigment stretching from the fourth or fifth dorsal spine to the pigmentation over the dorsal surface of the gut just posterior to the pectoral fin base.

Juvenile pigmentation increases markedly in newly settled individuals 13 mm SL. Numerous melanophores are added over the dorsolateral surface of the head and become concentrated in the parietal-interorbital region. Additional melanophores extend down onto the snout and lips. Laterally, melanophores are added in the cheek region between the eye and the preopercle and the dorsal portion of the opercle. Several melanophores are clustered at the posterior edge of the lower jaw. The ventral surface of the head remains unpigmented. Pigmentation gradually extends from the head posteriorly across the dorsolateral surface of the body until it fuses with bands of pigment reaching from the middle of the spinous dorsal fin to the gut. Pigmentation increases on the anterior end of the dorsal fin creating a dark blotch of pigment across the first four dorsal spines. Melanistic pigmentation also increases on the pectoral fin base with melanophores extending onto the pectoral fin rays and eventually forming several bands of pigmentation. Several irregular clusters of melanophores appear along the lateral midline and gradually form a band of pigment reaching from the gut to the caudal peduncle.

As juvenile pigmentation develops, saddles of pigment form along the dorsum in an anterior to posterior sequence. The first saddle or band of pigment forms under the 4th–7th dorsal fin rays. Gradually, melanophores extend ventrally from the pigment saddle and merge with the lateral midline melanophores. Concurrently, a second saddle of pigment forms under the 9th–10th dorsal fin rays, while a third saddle of pigment begins to develop under the 13th–15th dorsal fin rays. Melanophores from these pigment saddles also extend ventrally and fuse with the lateral midline pigment. At the same time, melanophores are added on the dorsal fin forming three to four bands. Melanophores extend ventrally from the lateral midline band and form a series of five to eight scallops which reach just below the lateral midline. The rest of the ventrolateral surface of the body remains characteristically unpigmented until juveniles reach about 19–20 mm. As the dorsal pigment saddles are forming, the

lateral midline melanophores extend posteriorly to the base of the caudal fin where they form a dark band. Gradually, melanophores extend onto the caudal fin rays forming three or five indistinct bands of pigment. Approximately 13–16 ventral midline melanophores remain visible in juveniles up to ~20 mm long.

MORPHOLOGY.—Larvae of *Artedius fenestralis* hatch at ~3.5–3.8 mm NL. Flexion of the notochord occurs between 5.9 and 6.8 mm NL. The largest planktonic larva collected is 13.9 mm and is beginning to undergo transformation. The smallest benthic juvenile examined is 13.1 mm. Thirty-four selected specimens, 3.2–21.2 mm, were examined for developmental morphology.

Larval *A. fenestralis* have stubby bodies with a humped appearance in the nape region. Distinctive diverticula extend dorsolaterally from the dorsal surface of the gut just posterior to the origin of the pectoral fin base. These diverticula are present in newly hatched larvae and remain prominent in the largest planktonic larvae. The diverticula completely disappear in benthic juveniles shortly after settling. The gut itself is moderately long and the posterior portion of the hindgut trails well below the rest of the body. Snout to anus length increases from 43% to 45% SL during larval development, then increases to 49% SL in benthic juveniles. *Artedius fenestralis* larvae have a short, rounded snout with snout length increasing from 15% HL in preflexion larvae to 23% HL in postflexion larvae and juveniles.

FIN DEVELOPMENT.—Caudal fin rays begin to form at ~6 mm. The adult complement of principal caudal rays is present in larvae ~7 mm long. The bases of the dorsal and anal fin rays appear in 7–7.5 mm larvae. The full complement of fin rays is formed by ~8.5–9 mm. Dorsal fin spines begin to form at ~8 mm, and the full complement of spines (VIII–IX) is present by ~9.5 mm. Although pectoral fin rays are visible by ~7 mm, the adult complement (14–16) is not formed until ~9 mm. Pelvic buds form between 6.5 and 7 mm and the adult complement of 1,3 pelvic fin rays is formed in larvae ~10 mm long.

SPINATION.—Seven to 13 tiny spines begin to form along the posterior margin of the preopercle in larvae ~4.7 mm NL. The preopercle appears to develop in two arc-shaped sections, which overlap slightly at the angle of the preopercle. Three to 7 spines are present along the dorsalmost section and 6–8 spines occur on the lower

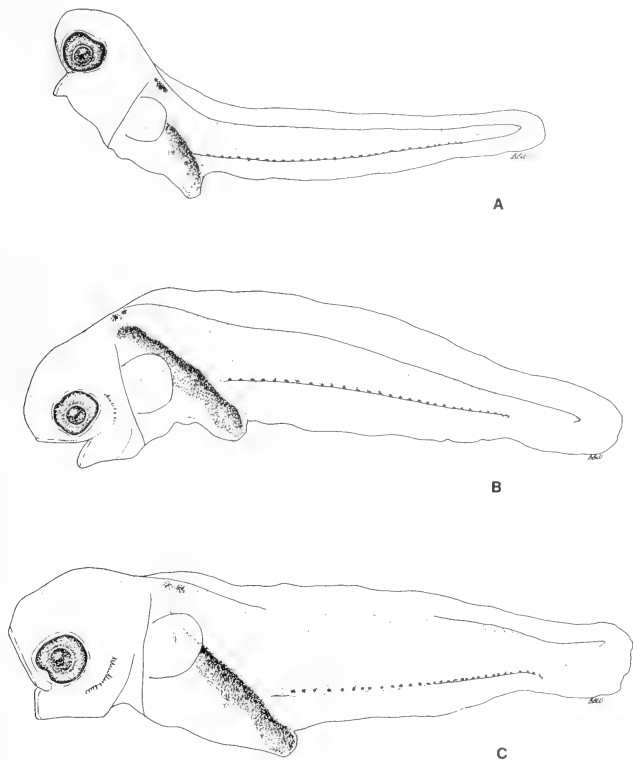


FIGURE 9. Larvae of *Artedius harringtoni*: A) 3.0 mm NL, B) 4.7 mm NL, C) 6.9 mm NL (from Richardson and Washington 1980).

section. The two sections fuse together in post-flexion 7 mm long. Two spines located at the site of fusion begin to increase in length relative to the other preopercular spines. Concurrently, the preopercular spines increase in number during larval development and range between 18 and

21 in larvae >8 mm long. The dorsalmost and middle two spines continue to increase in size relative to the other spines, becoming nearly three times as long. The ventralmost 2 or 3 spines also increase in size, becoming 1.5 to 2 times as long as the other spines. The number of preopercular

spines decreases in transforming larvae > 13 mm long. The smaller spines (4–6, 8–10, and 13–15) begin to regress first. Newly settled juveniles possess one large dorsal preopercular spine. The lower spines are visible only as serration, or bumps, on the preopercular margin. The dorsalmost spine continues to increase in size while the lower bumps eventually disappear in juveniles ~ 19 mm long.

Clusters of spines also develop in the parietal and supracleithral-posttemporal regions. One or two spines form at the posterior end of the parietal in larvae ~ 6 or 7 mm long. A third spine is added in 7–8-mm larvae. Larvae > 8 mm have four to six spines located in two rows on each side of the head. Usually, three spines occur in the anterior row while two or three spines are present in a second row posterior to and parallel to the first row. These spines begin to regress in size in transforming larvae > 12–13 mm long. The anterior spines curve posteriorly, eventually fusing with spines from the posterior row forming a hollow arch and canal. This canal develops into part of the cranial lateral line system in juveniles ~ 14–15 mm long.

Two small spines develop on the ventral portion of the posttemporal in larvae 6–7 mm long. A third spine is added on the posttemporal in larvae > 8 mm long. Concurrently, another spine develops on the dorsal tip of the supracleithrum. These spines remain prominent in planktonic larvae ≤ 12 mm long; however, in transforming juveniles the spines gradually curve dorsally and ventrally and fuse together forming a bony tube or canal. This canal becomes the anteriormost juncture of the lateral line and cephalic lateral line systems in juveniles.

Artedius harringtoni

(Figures 9–11; Table 4)

LITERATURE.—Blackburn (1973) described a 4.6 mm larva that he called Cottid 6 that is similar to *A. harringtoni*. Richardson and Washington (1980) illustrated and described specimens 3.0, 4.7, 6.9, 7.3, 9.3, and 13.6 mm long.

IDENTIFICATION.—Juveniles and adults were identified primarily on the basis of the following characters: high dorsal fin ray counts (16–18), low pectoral fin ray counts (usually 14), presence of seven branchiostegals, presence of a preorbital cirrus, scales extending onto the head under only the posterior portion of the orbit, and scales ab-

sent on the snout. The developmental series of larvae was linked together by pigmentation, preopercular spination, absence of gut diverticula, body shape, and the possession of seven branchiostegals. Postflexion and transforming larvae were linked with juveniles primarily on the basis of pigmentation, meristics, and presence of a preorbital cirrus.

DISTINGUISHING FEATURES.—Characters useful in distinguishing small larval *A. harringtoni* are a combination of presence of melanistic nape pigment, lack of head pigmentation, a series of 21–33 pigment slashes along the ventral midline of the tail, and a humped appearance in the nape region. Absence of dorsal gut diverticula distinguishes larval *A. harringtoni* from similarly pigmented larvae of *A. lateralis*, *A. fenestralis*, and *A. Type 3*.

Postflexion larvae 6.5 mm are distinguished by the presence of 18–22 spines along the posterior margin of the preopercle. The dorsalmost and middle preopercular spines are characteristically larger than the other spines. Larvae > 7 mm have seven branchiostegal rays. Larvae of all other species of *Artedius* have only six branchiostegal rays.

Juvenile *A. harringtoni* may be recognized by the dark pigmentation over the head and nape, possession of seven branchiostegals, retention of 18–22 ventral midline melanophores, possession of a preorbital cirrus, and dorsal and pectoral fin ray counts.

PIGMENTATION.—Preflexion larvae have no melanistic pigmentation on the head; however, 3–5 small, external melanophores are concentrated in a dense patch on the nape. The dorsolateral surface of the gut is covered with numerous large, intense melanophores. One to 8 tiny melanophores encircle the anus. Posterior to the anus, the only pigmentation consists of a series of 23–33 melanophores positioned along the ventral midline. This series originates under the first to third postanal myomere and extends posteriorly toward the tail tip with 1 or 2 melanophores positioned under each myomere. An additional 1 to 3 melanophores frequently occur on the caudal finfold near the tail tip.

During larval development the head region remains unpigmented. The nape melanophores become embedded in the musculature over the notochord in larvae > 7 mm. Concurrently, the number of ventral midline melanophores decreases to between 21 and 30, and the posterior

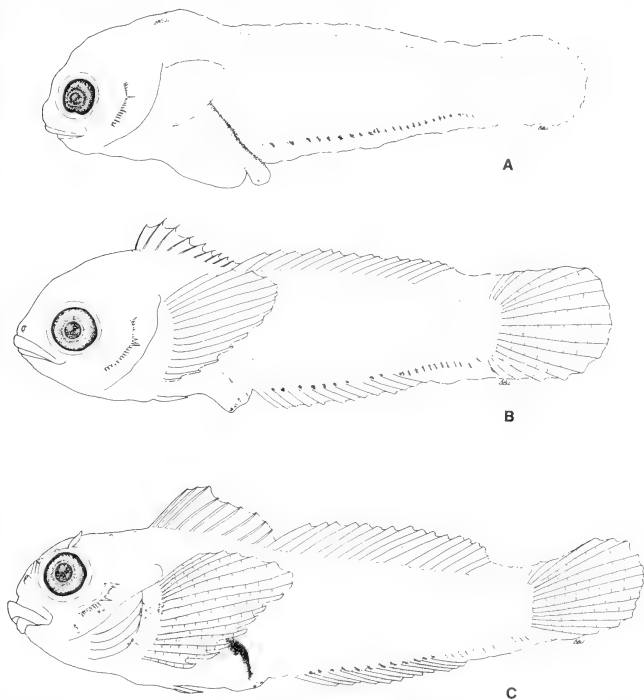


FIGURE 10. Larvae of *Artedius harringtoni*: A) 7.3 mm SL, B) 9.3 mm SL, C) 13.6 mm SL (from Richardson and Washington 1980).

half of the series appears as characteristic pigment slashes that extend onto the ventral finfold.

During transformation, planktonic larvae > 10 mm begin to develop juvenile pigmentation. Melanophores are added on the tip and base of the lower jaw, on the cheek between the eye and the dorsalmost preopercular spine, on the operculum, and on the isthmus.

Pigmentation increases markedly over the head

in newly settled benthic juveniles. Melanophores develop on the snout and upper lip and on the dorsal surface of the head over the brain. Melanophores gradually extend posteriorly from the head and eventually join with the nape pigmentation. Concurrently, melanophores extend posteroventrally from the posttemporal region toward the dorsal gut pigment. Numerous large melanophores form over the base of the pectoral

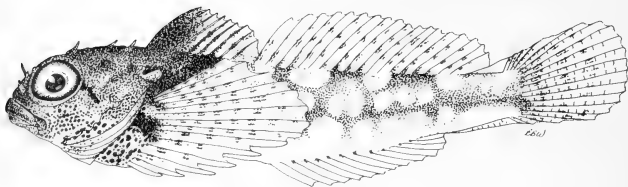


FIGURE 11. Juvenile of *Artedius harringtoni*, 13.9 mm SL.

fin, and subsequently extend onto the pectoral fin rays forming four or five distinct pigment bands across the fin. A band of melanophores also extends ventrally from the pectoral fin base and covers the isthmus.

In juveniles >13 mm long, the entire head is heavily pigmented. Melanophores extend posteriorly from the head to a vertical line under the seventh dorsal fin spine. A dense patch of melanophores develops at the anterior end of the spinous dorsal fin forming a dark blotch across the fin membrane between the first four dorsal spines. Scattered melanophores are added along the rest of the dorsal fin eventually forming three or four bands of pigment.

Posterior to the head, pigmentation is added in three saddles along the dorsum. The first saddle of pigment forms under the 2nd–4th dorsal fin rays, the second saddle forms under the 7th–10th dorsal fin rays, and the third forms under the 13th–15th fin rays. Concurrently, an irregular band of faint melanophores develops along the lateral midline. This lateral pigmentation gradually extends posteriorly from the abdominal region to the caudal peduncle. As development proceeds, bands of melanophores extend ventrally from each of the saddles on the dorsum and merge with the lateral midline pigment. As a result, the dorsolateral surface of the tail is covered by bands of pigmentation, which enclose small unpigmented saddles and circles creating a characteristic pattern.

Subsequently, groups of melanophores extend ventrally from the lateral midline pigmentation creating a scalloped edge of pigment along the ventrolateral body surface. Eventually, melanophores from the tips of each scallop extend laterally and join together enclosing four to six distinctive unpigmented circles, characteristic of juvenile *A. harringtoni*.

In late stages of juvenile pigmentation, the lateral band of melanophores extends posteriorly to the base of the caudal fin. Melanophores are added on the caudal fin rays forming five to seven bands of pigmentation.

Between 18 and 21 ventral midline melanophores remain visible in juveniles <15 mm.

MORPHOLOGY.—The smallest *A. harringtoni* larva from plankton collections is 3.0 mm NL and still retains remnants of its yolk. Larvae undergo flexion of the notochord between 5.2 and 6.4 mm NL. The largest planktonic larva examined is 13.6 mm long and beginning to undergo transformation. The smallest benthic juvenile collected in tidepools is 12.9 mm and is just beginning to develop juvenile pigmentation on the head and pectoral fin base. Thirty-five selected specimens, 3.0–13.7 mm, were examined for morphometrics.

Larvae of *A. harringtoni* are stubby with a distinctive humped appearance in the nape region. Unlike larval *A. fenestralis*, *A. lateralis*, and *A. Type 3*, larval *A. harringtoni* have no dorsal gut diverticula. The gut is moderately long with snout to anus length ranging from 42% in preflexion larvae to 50% SL in postflexion larvae. Relative snout to anus length decreases slightly in benthic juveniles. The hindgut appears to trail below the rest of the body. Relative body depth at the pectoral fin base increases from 23% in preflexion larvae to 30% in flexion and postflexion larvae.

Artedius harringtoni have blunt heads and rounded snouts. Head length increases relative to body length during development, averaging 21% in preflexion larvae, and 34% SL in juveniles. Snout length increases from 19% to 22% HL during larval development.

FIN DEVELOPMENT.—A thickening in the hypural region of the developing caudal fin is first visible at 4.7 mm NL, just prior to the onset of

notochord flexion which occurs at ~5.2 mm NL. Caudal fin rays begin to form in larvae ~6 mm; however, the adult complement of principal caudal rays is not complete until larvae reach ~7 mm long.

Bases of the dorsal and anal fin rays form in larvae ~6–7 mm long. Dorsal spines begin to form in larvae ~7–8 mm long. The adult complement of dorsal and anal fin rays is complete at 9.3 mm. Pectoral fin rays are first visible between 6 and 7 mm, and the adult complement (13–15) is countable at ~7.5 mm. The pelvic fin bud begins to form at ~7.1 mm, and the adult complement of I,3 is complete by ~10 mm.

SPINATION.—Eight to ten tiny spines begin to form along the posterior margin of the preopercle in larvae ~4.5 mm NL. The number of spines increases to 18–22 in flexion and postflexion larvae. By the end of flexion, ~6.7 mm, the middle two spines (7–9) begin to increase in size relative to the other preopercular spines. In larvae >7.5 mm, the dorsalmost two or three spines also increase in size relative to other spines. As development proceeds, the dorsalmost and middle spines increase in length and diameter creating a characteristic pattern with small, inconspicuous spines situated between the dorsalmost and middle spines, and ventral to the middle spines. In larvae >8.5 mm, the ventralmost four or five spines also become somewhat larger than the spines directly above them. When larvae reach ~10–11 mm SL, the preopercular spines begin to regress with the small, inconspicuous spines disappearing first. At the onset of transformation (~12–13 mm) only four spines remain in the approximate position of the original spines (1–2, 4–9, 12–14, and 18–22). In newly settled juveniles, the dorsalmost preopercular spine becomes quite long and stout while the lower three spines gradually become smaller and visible only as slight bumps on the margin of the preopercle.

Spines never develop in the parietal and post-temporal region of the head. However, in cleared and stained larvae, bony thickenings are visible in the parietal region at the same position as parietal spines found in other cottid larvae.

Artedius lateralis

(Figures 12, 13; Table 4)

LITERATURE.—Budd (1940) described and illustrated a newly hatched larva of *A. lateralis* 4.1 mm TL. Marliave (1975) described larvae of *A. lateralis* and illustrated specimens 4 mm TL, 8 mm TL, 11 mm TL, and 14 mm TL long.

IDENTIFICATION.—Small larval *A. lateralis* were reared from eggs spawned from known adults. Juveniles and adults were identified using the following characters: pigmentation, absence of scales on the head and caudal peduncle, absence of nasal and preorbital cirri, and the presence of 3–11 scales in the longest row in the dorsal scale band. The developmental series was linked together primarily on the basis of pigmentation, preopercular spination, presence of gut diverticula, and body shape. Postflexion and transforming larvae were linked to juveniles by pigmentation, cirri patterns, spination, and meristics.

DISTINGUISHING FEATURES.—Characters useful in distinguishing preflexion larvae of *Artedius lateralis* are prominent diverticula which extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin bases, the lack of head and nape pigment in larvae <6 mm NL, and a series of 22–32 melanophores that lie along the ventral midline posterior to the anus. The anterior half of the series is characterized by one large melanophore per myomere while the posterior half of the series consists of two or three smaller pigment slashes per myomere.

Postflexion larvae of *A. lateralis* >6.2 mm can be distinguished from other *Artedius* larvae by melanistic pigmentation over the brain. Juvenile *A. lateralis* are distinguished by two dark bars of melanophores extending ventrally from the dorsal fins across the lateral surface of the body trunk, the series of 11–21 ventral midline melanophores, and meristics.

PIGMENTATION.—Newly hatched larvae of *A. lateralis* have no melanistic pigmentation on the head or nape. Dense, round melanophores are concentrated over the dorsolateral surface of the gut and extend dorsally onto the gut diverticula. A cluster of 4 to 6 small melanophores surrounds the anus. Posterior to the anus, a series of 22–32 melanophores lies along the ventral midline of the body. These melanophores originate under the third or fourth postanal myomere and extend posteriorly toward the tail tip where several additional melanophores extend onto the caudal finfold. Melanophores in the anterior half of this series are relatively large and spaced one per myomere. The posteriormost melanophores appear as small pigment slashes, which extend onto the ventral finfold and are closely spaced two or three to every myomere.

During larval development, melanophores form on the dorsal surface of the head in larvae >6.3 mm. Two to five melanophores also form

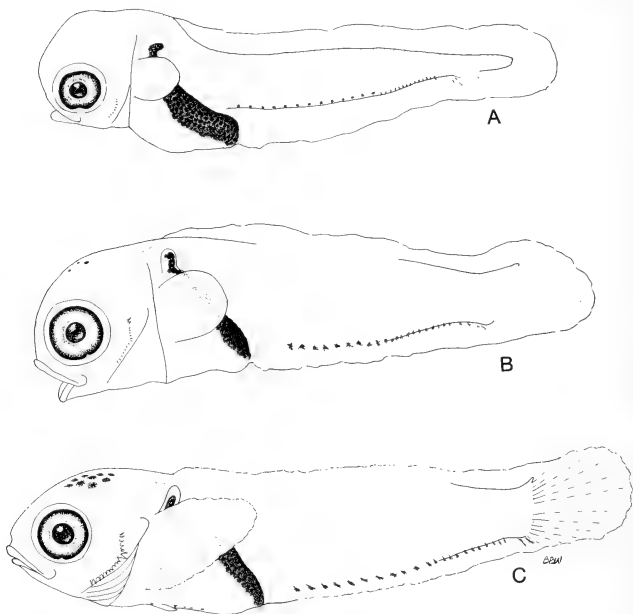


FIGURE 12. Larvae of *Artedius lateralis*: A) 4.6 mm NL, B) 6.4 mm SL, C) 7.1 mm SL.

at the base of the cleithrum and along the ventral midline of the gut in larvae >5.2 mm. These melanophores are arranged in a characteristic T shape with two melanophores positioned as horizontal slashes at the base of the cleithrum and one to three melanophores extending posteriorly along the ventral midline of the gut.

During transformation, in planktonic larvae >8 mm, melanistic pigmentation increases markedly on the dorsal surface of the head with 33–44 dark melanophores covering the brain. Melanophores also form just posterior to the lower jaw, on the cheek between the eye and the preopercle and on the operculum. Ventral mid-

line melanophores remain unchanged in number and spacing.

Pigmentation increases markedly in newly settled juveniles >10 mm long. Dark melanophores form on the dorsolateral surfaces of the head and extend anteriorly onto the snout and upper and lower lips. Several melanophores are added to the gular region beneath the lower jaw. Intense pigment forms on the bases of the pectoral fins and several large melanophores extend onto the pectoral fin rays. Gradually, melanophores from the base of the pectoral fin extend ventrally forming a band of pigment across the isthmus. With development, pigmentation increases on the head

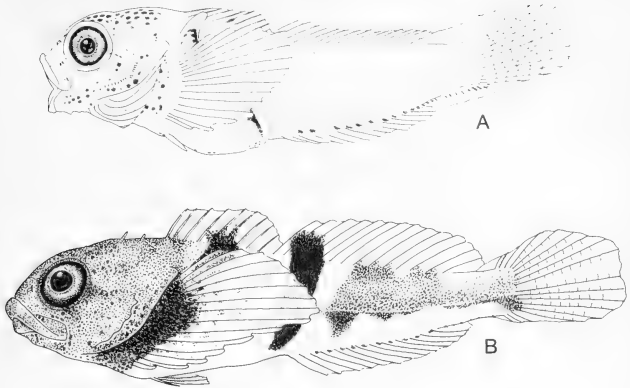


FIGURE 13. Young of *Artedius lateralis*: A) 9.1 mm SL, B) 13.3 mm SL.

so that in larvae ≥ 12 mm SL, the entire head is darkly pigmented.

Shortly after settling, in larvae between 10 and 11 mm, a patch of melanophores is added to the dorsal fin between the fourth and sixth spines. These melanophores extend ventrally across the dorsum toward the pigmentation on the pectoral fin base. A second band of melanophores forms on the second dorsal fin membrane between the 2nd and 4th fin rays. Gradually this band extends anteroventrally below the lateral midline. With development, the two vertical bands of pigment become very dark and intense. Melanophores from these bands extend dorsally across the dorsal fins. Concurrently, three saddles of faint melanophores are added posteriorly along the dorsum. The first saddle of pigment forms under the 8th–10th dorsal fin rays, the second saddle is added under the 12th–15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Gradually, melanophores from these pigmented saddles extend ventrolaterally and join together forming a band along the lateral midline. Lateral pigmentation extends posteriorly and forms a band along the base of the caudal fin. Melanophores extend onto the caudal fin rays,

gradually forming two or four distinct bands across the caudal fin. Ventral midline melanophores decrease in number in juveniles from 11 to 21. These melanophores remain visible in juveniles < 15 mm long.

MORPHOLOGY.—*Artedius lateralis* larvae are 3.9–4.5 mm long at hatching. Flexion of the notochord occurs between 5.0 and 6.3 mm NL. The largest planktonic specimen observed is 9.2 mm and beginning to develop juvenile pigmentation. *A. lateralis* settle at a relatively small size, ~ 9.5 to 10.5 mm. Thirty-three specimens (4.1–12.1 mm) were examined for developmental morphometrics.

Larvae of *A. lateralis* are rather stubby with a moderately short gut. Snout to anus length averages 40% in preflexion larvae, then increases to 48% SL in postflexion larvae and juveniles. Pronounced diverticula extend dorsally from each side of the gut just posterior to the pectoral fin base. The diverticula are present in newly hatched larvae and remain prominent throughout larval development. Tiny remnants of the diverticula are present in newly settled juveniles between 9 and 10.5 mm long.

Larvae of *A. lateralis* have a long rounded snout

relative to other *Artedius* Group A larvae. Snout length decreases from 28% to 24% HL during larval development.

FIN DEVELOPMENT.—The notochord begins to flex in larvae ~5 mm long, and is fully flexed in larvae between 5.7 and 6.3 mm. Caudal rays begin to form during flexion in larvae ~5.5 mm; however, the adult complement of 6 + 6 principal caudal rays is not complete until ~6 mm. Bases of the dorsal and anal fins are first visible in larvae between 6 and 6.5 mm and the adult complement of dorsal (15–17) and anal (12–14) rays is complete by about 7.5–8 mm.

Pectoral fin rays begin to form between 7 and 8 mm, but the full complement of rays (14–16) is not formed until larvae are ~8 mm long. Pelvic fin buds are first visible in a 7.4 mm larva; however, the fin rays are not countable until 9 mm.

SPINATION.—In preflexion larvae ~4.5 mm NL 8–9 tiny spines are visible on the posterior margin of the preopercle. As larvae undergo flexion of the notochord, the number of preopercular spines increases to 9–14. By the end of flexion, larval *A. lateralis* have 14–16 preopercular spines. In larvae >7 mm, the dorsalmost and middle (spines 6–9 from the top of the preopercle) become slightly longer than the other preopercular spines. These spines never become more than 1.5 times larger than the other preopercular spines, in contrast to the situation in larvae of *A. harringtoni*, *A. fenestralis*, and *A. Type 3* in which the dorsalmost and middle preopercular spines may be nearly 2.5 times larger than the other spines. Preopercular spines begin to regress in transforming specimens >9 mm. The dorsalmost spine increases in size while the lower spines (4–6 and 9–12) decrease in size becoming visible only as small serrations or irregularities on the preopercular margin. Spines 7–8, 12–13, and 16–18 fuse together to form blunt bumps along the preopercular margin. In juveniles >13 mm, only the large, dorsalmost spine remains. Transforming larvae reared in the laboratory possess 4–5 small spines at the posterior margin of the parietals. These spines are not present in planktonic larvae from field collections, nor are they visible in newly settled juveniles from tidepools.

Artedius Type 3

(Figures 14, 15; Table 4)

LITERATURE.—Larvae of *Artedius* Type 3 have not been previously described.

IDENTIFICATION.—Only a partial size series (2.9–7.6 mm) of *Artedius* Type 3 larvae are available, all from California collections. The presence of prominent gut diverticula and the characteristic *Artedius*-type preopercular spine pattern (dorsalmost, middle, and ventralmost spines larger than the others) identifies this larval type as an *Artedius*. Larvae remain unknown for only two species of *Artedius*, *A. corallinus* and *A. notospilotus*. Meristics of the largest larva of *Artedius* Type 3 coincide with those recorded for both *A. corallinus* and *A. notospilotus*. However, pectoral counts fit those of *A. notospilotus* most closely. The 7.6 mm larval *A. Type 3* possesses 16 pectoral fin rays. Ninety % of the *A. notospilotus* examined by Howe and Richardson (1978) possessed 16 pectoral fin rays while only 10% of *A. corallinus* specimens possessed 16 pectoral fin rays.

Pigmentation along the ventral midline posterior to the anus of *A. Type 3* larvae (9–13 widely spaced melanophores) coincides most closely with that of juvenile *A. corallinus*. Several *A. corallinus* 13.5–14 mm long, possess 3–6 widely spaced ventral midline melanophores. In contrast, a 16-mm juvenile *A. notospilotus* possesses 24 ventral midline melanophores spaced one every one or two myomeres.

Adult *A. corallinus* are common in the intertidal areas of the southern California coast where *Artedius* Type 3 larvae were collected (Miller and Lea 1972). *Artedius notospilotus* adults are rare in the same area.

Additional larger specimens are needed before larvae of *Artedius* Type 3 can be specifically identified.

DISTINGUISHING FEATURES.—*Artedius* Type 3 larvae are distinguished as an *Artedius* by the distinctive diverticula that extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin base. *Artedius* Type 3 larvae are distinguished from small larvae of *A. fenestralis*, which possess similar diverticula, by the low number (9–13) of ventral midline melanophores posterior to the anus. Other characters useful in distinguishing small *A. Type 3* larvae are absence of head pigmentation and presence of a cluster of 2–4 melanophores in the nape region. Preopercular spines begin to form in larvae <4.1 mm NL. Preopercular spines do not form in other *Artedius* larvae with multiple preopercular spines until ~4.5 mm NL. Flexion and postflexion larval *Artedius* Type 3 possess 21–

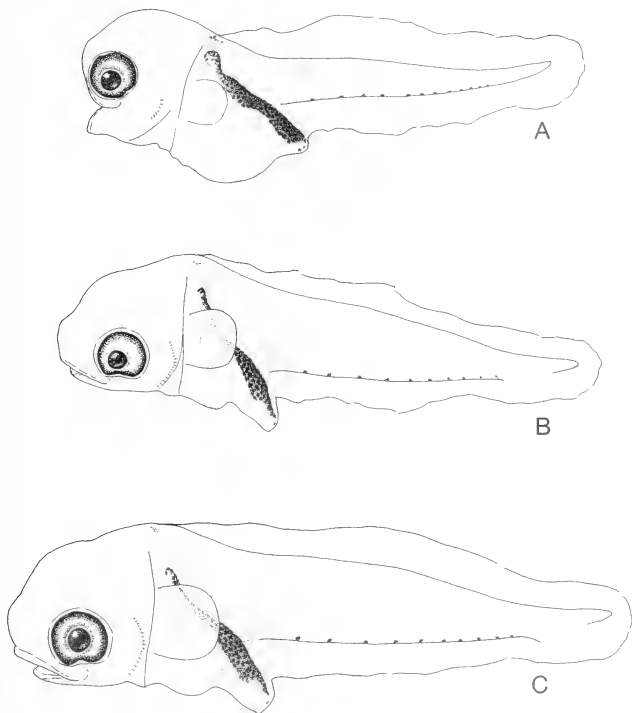


FIGURE 14. Larvae of *Artedius* Type 3: A) 3.2 mm NL, B) 4.1 mm NL, C) 4.9 mm NL.

24 preopercular spines, more than other larval *Artedius* (groups A and D), all of which have ≤ 21 preopercular spines.

PIGMENTATION.—Small preflexion larvae of *Artedius* Type 3 possess no melanistic head pigmentation. Two to four small external melanophores are clustered on the surface of the nape. Numerous dark, rounded melanophores are concentrated over the dorsolateral surface of the gut

and extend dorsally onto the gut diverticula. One to four small melanophores are clustered around the anus.

Posterior to the abdominal cavity, the only pigmentation consists of a series of 9–13 melanophores located along the ventral midline. This series of melanophores originates under the third to fourth postanal myomere and extends posteriorly toward the tail tip. Each melanophore is

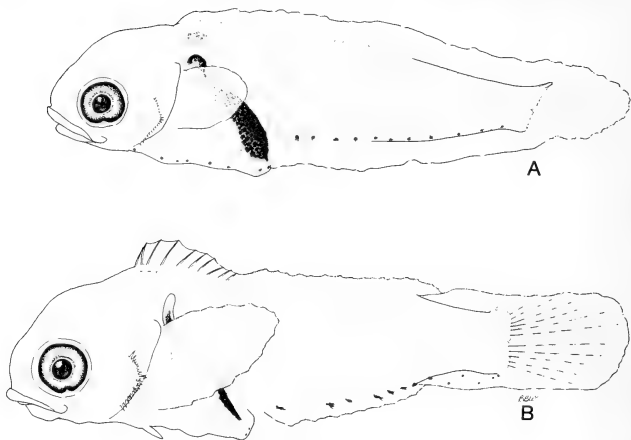


FIGURE 15. Larvae of *Artedius* Type 3: A) 6.8 mm SL, B) 7.3 mm SL.

spaced approximately two to three myomeres apart. An additional one to five pigment slashes extend onto the caudal finfold near the tail tip.

Pigmentation changes little during larval development. Melanophores are added in the nape region and become embedded in the musculature over the notochord in larvae < 5.5 mm. Melanophores are also added in the isthmus region and along the ventral midline of the gut.

MORPHOLOGY.—The smallest larval *Artedius* Type 3 is 2.9 mm NL and possesses remnants of the yolk sac. Larvae undergo flexion of the notochord between 5.6 and 6.9 mm NL. The largest specimen examined is 7.6 mm long and has recently completed notochord flexion. Size at transformation is unknown. Thirteen larvae (2.9–7.6 mm long) were examined for developmental morphology.

Larvae of *Artedius* Type 3 are rather stubby with a moderately long gut; the posteriormost portion of this gut trails somewhat below the rest of the body. A prominent diverticulum extends dorsally from each side of the gut just posterior to the base of the pectoral fin. Diverticula are present in the smallest larva examined (2.9 mm

NL) and remain pronounced in the largest specimen.

Snout to anus length averages 45% SL in both preflexion and flexion larvae. Body depth at the pectoral fin base increases during development from 26% in preflexion larvae, to 28% in flexion larvae, and 32% SL in the single postflexion larva. Relative body depth at the anus also increases with development, from 23 to 30% SL. The distances from the snout to the origin of the pelvic fins and from the origin of the pelvic fins to the anus averages 26 and 22% SL, respectively, in late flexion and early postflexion larvae.

Artedius Type 3 larvae have a rather large head with a blunt, rounded snout. With development relative head length increases from an average of 22% in preflexion larvae to 25% in larvae undergoing flexion of the notochord, and 29% SL in the postflexion larva. Jaw length averages about 43% HL throughout early larval development. In contrast, eye diameter decreases during development from an average of 47% in preflexion larvae to 37% HL in flexion and early postflexion larvae.

FIN DEVELOPMENT.—A 4.9-mm NL larva ex-

hibits a slight thickening of the hypural region of the forming caudal fin. By 5.6 mm, the notochord of larval *A.* Type 3 is strongly flexed and caudal rays are beginning to form. Notochord flexion is nearly complete by ~7 mm and the adult complement (6 + 6) of principal caudal rays is countable.

The dorsal and anal fin bases are first visible in larvae between 6.8 and 6.9 mm long. In the largest specimen examined, 7.6 mm, the adult complement of dorsal spines (IX), dorsal rays (13–15), and anal fin rays (12) is complete. Pectoral fin rays begin to form in a larva 6.8 mm NL, and 16 pectoral fin rays are countable in a larva 7.6 mm. Pelvic fin buds are first visible at ~6.8 mm NL; however, pelvic fin rays are not yet formed in the largest specimen.

SPINATION.—Preopercular spines begin to form in small preflexion larvae of *A.* Type 3 at ~4.1 mm NL. A series of 15–17 tiny, equal-sized spines is visible along the posterior margin of the preopercle in preflexion larvae between 4.1 and 5 mm NL. During development, preopercular spines increase in number ranging from 21 to 24 in flexion and early postflexion larvae.

In late flexion larvae (~6.8–6.9 mm NL) the middle 2 or 3 preopercular spines (the 8th–11th spine from the dorsal margin of the preopercle) begin to increase in size relative to other preopercular spines. In the 7.6-mm larva, the dorsalmost and ventralmost 1 or 2 spines are also larger than other preopercular spines. This forms the characteristic preopercular spine pattern found in *Artedius* larvae with multiple preopercular spines: the dorsalmost, middle, and ventralmost spines are markedly larger than the other preopercular spines.

No other spines develop on the head in larvae ≤7.6 mm. Head spination in larger larvae remains unknown.

Oligocottus maculosus

(Figures 16, 17; Table 5)

LITERATURE.—Stein (1972, 1973) described *O. maculosus* larvae and illustrated specimens 4.6, 6.0, 6.6, and 9.2 mm TL.

IDENTIFICATION.—Larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (33–34) and dorsal fin ray (15–18) counts, small size at transformation (8–9 mm), absence of cirri

on the nasal spines and along the base of the dorsal fins, and pigmentation. The developmental series was linked together primarily on the basis of pigmentation, preopercular and parietal spination, and body shape. Postflexion and transforming larvae were linked to juveniles by the serial method utilizing pigmentation, spination, and size at transformation.

DISTINGUISHING FEATURES.—Newly hatched larvae of *O. maculosus* reared in the laboratory are distinguished by the following pigmentation characters: intense melanistic nape pigment, dark dendritic melanophores that extend onto a prominent bubble of skin in the nape region just anterior to the origin of the dorsal finfold, 1 or 2 melanophores situated anteriorly on the visceral mass beneath the pectoral fins, and a series of 18–36 ventral midline melanophores posterior to the anus. In addition to distinctive pigmentation, larvae possess two rounded humps or protrusions that extend dorsally on either side of the gut just posterior to the pectoral fin bases. These protrusions are similarly positioned and reminiscent of the gut diverticula found in larvae of *Artedius*; however, they never develop into distinct diverticula. These protrusions disappear at the completion of yolk absorption about five to ten days after hatching. *Oligocottus maculosus* larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to 7.5 mm SL.

Flexion and postflexion larvae >6.5 mm possess a relatively low number of preopercular spines (9–13).

Postflexion larvae and juveniles may be distinguished by meristics, especially the high vertebral and dorsal fin ray counts, and the small size at transformation (8–9 mm SL). In addition, juveniles possess a slender postorbital cirrus and two frontoparietal cirri.

PIGMENTATION.—Newly hatched larvae of *O. maculosus* possess no melanistic head pigmentation. Fourteen to 16 intense, stellate melanophores are concentrated in the nape region. One to 3 dendritic melanophores extend anteriorly from the nape pigment patch onto a prominent elevation or bubble of skin located just anterior to the origin of the dorsal finfold. In live larvae, xanthophores cover the bubble of skin and the nape. Three to 4 dendritic, embedded melanophores are positioned in the otic capsule.

The dorsal surface of the gut is darkly pig-

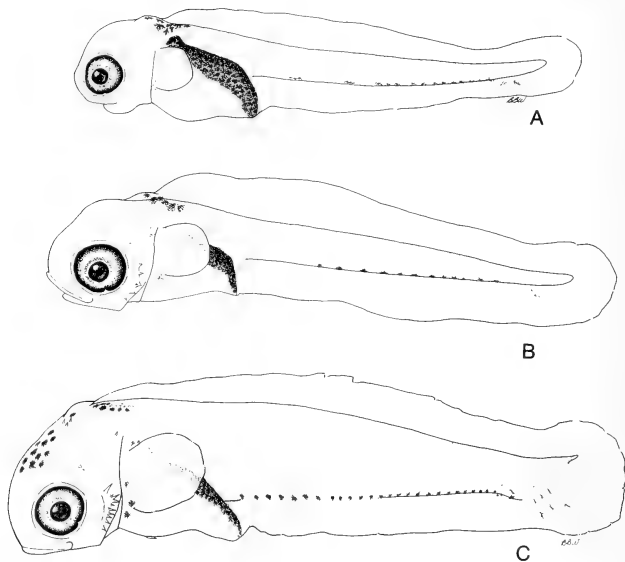


FIGURE 16. Larvae of *Oligocottus maculosus*: A) 4.3 mm NL, B) 7.2 mm NL, C) 6.9 mm NL.

mented with 100–150 dark melanophores. Two to 4 pale, dendritic melanophores are located along the anteroventral margin of the gut, just beneath the pectoral fins. These melanophores are frequently embedded in the gut musculature and are difficult to see. One to 5 small melanophores are clustered around the anus.

Posterior to the anus, larvae of *O. maculosus* possess a relatively high number of ventral midline melanophores. The actual number of melanophores appears to vary with the geographic location at which the larvae were collected. Stein (1973) recorded between 11 and 20 ventral midline melanophores in his reared larvae, while larvae reared in Oregon possessed between 16 and 20 melanophores along the ventral midline. J. B. Marliave (Vancouver Public Aquarium, Van-

couver, B.C., Canada, pers. comm.) found between 26 and 36 ventral midline melanophores in reared larvae from the Straits of Georgia in British Columbia. Regardless of the number of melanophores, this series begins under the third or fourth myomere posterior to the anus and extends toward the tail tip. The first four melanophores in the series are usually spaced one every two to three myomeres, while the remainder of the melanophores are spaced one per myomere. Five or nine additional pigment slashes extend onto the ventral finfold near the tail tip.

During larval development in larvae <6 mm, 15–20 melanophores form over the midbrain and interorbital region of the head. Two to 5 melanophores form on the snout and 1–3 melanophores form on the cheek just anterior to the



FIGURE 17. Young of *Oligocottus maculosus*: A) 7.8 mm SL, B) 10.4 mm SL.

dorsalmost preopercular spine in larvae >7 mm. At this size, melanophores are also added in the otic capsule; however, they become obscured by the developing musculature and are difficult to see. By ~ 6 mm, several melanophores are added just ventral to the nape pigment patch. Five to 7 of the centrally positioned melanophores become embedded while the other nape melanophores form a prominent U-shape anterolaterally around the central melanophores.

During transformation, ~ 7 –8 mm, melanistic pigmentation increases markedly over the dorsal surface of the head. Melanophores are added on the snout, on the cheek region anterior to the preopercle and on the dorsal portion of the operculum. Melanophores also form on the pectoral fin base and gradually extend ventrally onto the isthmus.

Pigmentation over the dorsal surface of the head is intense in benthic juveniles. A band of melanophores forms on either side of the snout, extending from the upper lip to the ventral margin of each eye. Each band continues posteriorly reaching from the eye to the dorsalmost preopercular spine. Melanophores are also added ventrally along the entire margin of the pre-

operculum and on the anterior tip of the lower lip. In juveniles >8.5 mm, tiny melanophores cover the entire dorsolateral surface of the head; however, the bands of pigment extending through each eye remain prominent. An irregular band of tiny melanophores forms along the surface of the lateral midline in juveniles ≥ 9 mm. This band gradually extends posteriorly to the caudal fin base. Two additional bands of pigment form along the dorsum. A third band forms under the 8th–10th dorsal rays and a fourth band develops under the 14th–16th dorsal fin rays. These pigment bands eventually extend ventrally and fuse with the lateral midline pigmentation. Tiny melanophores are added over the dorsolateral body surface in juveniles ~ 13 mm; however, the intense pigment bands along the dorsum remain distinct. Melanophores extend out onto the dorsal and caudal fin rays, forming three or five bands of pigment.

MORPHOLOGY.—Newly hatched *Oligocottus maculosus* larvae range in length from 4.2 to 4.5 mm NL. Larvae undergo flexion of the notochord at 7.2–7.6 mm NL. Transformation occurs at a relatively small size, ~ 7.5 –8 mm. The smallest benthic juvenile examined was 8 mm long.

TABLE 5. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *OLIGOCOTTUS MACULOSUS* AND *O. SNYDERI*. Values are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

| Item | <i>Oligocottus maculosus</i> | <i>Oligocottus snyderi</i> |
|-------------------------------------|------------------------------|-----------------------------|
| Head length/SL: | | |
| Preflexion | 17.3 \pm 0.61 (17.2–18.3) | 21.4 \pm 1.26 (20.1–23.4) |
| Flexion | 19.7 \pm 1.84 (18.4–21.0) | 20.8 \pm 1.34 (18.9–23.1) |
| Postflexion | 25.3 \pm 1.89 (22.3–26.6) | 23.4 \pm 1.71 (21.4–28.2) |
| Juvenile | 30.1 \pm 3.06 (27.1–32.8) | 26.9 \pm 1.00 (26.5–28.0) |
| Snout length/HL: | | |
| Preflexion | 25.7 \pm 2.08 (24.3–27.9) | 23.7 \pm 3.37 (21.2–25.9) |
| Flexion | 26.5 \pm 1.08 (26.0–28.1) | 21.4 \pm 2.43 (16.9–23.3) |
| Postflexion | 29.3 \pm 2.83 (24.4–33.0) | 16.1 \pm 2.87 (13.9–20.4) |
| Juvenile | 27.1 \pm 3.22 (24.9–31.4) | 32.0 \pm 0.00 (32.0–32.0) |
| Eye diameter/HL: | | |
| Preflexion | 55.6 \pm 2.08 (53.9–57.2) | 47.8 \pm 4.80 (40.1–52.3) |
| Flexion | 44.9 \pm 4.24 (42.3–48.2) | 42.1 \pm 2.95 (37.6–46.1) |
| Postflexion | 41.2 \pm 4.03 (33.1–45.0) | 33.3 \pm 3.21 (31.2–37.9) |
| Juvenile | 31.4 \pm 2.01 (28.9–34.1) | 31.0 \pm 2.52 (29.0–34.3) |
| Snout to anus length/SL: | | |
| Preflexion | 39.1 \pm 1.53 (37.2–40.4) | 42.1 \pm 1.47 (40.1–44.4) |
| Flexion | 39.8 \pm 2.83 (38.1–42.3) | 41.8 \pm 2.30 (39.2–44.9) |
| Postflexion | 43.9 \pm 3.39 (40.8–48.1) | 44.5 \pm 1.83 (42.1–46.4) |
| Juvenile | 45.0 \pm 2.65 (42.7–48.5) | 42.2 \pm 1.53 (40.3–43.1) |
| Snout to pelvic fin origin/SL: | | |
| Preflexion | — | — |
| Flexion | 24.0* | 21.0 \pm 1.00 (20.0–22.0) |
| Postflexion | 24.9 \pm 2.15 (23.1–26.9) | 23.3 \pm 1.71 (21.0–25.5) |
| Juvenile | 28.1 \pm 3.61 (25.3–32.1) | 24.6 \pm 1.53 (22.9–26.1) |
| Pelvic fin origin to anus/SL: | | |
| Preflexion | — | — |
| Flexion | 18.0* | 20.0 \pm 1.15 (19.1–21.1) |
| Postflexion | 20.2 \pm 1.89 (18.1–22.8) | 21.2 \pm 1.50 (20.1–23.3) |
| Juvenile | 16.9 \pm 1.73 (16.1–19.4) | 18.1 \pm 3.21 (16.0–22.1) |
| Body depth at pectoral fin base/SL: | | |
| Preflexion | 19.4 \pm 1.00 (17.8–20.2) | 23.2 \pm 1.17 (21.8–25.5) |
| Flexion | 24.0 \pm 0.00 (24.0–24.0) | 23.4 \pm 2.00 (20.2–26.6) |
| Postflexion | 25.9 \pm 2.17 (23.7–29.1) | 20.6 \pm 1.50 (19.4–21.8) |
| Juvenile | 23.9 \pm 3.06 (20.6–27.2) | 21.2 \pm 2.00 (19.0–23.4) |
| Body depth at anus/SL: | | |
| Preflexion | 15.5 \pm 0.61 (14.9–16.2) | 21.0 \pm 2.37 (18.1–24.9) |
| Flexion | 18.0 \pm 0.00 (18.0–18.0) | 24.3 \pm 2.91 (17.9–28.1) |
| Postflexion | 25.9 \pm 2.17 (23.7–29.1) | 26.2 \pm 1.50 (21.9–27.3) |
| Juvenile | 20.3 \pm 2.08 (18.1–22.3) | 22.1 \pm 2.31 (19.0–23.0) |
| Pectoral fin length/SL: | | |
| Preflexion | 10.1 \pm 0.61 (9.8–11.2) | 8.2 \pm 2.53 (6.1–12.1) |
| Flexion | 18.0 \pm 0.00 (18.0–18.0) | 10.1 \pm 1.77 (9.3–13.4) |
| Postflexion | 21.7 \pm 2.96 (17.3–26.3) | 14.4 \pm 1.41 (13.1–16.0) |
| Juvenile | 29.1 \pm 2.65 (26.8–31.9) | 24.3 \pm 1.53 (22.9–26.3) |

— = Not present at this stage.

* = Only one specimen available in this stage.

Eighteen specimens of *O. maculosus* (4.3–10.8 mm) were examined for developmental morphology.

In newly hatched larvae two prominent bumps

or protrusions appear on the dorsal surface of the gut just posterior to the pectoral fin base. These bulges are similar to the dorsal gut diverticula of *Artedius* larvae; however, they never

develop into distinct diverticula. The gut protrusions disappear approximately 5–10 days after hatching. *Oligocottus maculosus* larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae ≤ 7.5 mm.

Small *O. maculosus* are slender with a relatively short gut. Snout to anus length averages 39% in preflexion larvae and increases to 44% in postflexion larvae and 45% SL in juveniles. Body depth at both the pectoral fin base and the anus increases during larval development from 19% and 15%, respectively, to 25% SL.

FIN DEVELOPMENT.—Larval *Oligocottus maculosus* begin to undergo notochord flexion at ~6–7 mm. The adult complement of 12 principal caudal rays is complete in larvae ~6.8–7 mm long at about the completion of notochord flexion.

Dorsal and anal fin rays begin to form in larvae ~6.6 mm long; however, the full complement of fin rays (15–18, 12–14, respectively) is not complete until larvae are 8 mm long. Dorsal spines (VIII–IX) also form between 7 and 8 mm. Although pectoral fin rays are visible in larvae by 6.6 mm, the adult complement (12–15) is not fully formed until larvae reach about 7.6 mm. Pelvic buds are first visible in 7 mm larvae but the fin rays are not formed until ~8.5 mm.

SPINATION.—Six to 7 tiny spines are first visible on the posterior margin of the preopercle in larvae ~5.8 mm long. Spines increase in number to 9 or 10 in larvae undergoing notochord flexion. In postflexion larvae 6.9–7.8 mm long, preopercular spines number 10 or 11. Two or 3 of these spines appear as tiny accessory spines that form just anterior to the bases of the other spines. The dorsalmost spine becomes slightly larger than the lower spines. The 3rd, 4th, and 5th preopercular spines also increase slightly in size relative to the lower spines. In the largest planktonic larvae (~8 mm long) the preopercular spines begin to decrease in size and number and are covered with skin. In newly settled benthic juveniles ~8–10 mm long, the dorsalmost spine is quite large and stout with a strong upward curvature. The lower spines persist only as three blunt, bony protrusions on the preopercular margin.

Three tiny spines also form in the parietal region in larvae ~6–7 mm long. Two spines develop anteriorly with a third nuchal spine forming just posterior to them. These parietal spines persist through the larval period, but they regress

in benthic juveniles. During regression, the anterior spines decrease in size and their tips bend posteriorly and fuse with the nuchal spine, forming an arch. This canal and arch become incorporated into the cephalic lateral line system.

Two spines also form on the posttemporal in larvae ~6–7 mm long. By ~7–8 mm, a third spine forms on the posttemporal and a fourth spine forms on the supracleithrum. These supracleithral-posttemporal spines persist through larval development and eventually form the junction of the cephalic and lateral line systems.

Oligocottus snyderi

(Figures 18, 19; Table 5)

LITERATURE.—Stein (1973) described and illustrated 4.5- and 5.5-mm TL larvae of *O. snyderi*. Richardson and Washington (1980) called these larvae Cottidae Type 1 and illustrated specimens 4.2, 6.7, and 9 mm long.

IDENTIFICATION.—Small larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (34–37) and dorsal fin ray (17–20) counts, light pigmentation, the presence of cirri on the nasal spines and along the bases of the dorsal fins, and the absence of scales (prickles). The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular and parietal spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, meristics, and preopercular and parietal spination.

DISTINGUISHING FEATURES.—Distinguishing pigmentation of preflexion larval *O. snyderi* are melanistic nape pigmentation, relatively light pigmentation over the dorsolateral surfaces of the gut, and a low number of ventral midline melanophores (5–9) situated posterior to the anus. This series of ventral midline melanophores originates beneath the fifth to seventh postanal myomeres and extends posteriorly toward the tail tip. One melanophore is spaced approximately every four or five myomeres. This characteristic pigmentation changes little during larval development.

In newly hatched larvae, a hump or bubble of skin is present just anterior to the origin of the dorsal finfold. Although diffuse xanthophores are present over this bump in laboratory-reared larvae, no melanophores extend onto this bubble of skin. In contrast, *O. maculosus* larvae, which

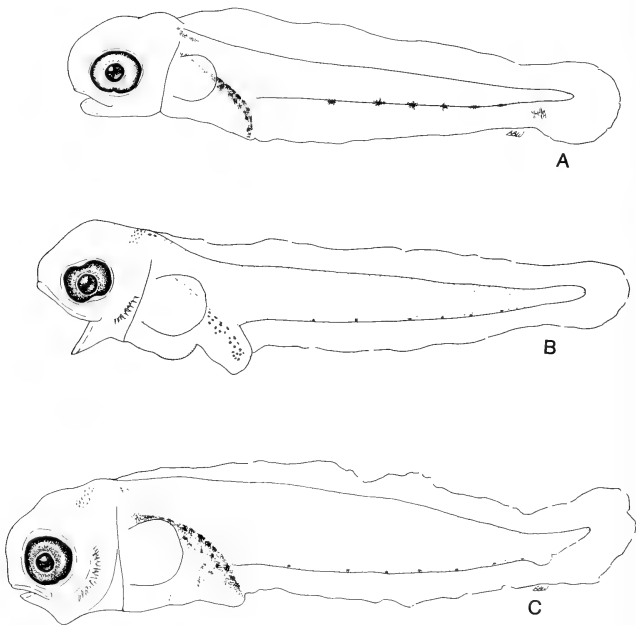


FIGURE 18. Larvae of *Oligocottus snyderi*: A) 4.7 mm NL, B) 5.1 mm NL, C) 6.7 mm NL (C from Richardson and Washington 1980).

also possess this distinctive bubble of skin at the nape, have one to three large dendritic melanophores that extend up onto the bubble of skin from the nape pigment patch.

Larvae of *O. snyderi* >4.2 mm NL may be further distinguished from all other known cottid larvae by the presence of a cluster of 10–20 minute prickles situated in the parietal region of the head.

Larvae undergoing notochord flexion, >6 mm long, possess a distinctive pattern of multiple preopercular spination, in which approximately 15 equal-sized spines are positioned along the

posterior margin of the preopercle. Ten to 11 small, accessory spines are situated at the anterior bases of the other spines and point anterolaterally.

Postflexion larvae and juveniles may be distinguished by their relatively light pigmentation, the prominent bands of pigment through the eye, and the low number of widely spaced ventral midline melanophores. In addition to pigmentation, juvenile *O. snyderi* are characterized by high vertebral and dorsal fin ray counts (34–37 and 17–20, respectively), and by the presence of very long, slender nasal, postorbital, and fron-

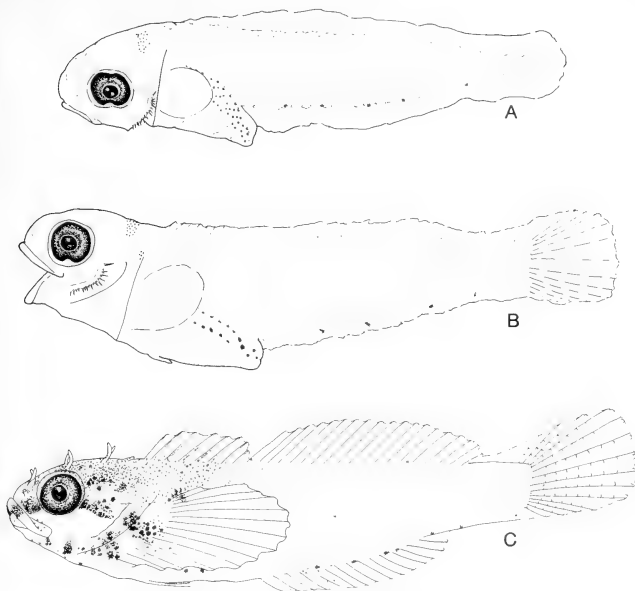


FIGURE 19. Young of *Oligocottus snyderi*: A) 8.2 mm SL, B) 10.2 mm SL, C) 14.4 mm SL.

toparietal cirri. In juveniles >15 mm, a row of distinctive cirri develop along either side of the bases of the dorsal fins.

PIGMENTATION.—Newly hatched, reared larval *O. snyderi* are lightly pigmented with no melanistic head pigmentation. Several xanthophores are situated over the midbrain in live larvae. Two to 8 external melanophores are clustered over the notochord in the nape region. In live specimens several diffuse xanthophores extend dorsally from the nape onto a distinctive bump or bubble of skin just anterior to the origin of the dorsal finfold. In contrast to larvae of *O. maculosus*, however, melanophores never extend onto this bubble of skin in larvae of *O.*

snyderi. The dorsolateral surface of the gut is lightly pigmented with 50–60 small melanophores forming an elliptical patch over the body cavity. Intense xanthophores also cover the dorsolateral surfaces of the gut. The only pigmentation posterior to the anus consists of a series of 5–9 melanophores that originates under the fifth to seventh postanal myomere and extends posteriorly. Each melanophore is positioned four to six myomeres apart. Occasionally, one or two melanistic pigment slashes extend onto the caudal finfold just beneath the notochord tip.

During larval development, several melanophores form on the dorsal surface of the head. Size of larvae at formation of this melanistic pig-

mentation appears somewhat variable. One or two melanophores are present over the midbrain in 21-day-old, laboratory-reared larvae (~6.5 mm long). Morris (n.d.) reported that four or five melanophores develop in the midbrain region of larvae at four weeks of age (~8.5 mm). Melanistic pigmentation does not appear over the brain in field-caught larvae until about 10 mm.

During transformation, head pigmentation increases markedly in late postflexion larvae 10–14 mm long. Thirteen to 18 large, stellate melanophores form over the midbrain and interorbital regions of the head. Concurrently, several small melanophores form anterior to the orbit and extend anteriorly across the snout onto the upper lip forming a distinct band. Several intense melanophores develop posterior to the orbit forming a dark band extending from the orbit to the dorsalmost preopercular spine. Melanophores are also added at the posterior margin of the lower jaw just ventral to the preopercle, along the dorsal margin of the operculum, and along the pectoral fin rays. A row of intense, embedded melanophores forms just above the spinal cord and extends posteriorly from the nape region two-thirds of the way to the caudal fin. The ventral midline melanophores remain unchanged.

In juveniles between 13 and 15 mm long, numerous tiny melanophores form over the dorsolateral surfaces of the head and extend anteriorly onto the snout between the eyes, ventrally along the preopercle, and along the opercular margin. These diffuse melanophores extend posteriorly to the seventh dorsal spine. Numerous small melanophores also form posterior to the pectoral fin base in an irregular band of pigment along the lateral midline. With development, melanophores are added along the dorsum in an anterior to posterior sequence. Concurrently, melanophores extend dorsally onto the dorsal fins forming four to five distinct bands of pigment. Gradually, the melanophores along the dorsal midline extend ventrally and posteriorly and join the dorsal and lateral areas of pigmentation. This lateral pigmentation extends posteriorly and forms a dark band at the base of the caudal fin. Melanophores extend onto the caudal fin rays forming four to five bands of pigment. Juvenile *O. snyderi* are characterized by uniform diffuse pigmentation over the head and dorsolateral surfaces of the body with a distinct, dark band of pigment extending from the snout, through the orbit, to the dorsalmost preopercular

spine. The characteristic low number of widely spaced ventral midline melanophores remains visible in juveniles ≤ 18 mm.

MORPHOLOGY.—Newly hatched *O. snyderi* larvae range in size from 4 to 4.5 mm NL. Notochord flexion occurs between 6.2 and 8.4 mm NL. The largest planktonic specimen taken in the field is 10.2 mm and has not yet begun to undergo transformation. The smallest benthic juvenile examined is 12.4 mm. Twenty-four specimens, ranging in length from 4 to 15.1 mm, were examined for development morphology.

Newly hatched *O. snyderi* larvae are rather slender with a relatively short gut, the posteriormost portion of which trails well below the body. Snout to anus length averages 42% in preflexion and flexion larvae, then increases slightly to 44% SL in postflexion larvae. Relative body depth at the pectoral fin base increases from 23% to 25% SL during larval development. A small, rounded protrusion extends dorsally from the dorsal surface of the gut just posterior to the pectoral fin base in newly hatched larvae. This protrusion is reminiscent of the gut diverticula found in larvae of several species of *Artedius* but is much less pronounced and never develops into distinct diverticula. This protrusion decreases in size shortly after hatching and is no longer visible by yolk absorption five days after hatching. In addition, *O. snyderi* larvae possess a prominent bump or bubble of skin that protrudes dorsally in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to ~6.5–7 mm.

FIN DEVELOPMENT.—Larvae of *O. snyderi* undergo notochord flexion between 6.2 and 8.4 mm. Caudal fin rays first appear at 7.8 mm; however, the full adult complement of 6 + 6 principal caudal rays is not complete until larvae reach ~9–10 mm. Rays begin to form in the dorsal and anal fins of larvae between 7.5 and 8 mm long; however, these rays are not fully formed in larvae <9 mm. Adult complements are 17–20 and 12–15, respectively. Dorsal fin spines begin forming in larvae 9–10 mm long, and the adult complement of spines (VIII–IX) is countable in a 10.2 mm specimen. Pectoral fin rays (12–15) form at 9 mm and are complete by 10 mm. Pelvic buds are first visible in larvae between 8.2 and 9 mm, but the fin rays are not fully formed until larvae reach 10–12 mm.

SPINATION.—Five to nine tiny bumps form along the posterior margin of the preopercle

in larvae >4.2 –5 mm. By ~ 5.1 mm, 10–15 tiny equal-sized spines are visible. During notochord flexion the preopercular spines increase in size and number, ranging between 17 and 22. The preopercular spines of *O. snyderi* larvae are unique in that 10–12 spines form along the posterior margin of the preopercle as in other cottids with preopercular spines, yet by ~ 7 mm NL, between 8 and 10 small accessory spines form anteriorly at the bases of the original spines. In larvae >9 mm, the dorsalmost preopercular spine becomes stouter and longer than the other spines and is separated from the lower spines by a short gap on the preopercular margin. The 5–8 spines just ventral to the dorsalmost spine also become slightly larger relative to the lower preopercular spines. Between 12 and 14 preopercular spines are visible in newly settled benthic juveniles. The dorsalmost spine becomes much larger relative to the other spines. The smaller, accessory spines begin to atrophy and are represented only by small bumps or irregularities on the preopercle. By ~ 14 mm, only the dorsalmost spine persists.

Distinctive spines also form in the parietal region of the head of young *O. snyderi*. Larvae as small as 4.2 mm have 7–10 small bumps or prickles visible over the parietals. These prickles increase in number during development; 10–20 prickles are present in the parietal region in larvae ≥ 6.2 mm. Eight to 12 tiny prickles remain visible along the posterolateral margin of the parietal bones in 12–13-mm cleared and stained benthic juveniles.

A cluster of spines also develops in the supracleithral-posttemporal region in larvae >8 mm. One spine forms on the supracleithrum and five spines, situated in two rows, form on the dorsal portion of the posttemporal. These persist throughout larval development but atrophy during transformation until only three bony projections are present in benthic juveniles. These bony projections represent the rudiments of the incipient lateral line system.

Clinocottus acuticeps

(Figures 20–22; Table 6)

LITERATURE.—Blackburn (1973) illustrated and described an 8.6-mm specimen, which he called Cottid 1 "*Biramous anus*." Richardson (1977) and Richardson and Percy (1977) listed larvae of *C. acuticeps* as Cottidae sp. 12. Larvae of this species were described by Richardson and Wash-

ington (1980). They illustrated specimens 3.7, 3.9, 6.9, 7.6, 10.4, 13.8, and 16.5 mm long.

IDENTIFICATION.—Small larval *C. acuticeps* were reared from eggs spawned from known adults. Adults and juveniles were identified by low dorsal fin ray (13–17) and anal fin ray (9–13) counts, the presence of nasal cirri, and a membrane connecting the innermost pelvic fin ray with the abdomen. The developmental series was linked together primarily by pigmentation, body shape, and hindgut diverticula. Postflexion and transforming larvae were linked with juveniles by pigmentation, meristics, and the membrane attaching the pelvic fin rays to the abdomen.

DISTINGUISHING FEATURES.—*Clinocottus acuticeps* larvae are distinguished from all other known cottid larvae by long protrusions (diverticula) that extend posteriorly from the gut on either side of the anus. These diverticula are present in yolk-sac larvae and persist in the largest pelagic specimens (14.5 mm). The gut itself is distinctively long and the posterior portion trails well below the body. Snout to anus length, averaging 62.5% SL, is greater than in other known larvae of *Artedius*, *Clinocottus*, or *Oligocottus*. In addition, these larvae have a flabby appearance with an outer bubble of skin, which is especially pronounced in the head region.

Other characters useful in distinguishing *C. acuticeps* larvae are melanistic pigmentation on the snout and head, and relatively few ventral midline melanophores (4–10).

Transforming and juvenile *C. acuticeps* are distinguishable from all other known cottids by the presence of a membrane attaching the inner pelvic fin ray to the belly. Other characters useful in separating juveniles are the relatively light, uniform pigmentation over the body; a band of pigment extending from the snout posteriorly through the orbit toward the preopercle; a dark blotch of pigment at the anterior end of the spinous dorsal; and a low number of ventral midline melanophores.

PIGMENTATION.—Newly hatched larvae reared in the laboratory exhibit 4 or 5 dendritic melanophores on the snout and 2 faint melanophores in each otic capsule. In field-collected larvae <3.7 mm NL, the presence of snout pigment varies; however, all larvae >3.7 mm NL possess at least 2 melanophores on the snout. Eight to 15 melanophores are clustered in the nape region of even the smallest larvae. Numerous melano-

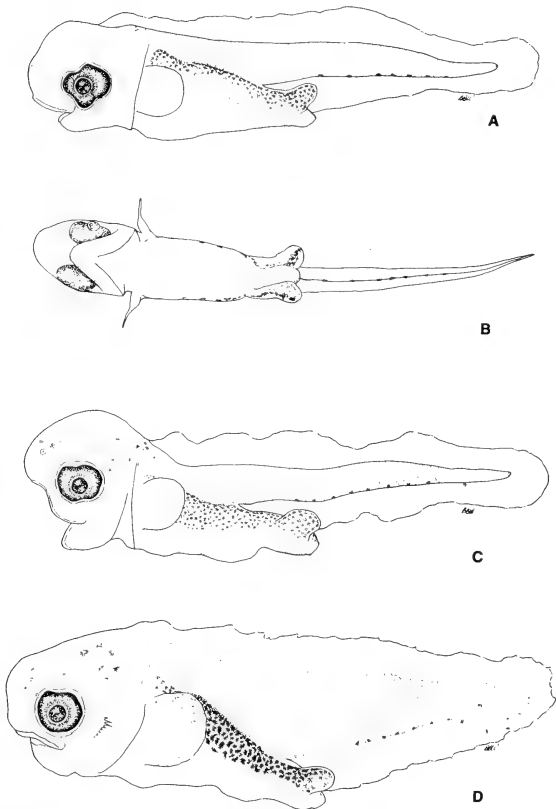


FIGURE 20. Larvae of *Clinocottus acuticeps*: A) 3.7 mm NL, B) 3.7 mm NL, C) 3.9 mm NL, D) 6.9 mm NL (from Richardson and Washington 1980).

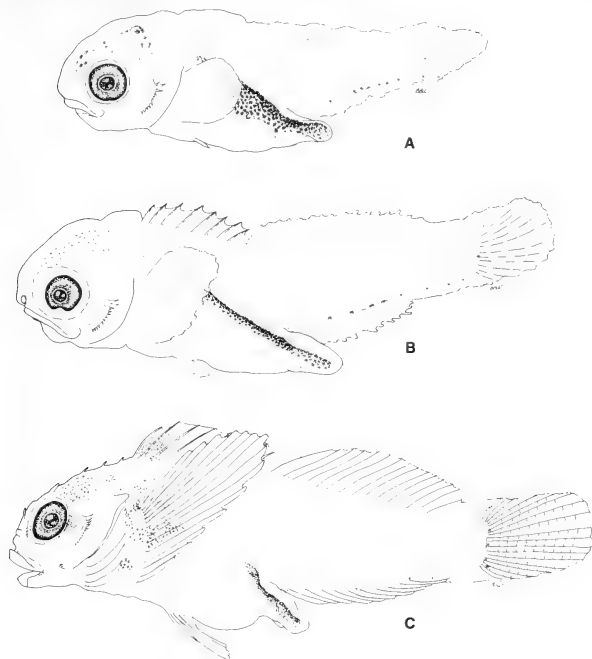


FIGURE 21. Larvae of *Clinocottus acuticeps*: A) 7.6 mm SL, B) 10.4 mm SL, C) 13.8 mm SL (from Richardson and Washington 1980).

phores are scattered over the dorsolateral surface of the gut extending posterolaterally over the surface of the gut diverticula. These melanophores are much fainter and more irregular in shape than in larvae of other species of *Clinocottus*.

A series of 4–10 inconspicuous ventral midline melanophores originates beneath the 7th–10th postanal myomeres and extends posteriorly toward the tail tip. Several additional melanophores appear as streaks of pigment on the ventral finfold near the tail tip.

Pigmentation increases on the head during larval development. Melanophores form first on the head over the midbrain in larvae 5.5 mm NL. Concurrently, several embedded melanophores appear on the nape and extend anteriorly onto the head. Four to five internal melanophores occur in or near the otic capsule. In larvae >6.5 mm, scattered melanophores extend continuously from the snout to the nape region. Ventral midline melanophores persist in flexion and postflexion larvae, and the posteriormost mel-

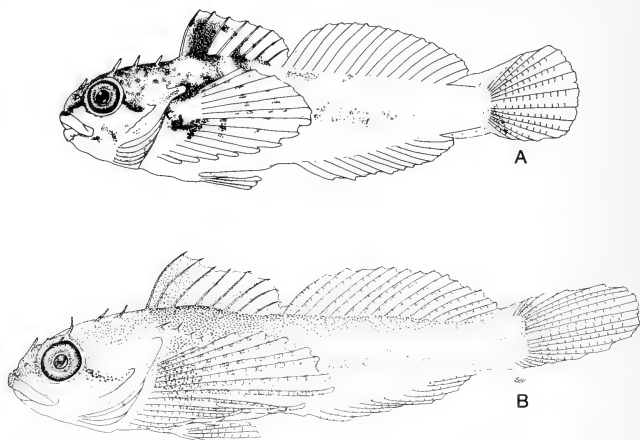


FIGURE 22. Young of *Clinocottus acuticeps*: A) 13.8 mm SL, B) 16.5 mm SL (B from Richardson and Washington 1980).

nophore, which is located near the notochord tip in small larvae, occurs near the middle of the caudal fin base between the forming hypural plates. The posteriormost melanophores which extended onto the ventral finfold now occur on the caudal fin. In the largest planktonic larvae, which are beginning to undergo transformation, melanophores are added in a patch just posterior to the orbit. Melanophores also are added along the bases of the pectoral fins and extend onto the pectoral fin rays.

In newly settled benthic juveniles (13–14 mm) head pigmentation increases markedly. Melanophores extend anteriorly across the dorsal surface of the snout and onto the upper lip. The melanophores at the ventral margin of the snout are especially intense and closely spaced, forming a prominent band that extends from the upper lip to the ventral margin of the orbit. This band continues from the posterior margin of the orbit to the dorsal margin of the preopercle. Additional melanophores are added along the ventral edge of the lower lip, at the base of the preopercle, and on the dorsal portion of the operculum. As development proceeds, a second band of pig-

ment forms between the ventral margin of the orbit and the melanophores at the base of the preopercle. Simultaneously, pigmentation increases on the pectoral fin bases while two to three bands of pigment form across each fin.

Between 14 and 15 mm, a dense patch of melanophores forms at the anterior end of the first dorsal fin between the first and third spines. As juvenile pigmentation progresses this patch expands posteriorly to include the fourth dorsal spine, and a second patch of melanophores forms between the seventh and eighth dorsal spines. Melanophores extend ventrally from these two pigment patches forming two distinct bands across the dorsum. Pigmentation proceeds posteriorly along the dorsum. In juveniles between 15 and 16 mm long, a third band (or saddle) of pigment forms under the second to sixth dorsal fin rays; a fourth band forms under the 8th to 11th dorsal fin rays; and a fifth band forms under the last two dorsal fin rays. As these bands of pigment develop along the dorsum, they extend ventrally and eventually unite into a uniform band of pigment above the lateral midline. Concurrently, another band of pigment extends pos-

TABLE 6. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *CLINOCOTTUS ACUTICEPS*, *C. EMBRYUM*, *C. GLOBICEPS*, AND *C. ANALIS*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

| Item | <i>Clinocottus acuticeps</i> | <i>Clinocottus embryo</i> | <i>Clinocottus globiceps</i> | <i>Clinocottus analis</i> |
|--|------------------------------|---------------------------|------------------------------|---------------------------|
| Head length/SL: | | | | |
| Preflexion | 27.1 ± 3.44 (22.3–30.1) | 26.1 ± 2.65 (26.0–30.1) | 20.6 ± 2.21 (17.0–25.0) | – |
| Flexion | 29.2 ± 1.92 (26.8–32.4) | 23.9 ± 1.15 (21.8–25.3) | 23.0 ± 1.79 (21.0–27.2) | – |
| Postflexion | 27.9 ± 2.71 (22.9–32.6) | 24.0 ± 0.00 (24.0–24.0) | 27.3 ± 4.09 (22.4–33.3) | 30.1 ± 1.25 (27.8–32.1) |
| Juvenile | 32.2 ± 0.65 (31.5–32.7) | 31.5 ± 1.13 (30.2–32.2) | 31.6 ± 0.46 (31.2–32.1) | – |
| Snout length/HL: | | | | |
| Preflexion | 24.6 ± 4.80 (21.3–25.9) | 21.3 ± 1.53 (19.9–23.7) | 21.3 ± 4.40 (14.5–26.7) | – |
| Flexion | 26.4 ± 2.97 (22.9–30.6) | 24.1 ± 3.83 (18.4–30.8) | 25.7 ± 3.39 (20.0–30.5) | – |
| Postflexion | 23.6 ± 4.38 (16.3–30.9) | 22.2 ± 0.58 (21.8–23.6) | 25.3 ± 4.84 (20.0–33.0) | 28.3 ± 2.70 (22.3–32.2) |
| Juvenile | 27.5 ± 4.36 (26.8–29.4) | 27.5 ± 1.47 (22.7–31.2) | 27.1 ± 0.92 (26.1–27.9) | – |
| Eye diameter/HL: | | | | |
| Preflexion | 39.7 ± 6.63 (31.5–54.2) | 39.3 ± 3.06 (35.8–42.1) | 50.4 ± 9.16 (46.2–63.1) | – |
| Flexion | 34.6 ± 2.41 (31.9–36.4) | 35.7 ± 3.79 (34.8–39.5) | 43.7 ± 7.39 (37.9–51.4) | – |
| Postflexion | 32.7 ± 3.30 (27.1–38.2) | 32.1 ± 3.06 (29.0–35.3) | 38.2 ± 8.09 (24.4–46.0) | 31.3 ± 1.41 (27.8–33.0) |
| Juvenile | 27.9 ± 2.06 (25.5–29.3) | 29.8 ± 0.74 (29.2–30.6) | 27.1 ± 0.91 (26.1–27.9) | – |
| Snout to anus length/SL: | | | | |
| Preflexion | 60.7 ± 4.64 (54.4–67.2) | 51.6 ± 3.51 (48.2–55.1) | 44.0 ± 3.59 (39.6–52.9) | – |
| Flexion | 62.8 ± 2.74 (60.3–67.1) | 49.9 ± 3.87 (43.9–54.4) | 48.2 ± 3.27 (44.4–56.0) | – |
| Postflexion | 62.5 ± 4.61 (57.5–70.3) | 50.0 ± 3.06 (47.3–53.8) | 50.0 ± 3.48 (44.7–56.8) | 48.9 ± 2.40 (46.4–54.3) |
| Juvenile | 50.2 ± 1.64 (48.4–51.6) | 49.0 ± 3.10 (47.0–52.6) | – | – |
| Snout to pelvic fin origin/SL: | | | | |
| Preflexion | – | – | – | – |
| Flexion | – | 28.0* | 24.6 ± 2.94 (21.4–28.0) | – |
| Postflexion | 33.4 ± 2.63 (29.4–39.5) | 32.1 ± 3.54 (29.0–34.2) | 26.7 ± 2.33 (23.4–30.9) | 29.3 ± 1.34 (27.2–31.4) |
| Juvenile | 33.3 ± 1.16 (32.5–34.6) | 31.1 ± 1.31 (29.6–32.1) | 30.7 ± 1.04 (29.5–31.4) | – |
| Pelvic fin origin to anus/SL: | | | | |
| Preflexion | – | – | – | – |
| Flexion | – | 26.1* | 21.5 ± 1.77 (18.7–23.4) | – |
| Postflexion | 29.4 ± 4.56 (23.1–37.3) | 18.2 ± 0.71 (17.1–18.4) | 22.9 ± 1.42 (21.4–25.2) | 19.9 ± 2.26 (17.3–22.3) |
| Juvenile | 16.9 ± 1.70 (15.9–18.9) | 17.9 ± 2.50 (15.4–20.4) | 20.7 ± 0.64 (20.0–21.2) | – |
| Body depth at pectoral fin base/SL: | | | | |
| Preflexion | 24.3 ± 3.25 (17.8–29.1) | 25.8 ± 4.36 (21.2–29.4) | 20.8 ± 2.87 (15.8–25.5) | – |
| Flexion | 27.6 ± 2.30 (24.3–30.2) | 26.3 ± 2.29 (23.7–30.2) | 23.9 ± 2.02 (22.2–29.3) | – |
| Postflexion | 31.3 ± 2.29 (28.4–35.0) | 26.1 ± 1.53 (25.0–28.2) | 26.8 ± 2.78 (22.1–30.9) | 28.1 ± 1.36 (25.4–29.1) |
| Juvenile | 26.1 ± 1.99 (23.9–27.8) | 21.6 ± 1.01 (23.5–25.5) | 27.3 ± 0.53 (26.7–27.7) | – |
| Body depth at anus/SL: | | | | |
| Preflexion | 21.4 ± 2.94 (18.0–24.5) | 22.8 ± 4.36 (18.2–26.5) | 17.5 ± 2.46 (13.6–21.6) | – |
| Flexion | 25.4 ± 2.07 (23.3–28.1) | 25.1 ± 1.51 (22.9–27.3) | 21.2 ± 2.07 (17.7–24.0) | – |
| Postflexion | 28.4 ± 2.43 (26.4–35.2) | 27.0 ± 0.00 (27.0–27.0) | 25.7 ± 3.04 (21.1–30.4) | 25.7 ± 1.50 (25.0–29.1) |
| Juvenile | 24.0 ± 2.28 (21.4–25.4) | 23.3 ± 1.93 (22.1–25.5) | 25.7 ± 2.08 (23.3–27.0) | – |
| Pectoral fin length/SL: | | | | |
| Preflexion | 11.4 ± 1.27 (9.6–13.3) | 9.9 ± 3.46 (6.3–12.1) | 12.1 ± 1.19 (9.6–13.8) | – |
| Flexion | 11.0 ± 1.87 (9.9–14.5) | 11.2 ± 2.75 (7.1–17.5) | 12.3 ± 4.40 (7.5–22.0) | – |
| Postflexion | 26.4 ± 5.95 (18.2–35.0) | 32.0 ± 4.04 (30.1–37.0) | 22.7 ± 6.00 (11.1–30.4) | 29.3 ± 2.15 (24.8–32.3) |
| Juvenile | 32.1 ± 1.74 (30.8–34.1) | 33.4 ± 1.16 (32.1–34.2) | 29.0 ± 0.82 (28.1–29.7) | – |

– = Not present at this stage.

* = Only one specimen available in this stage.

teriorly along the lateral midline to the caudal fin where melanophores form a dark band at the base of the caudal fin. Melanophores extend onto the caudal fin rays where they form four or five bands across the fin. Clusters of melanophores extend first ventrally and then laterally from the lateral midline pigment band and gradually unite enclosing three to five small unpigmented circles below the lateral line. Three to six tiny melanophores remain visible along the ventral midline posterior to the anus in juveniles <17 mm long.

MORPHOLOGY.—*Clinocottus acuticeps* larvae hatch at the smallest length (3.1–3.3 mm NL) of any member of the genus. Notochord flexion occurs between 5.6 and 7.3 mm NL. The largest planktonic specimen collected is 14.5 mm and is beginning to undergo transformation. The smallest benthic juvenile examined is 12.6 mm. Thirty-seven selected specimens of *C. acuticeps*, ranging in length from 3.1–16.2 mm, were examined for developmental morphology.

Larvae of *C. acuticeps* have a distinctive, flabby appearance as if a loose bubble of outer skin surrounds the anterior part of the body.

Larvae are deep-bodied with a long, distinctive gut, the posterior portion of which trails well below the body. Snout to anus length remains relatively constant during larval development, averaging 63% SL. Prominent diverticula extend posteroventrally from the hindgut on either side of the anus. These diverticula are well developed throughout larval development but are not visible in benthic juveniles.

FIN DEVELOPMENT.—A 5.6 mm NL larva is just beginning notochord flexion and a concurrent thickening of the hypural region of the forming caudal fin. The adult complement of 6 + 6 principal caudal rays is present in a 6.8 mm specimen prior to completion of notochord flexion at ~7.5 mm. Bases of the dorsal and anal fin rays begin forming on a 6.9 mm larva. The full adult complement of dorsal (13–17) and anal (9–13) fin rays is present by ~8 mm. The adult complement of dorsal fin spines (VII–IX), however, is not present until ~8.7 mm.

Although pectoral fin rays are visible on a 6.9 mm larva, the full adult complement (13–15) is not complete until >7.6 mm. Pelvic fin buds appear just after completion of notochord flexion in a 7.6 mm larva; however, the fin rays are not fully formed until ~10 mm.

SPINATION.—Preopercular spines first appear as small bumps at 5.2 mm NL. Nine to 11 small spines are present by the onset of notochord flexion at ~6 mm. During flexion, spines remain small and evenly spaced with the 2nd and 3rd spines becoming slightly longer than the others. By completion of flexion, at 7.6 mm, 11–12 spines are present along the margin of the preopercle. The dorsalmost 3 spines are beginning to elongate and point dorsally. In a 10-mm cleared and stained specimen, the dorsalmost 3 spines are nearly four times as long as the ventral spines. In the largest planktonic larvae (13–14 mm long) the ventralmost spines are beginning to atrophy. The 3 dorsalmost spines are still prominent in a 15.2 mm juvenile, but the 8 ventral spines are minuscule, with their tips twisted and bent anteriorly. By ~19 mm, the lower spines have atrophied completely, and only the single large dorsalmost spine persists.

No spines develop in the parietal or supra-cleithral-posttemporal regions of the head in larvae or juveniles of this species.

Clinocottus embryum

(Figures 23–25; Table 6)

LITERATURE.—Richardson (1977) and Richardson and Percy (1977) listed larvae of this species as Cottidae sp. 20. Richardson and Washington (1980) described these larvae as Cottidae Type 2 and illustrated specimens 4.0, 6.4, and 7.4 mm long.

IDENTIFICATION.—Juveniles and adults were identified using a combination of the following characters: an advanced anus, light pigmentation, presence of a nasal cirrus, low anal fin ray counts (9–12), and absence of a membrane attaching the pelvic fin rays to the abdomen. The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, cirri patterns, meristics, and preopercular spination.

DISTINGUISHING FEATURES.—Characters useful in distinguishing preflexion larvae of *C. embryum* are lack of head pigment, relatively light gut pigmentation, large number of ventral midline melanophores (15–21), and relatively long, trailing gut. Head and/or snout pigment is present in larvae of all other species of *Clinocottus*. *C. embryum* larvae are further distinguished from

yolk-sac *C. acuticeps* larvae (in which snout pigment is sometimes absent) by the absence of distinct hindgut diverticula.

In addition to the pigmentation characters mentioned above, flexion and postflexion larvae of *C. embryo* are distinguished by their head spination. Larvae 7.3 mm have 11–14 preopercular spines; the dorsalmost spine is the largest.

In benthic juveniles of *C. embryo*, the anus is advanced midway between the origin of the pelvic fins and the anal fin, as in other members of the genus. Juvenile *C. embryo* are distinguished from *C. globiceps*, *C. analis*, and *C. recalvus* by relatively light, mottled body pigmentation and long and slender nasal, postorbital, and frontoparietal cirri. *Clinocottus embryo* juveniles are distinguished from *C. acuticeps* by the presence of a large number of ventral midline melanophores (15–21) and the absence of a membrane connecting the inner pelvic fin ray to the abdomen.

PIGMENTATION.—Melanistic pigmentation is absent on the head in preflexion *C. embryo* larvae. One to 5 melanophores are scattered over the nape region. The dorsolateral surface of the gut is relatively lightly pigmented and occasionally several faint melanophores are present on the anterolateral surface of the gut below the pectoral fins. Posterior to the anus, a series of 15–19 melanophores extends along the ventral midline. This series begins on the fourth or fifth myomere posterior to a vertical line through the anus; the melanophores are spaced approximately 1 per myomere. Several specimens have 1 or 2 melanophores on the ventral finfold near the notochord tip.

During larval development, the formation of head pigmentation varies in larvae between 6 and 9 mm long. Three out of eight larvae observed possess one to five tiny melanophores over the brain. One or two melanophores are consistently present beneath the pectoral fin on the anterolateral surface of the gut in larvae >6.5 mm. Otherwise, pigmentation remains unchanged.

In transforming larvae >9.6 mm long, numerous melanophores appear over the brain. Several melanophores appear on the cheek region between the orbit and the preopercle. Melanophores are also added on the pectoral fin base.

Melanistic pigmentation increases over the

head in newly settled juveniles. Large melanophores cover the surfaces of the head over the midbrain and interorbital regions. Several large, intense melanophores are embedded at the posterior margin of the parietal region. A distinct, dense band of melanophores extends from the orbit anteriorly onto the upper lip and posteriorly from the orbit to the dorsal tip of the preopercle. Several melanophores form a dark patch on the cheek beneath the orbit. Melanophores are also added to the dorsal surface of the operculum and to the pectoral fin base with several melanophores extending onto the pectoral fin rays.

As development proceeds, pigmentation increases markedly over the head. In a 16-mm juvenile, the bands of pigment extending through the eye are prominent, but numerous small melanophores cover the entire dorsal surface of the head above these bands of pigment. Pigmentation increases on the operculum and pectoral fin base. Three to four bands of melanophores are added across the pectoral fin rays.

Five bands of pigment develop on the body along the dorsal midline in an anterior to posterior sequence. The first band of pigment forms under the third to fifth dorsal fin spines, and a second smaller band begins to form under the seventh to ninth dorsal spines in juveniles between 13 and 14 mm long. By ~15 mm, three additional bands of pigment are present on the dorsum beneath the second dorsal fin. The third band forms under the 2nd–4th dorsal fin rays, the fourth band forms under the 7th–9th fin rays, and the fifth band forms under the 12th–15th rays. At the same time, a series of embedded melanophores develops in a row just above the notochord, extending from the nape region toward the caudal fin. A few diffuse patches of external melanophores also form along the lateral midline posterior to the gut.

As juvenile pigmentation develops, the dorsal bands of pigment extend ventrally until they unite above the lateral line, forming four unpigmented saddles between the bands. The melanophores lying along the lateral midline increase in number and extend posteriorly and ventrally toward the caudal fin. As this lateral pigmentation extends posteriorly, it fuses dorsally with the pigment bands. As pigmentation expands and unites over the lateral surface of the body, numerous, irregular, unpigmented circles remain above and below the lateral line, giving juvenile *C. embryo*

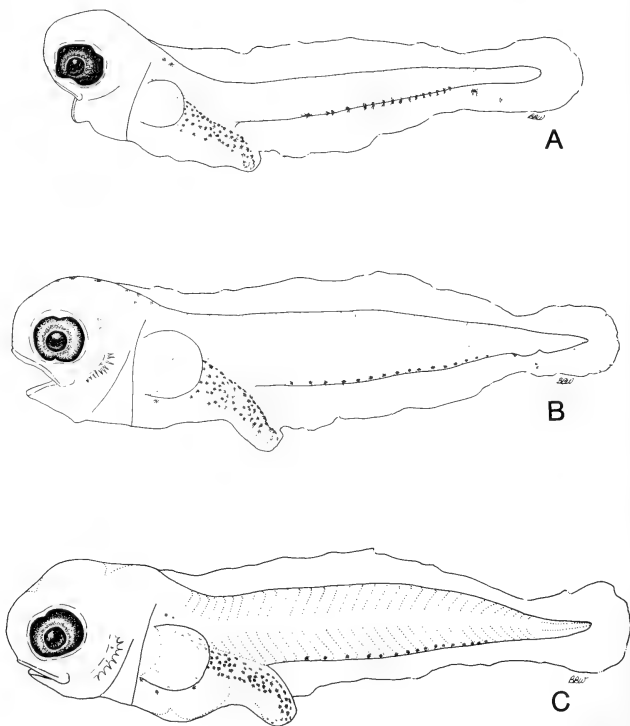


FIGURE 23. Larvae of *Clinocottus embryum*: A) 4.0 mm NL, B) 5.4 mm NL, C) 6.4 mm NL (A and B from Richardson and Washington 1980).

a distinctively mottled appearance. Eighteen to 21 small melanophores remain visible along the ventral midline in juveniles up to ~19 mm long.

MORPHOLOGY.—The smallest *C. embryum* examined is 4.0 mm NL and is recently hatched. Larvae undergo flexion of the notochord between 6.4 and 9.6 mm NL. The largest specimen taken

in the plankton is 14.0 mm and is beginning to undergo transformation. The smallest benthic juvenile is 13.7 mm. Eighteen *C. embryum*, ranging from 4 to 14 mm long, were examined for developmental morphology.

Larval *C. embryum* have a distinctively shaped gut with the posterior portion trailing well below

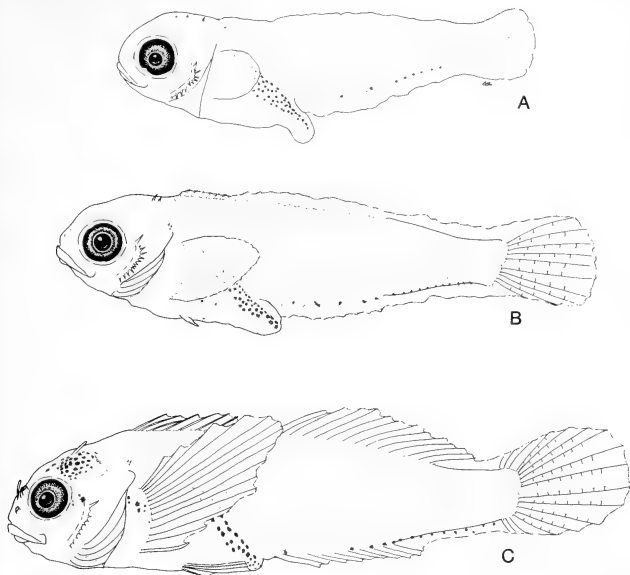


FIGURE 24. Larvae of *Clinocottus embryum*: A) 7.4 mm SL, B) 9.6 mm SL, C) 13.9 mm SL (A from Richardson and Washington 1980).

the body. The walls of the hindgut protrude on either side of the anus, reminiscent of the hindgut diverticula of *C. acuticeps*; however, these bulges never develop into pronounced diverticula. Snout to anus length is relatively long throughout larval development, averaging 50% SL.

FIN DEVELOPMENT.—The onset of notochord flexion is first apparent in a 6.4 mm larva. Caudal rays are present by ~7.4 mm but the adult complement of 6 + 6 principal caudal rays is not complete until about 8.4 mm. Bases of the forming dorsal and anal fin rays are first visible at ~7.4 mm; however, the adult complement of dorsal (14–17) and anal (9–12) fin rays is not present until ~8.3 mm. Dorsal spines (VIII–X)

are beginning to form at ~8.3 mm but are not fully formed until 9.6 mm. Pectoral fin rays begin to form at ~8 mm, and the adult complement of fin rays (12–15) is present by 9.6 mm. Pelvic fin buds are first apparent at ~9.6 mm, and the adult pelvic fin complement (I,3) is present in postflexion larvae >12.4 mm long.

SPINATION.—Eight to 10 tiny, evenly spaced spines increases, ranging in number from 11 to 14. opercle at ~5.2 mm NL. In larvae undergoing notochord flexion, the number of preopercular spines increases, ranging in number from 11 to 14. During the flexion stage, the dorsalmost preopercular spine increases in size relative to the rest of the preopercular spines so that by the end

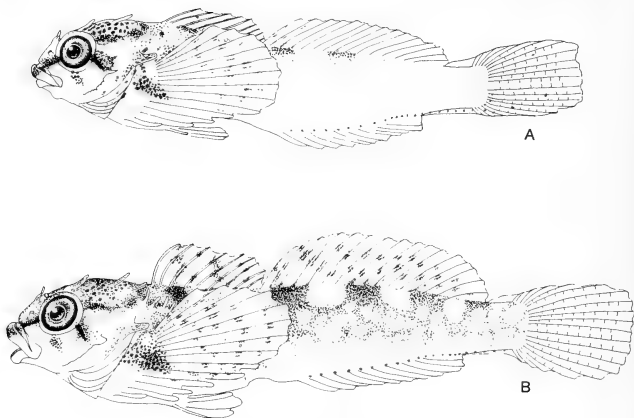


FIGURE 25. Juveniles of *Clinocottus embryum*: A) 13.7 mm SL, B) 16.2 mm SL.

of flexion, the dorsalmost spine is much longer and stouter than the other spines. In the largest planktonic larvae, 13–14 mm long, the upper spine is ≥ 2.5 times longer than the other spines and is separated from them by a slight gap. In newly settled benthic juveniles, the number and size of the lower preopercular spines are reduced. By > 15 mm, only a second, tiny spine persists just ventral to the large dorsal spine. The other spines appear as five to seven small bumps or irregularities along the preopercular margin. In completely transformed juveniles ≥ 16 mm long, only the uppermost spine is visible.

Two spines develop in the parietal region of *C. embryum* larvae. A single small spine is first present at the posterior margin of each parietal at ~ 6.7 mm. By 9.6 mm, this parietal spine has increased in size and a second smaller parietal spine is present just behind it. As larvae undergo transformation, between 12 and 14 mm, these spines undergo a reduction in size, and the first parietal spine eventually fuses with the second parietal spine, forming a hollow central canal between the spines. This canal is part of the incipient cephalic lateral line system. In newly set-

tled juveniles, only a skin-covered bony protuberance is visible in the parietal region.

Three spines also form in the supracleithral-posttemporal region of the head at ~ 9.6 mm. These spines persist through transformation and eventually become associated with the lateral line system in juveniles > 15 mm long.

Clinocottus globiceps

(Figures 26–28; Table 6)

LITERATURE.—Larvae of this species were listed by Richardson (1977) and Richardson and Percy (1977) as *Oligocottus* sp. 1. Richardson and Washington (1980) described larvae of this species as Cottidae Type 3. They illustrated specimens 6.3, 7.5, and 12.5 mm long.

IDENTIFICATION.—Larvae were reared from eggs spawned from known adults. Field-collected larvae were identified through comparison with reared larvae. Identification of larvae and juveniles was further confirmed by the following characters: pigmentation, body shape, an advanced anus, and absence of a nasal cirrus.

DISTINGUISHING FEATURES.—Preflexion and flexion larvae of *C. globiceps* may be distin-

guished from other cottid larvae, except *C. recalvus* and *C. analis*, by the presence of heavy pigmentation on the head, nape, and dorsolateral surface of the gut. Larval *C. globiceps* are distinguished from *C. recalvus* and *C. analis* by the number (4–8) and spacing of ventral midline melanophores. Late flexion and postflexion larvae of *C. globiceps* differ from all other *Clinocottus* larvae in preopercular and parietal spination.

Transforming and juvenile *C. globiceps* are distinguished from other cottid larvae by the combination of a blunt, rounded snout and head, heavy pigmentation over the anterior third of the body, and two or three inconspicuous ventral midline melanophores which persist on the caudal peduncle.

PIGMENTATION.—Newly hatched and preflexion larvae of *C. globiceps* have intense melanistic pigmentation on the head and nape. Eight to 11 large stellate melanophores are present over the midbrain and 21–30 melanophores are concentrated in the nape region. These nape melanophores are arranged in a distinctive pattern in which 7–10 melanophores are embedded along the dorsal midline of the nape and are surrounded anteriorly and laterally by 14–23 dark melanophores lying on the external surface of the nape. Eight to 10 dendritic melanophores occur on both the anterior and posterior walls of the otic capsules. The dorsolateral surface of the gut is heavily pigmented with 100–150 large, round melanophores. The only pigmentation occurring posterior to the anus is a series of 4–8 discrete, ventral midline melanophores. These are situated under the 10 posteriormost myomeres near the tail tip. Frequently, 2–5 additional small melanophores extend beyond the tail tip onto the caudal finfold.

Pigmentation changes little during larval development. The midbrain melanophores increase in number ranging from 12 to 16 in larvae >6 mm. By about 8 mm, melanophores are densely concentrated over the nape and extend anteriorly onto the head. Melanophores are added in the midbrain region and several melanophores extend anteriorly over the forebrain onto the snout. As head musculature develops, melanophores in the otic region become obscured so that only 5 or 6 melanophores are visible on the posterior wall of the otic capsule.

During transformation, in planktonic larvae 12–14 mm long, head pigmentation increases

markedly. Several melanophores are added on the upper lip and beneath the orbit. Melanophores are also added in a row along the preopercle and on the dorsal portion of the operculum. Pigmentation over the brain intensifies and expands posteriorly, merging with the nape pigmentation. Concurrently, nape melanophores extend ventrally from the nape forming a continuous band of pigment between the nape and gut. Pigmentation also increases over the body cavity as melanophores extend ventrally over the lateral surfaces of the gut. Several melanophores also are added on the pectoral fin base. Ventral midline melanophores decrease in size and number, until only two to four inconspicuous melanophores persist beneath the caudal peduncle.

Newly settled benthic juveniles of *C. globiceps* are distinctively pigmented with the anterior third of the body covered with dark melanophores extending posteriorly to about a vertical through the seventh dorsal spine. Only the posterior two-thirds of the pelvic fin rays remain unpigmented. Posterior to the intense head pigment, the two to four small, ventral midline melanophores constitute the only pigment. Between 14 and 16 mm SL, juvenile pigmentation is added posteriorly along the dorsum. By about 14 mm, a dark vertical bar of melanophores forms under the second to fourth dorsal fin rays and extends ventrally two-thirds of the way below the lateral midline. Between 15 and 16 mm, three additional saddles of melanophores are added posteriorly along the dorsum. The first saddle forms under the 8th–10th dorsal fin rays, the second forms under the 14th–15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Concurrently, melanophores are added posteriorly along the lateral midline forming a dark band of pigment at the base of the caudal fin. Several melanophores appear on the pectoral, dorsal, and caudal fin rays.

MORPHOLOGY.—Larval *C. globiceps* hatch at a relatively large size, 5.1–5.4 mm NL. Flexion of the notochord occurs between 6.2 and 8.1 mm NL. The largest planktonic larva taken in field collection is 12.9 mm and is beginning to undergo transformation. The smallest benthic juvenile is 13.5 mm long. Thirty-eight specimens (5.1–14.6 mm) were examined for developmental morphometrics. Because only 10 larvae were available from field collections, this morphometric series includes 25 laboratory-reared larvae.

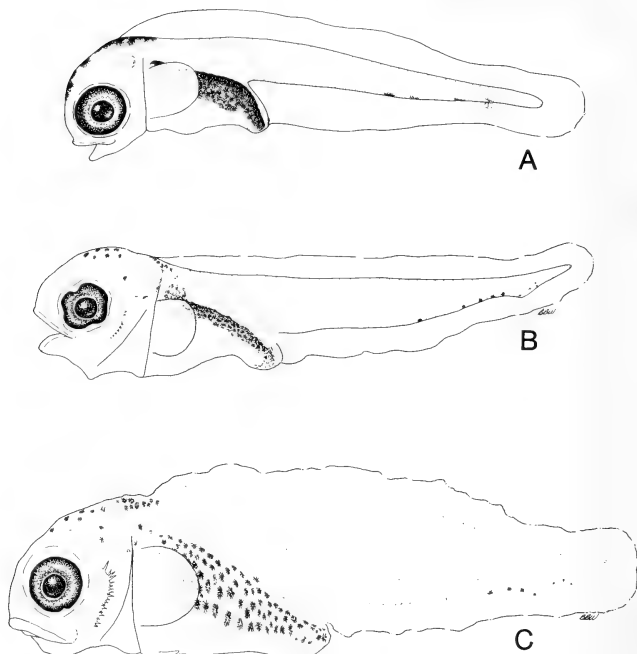


FIGURE 26. Larvae of *Clinocottus globiceps*: A) 5.0 mm NL, B) 6.3 mm SL, C) 7.5 mm NL (B and C from Richardson and Washington 1980).

Larval *C. globiceps* are relatively deep-bodied, and the posterior portion of the gut trails below the rest of the body. When viewed ventrally, the hindgut bulges slightly on either side of the anus similar to, but less pronounced than, the bulges in *C. embryum*.

Relative body depth at the pectoral fin base increases during larval development from 20.7% in preflexion larvae to 28.5% SL in transforming larvae and juveniles.

Larval *C. globiceps* have a notably blunt,

rounded head and snout with relative head length increasing from 17.0% in preflexion larvae to about 31% SL in transforming juveniles.

FIN DEVELOPMENT.—The smallest larva beginning to undergo flexion of the notochord is 6.2 mm long. Notochord flexion is complete in larvae between 7.5 and 8.0 mm long. Although caudal rays are present in late-flexion stage larvae (7.0–7.5 mm NL), the adult complement of 6 + 6 principal caudal rays is not countable until the completion of flexion at 7.4 mm.

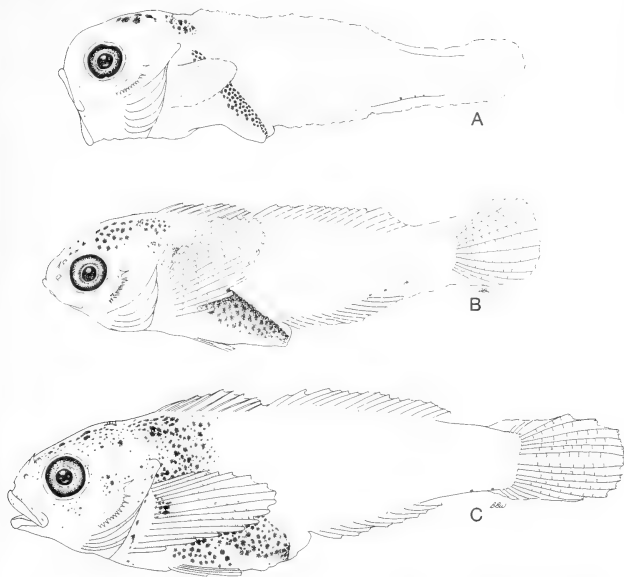


FIGURE 27. Larvae of *Clinocottus globiceps*: A) 8.5 mm SL, B) 12.5 mm SL, C) 12.9 mm SL (B from Richardson and Washington 1980).

Dorsal and anal fin bases are just beginning to form at completion of notochord flexion. The full complement of dorsal (13–17) and anal (11–12) fin rays is complete at ~9.5 mm. The dorsal spines (VIII–X) are completely formed at ~10 mm. Development of the pectoral fin corresponds to that of the dorsal and anal fins. Pectoral fin rays are visible on a 7.5 mm larva. The adult complement of rays (13–15) is fully formed by ~9–9.5 mm. Pelvic fin buds are first visible in larvae between 6.5 and 7 mm long. The adult complement (I,3) is present between 9.5 and 10 mm.

SPINATION.—Preopercular spines first appear as seven to nine small bumps along the posterior

margin of the preopercle in larvae 5.5–6 mm. Larvae undergoing notochord flexion have 9–14 small, evenly spaced spines along the preopercular margin. During postflexion, spines increase in number from 16 to 22, and the dorsalmost spine becomes separated from the rest of the preopercular spines by a short gap. Simultaneously, this dorsalmost spine becomes longer and stouter than the other preopercular spines. In the largest planktonic larvae (12.5 mm SL) this dorsalmost spine is about 2.5 times as long as the other spines. The lower preopercular spines decrease in size and number during transformation. The uppermost spine continues to become longer and stouter in benthic juveniles and is over four times

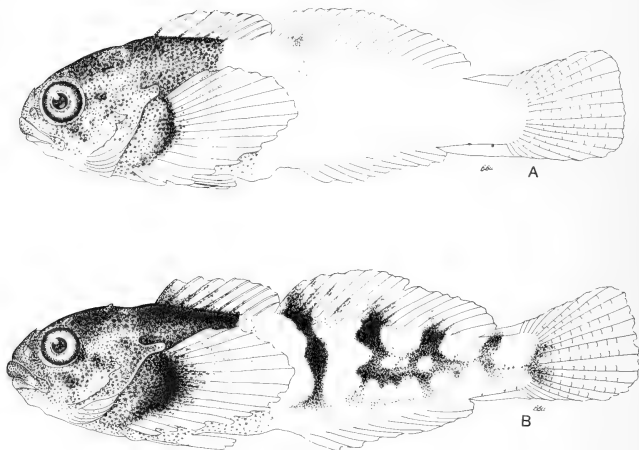


FIGURE 28. Juveniles of *Clinocottus globiceps*: A) 13.7 mm SL, B) 14.6 mm SL.

as long as the lower spines in a 14.5 mm specimen. The other preopercular spines are reduced to small bumps or serrations along the lower preopercular margin. In a 17-mm juvenile all remnants of the lower spines have disappeared and only the large dorsal spine persists.

Clusters of spines develop on the head in the parietal region of *C. globiceps* larvae. One tiny spine is visible on each side of the head in larvae 6–7 mm and two spines are present on each side of the head in larvae 7–8 mm. By ~9–10 mm, five to six spines are present on each side of the head, arranged in a parallel pair of rows with two to three spines in the anterior row and three spines in the posterior row. These spines persist in the largest planktonic specimens examined (12.9 mm). In newly settled benthic juveniles, however, these spines appear reduced and are present only as bony protuberances situated at the posterior margin of the parietals. Each protuberance has a hollow canal running through it which eventually forms the incipient cranial lateral line system in the parietal region of the head.

Similar spine clusters also form in the supra-cleithral-posttemporal region. One or two small spines are first visible in larvae ~9 mm long. Five or six spines, arranged in two rows of three spines each, are present in both of the 12-mm specimens. These spines eventually become associated with the lateral line system in benthic juveniles.

Clinocottus analis

(Figure 29; Table 6)

LITERATURE.—Eigenmann (1892) and Budd (1940) briefly described and illustrated 4-mm specimens of *C. analis*.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: an advanced anus, cirri, head shape, and pigmentation. Pigmentation, preopercular spination, and body shape linked postflexion larvae of *C. analis* with juveniles and adults.

DISTINGUISHING FEATURES.—Late postflexion and transforming specimens of *C. analis* were identified in collections from southern Califor-

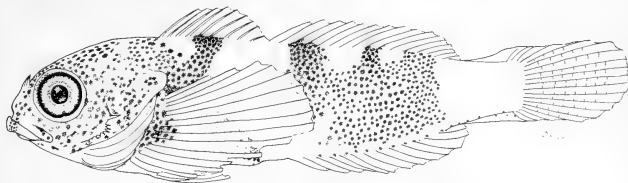


FIGURE 29. Young of *Clinocottus analis*: 10.5 mm SL.

nia. Apart from the two descriptions of newly hatched larvae, intermediate larval stages of *C. analis* are unknown. A brief diagnosis of postflexion larval *C. analis* is presented in the hope that this information may facilitate the identification of a complete developmental series of *C. analis*.

Eleven postflexion larval *C. analis* (9.9–11.4 mm SL) were examined for developmental morphology, pigmentation, and spination. *Clinocottus analis* postflexion larvae may be distinguished from all other larvae belonging to the *Arteidius*, *Clinocottus*, *Oligocottus* groups by the intense band of melanistic pigmentation on the lateral body surface between the bases of the second dorsal and anal fins. Intense melanophores are also present on the dorsolateral surface of the head, the snout, the tips of the lips, and on the operculum. A patch of melanophores is present on the pectoral fin base and in a band on the dorsum beneath the spinous dorsal fin. Sixteen to 22 small, round melanophores are situated on the ventral midline posterior to the anus.

Postflexion larval *C. analis* have blunt, rounded snouts and relatively large heads. Snout length and head length are 28% HL and 30% SL, respectively, longer than in other *Clinocottus* larvae. In addition, *C. analis* larvae have moderately long, bulging guts. Snout to anus length averages 49% SL in postflexion larvae. Body depth at the pectoral fin base is 28% SL, while body depth at the anus is 26% SL.

Six to 11 spines are present on the posterior margin of the preopercle. The dorsalmost spine is longer and stouter than the other spines. In the smallest specimens (9.9–11.0 mm) the spines are situated in two groups of three to five spines. The ventralmost spines begin to regress in larvae > 11

mm long; these spines decrease in size and number and gradually become covered by skin. Two small spines are also present in the parietal region of the head in the 9.9 mm specimen. These spines decrease in size and remain only as bony bumps by ~11 mm.

Arteidius creaseri

(Figures 30, 31; Table 7)

LITERATURE.—Larval *Arteidius creaseri* have not been previously described.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: low dorsal fin ray (12–14) and anal fin ray (9–10) counts, low vertebral counts (30–31), scales extending onto head under the orbit and on the snout, and the presence of a preorbital cirrus. The developmental series was linked together primarily by preopercular and parietal spination, pigmentation, body shape, and meristics. Postflexion and transforming larvae were linked to juveniles by the cirri pattern, pigmentation, body shape, and meristics.

DISTINGUISHING FEATURES.—Preflexion larvae of *A. creaseri* are characterized by a pointed snout, large head, and relatively deep body. Distinguishing pigmentation includes intense, large, round melanophores covering the dorsolateral surface of the gut, 1–3 large melanophores at the anteroventral margin of the gut, and a series of 7–11 large, evenly spaced melanophores along the ventral midline posterior to the anus. A large, distinctive, blotch-like melanophore is located on the ventral finfold near the tail tip, and another smaller melanophore occurs just beneath the tail tip.

Larvae of *A. creaseri* > 7 mm are further distinguished by the presence of four large, evenly

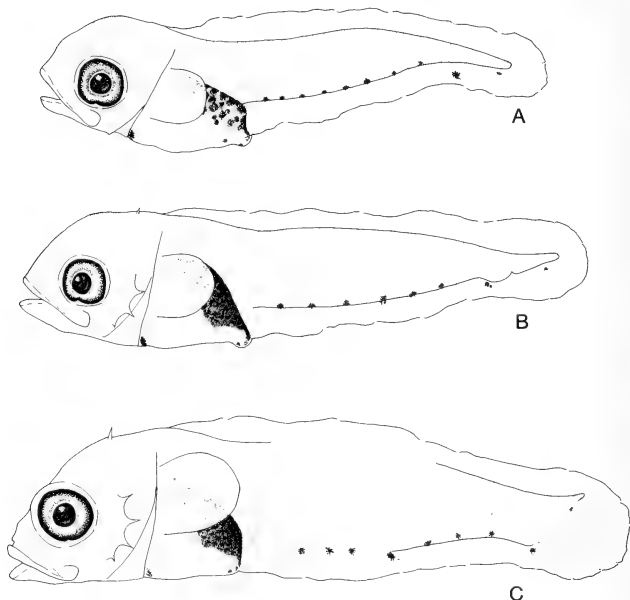


FIGURE 30. Larvae of *Artedius creaseri*: A) 5.0 mm NL, B) 6.6 mm NL, C) 7.9 mm SL.

spaced preopercular spines and a prominent parietal and nuchal spine. Late postflexion larvae may be recognized by their pointed snout and long jaw, large head, and the characteristic ventral midline pigmentation. In addition, meristics, especially the low dorsal fin, anal fin, and vertebral counts are diagnostic of this species. Small juveniles possess a long, slender nasal cirrus, a broad, ribbonlike postorbital cirrus with a fringed tip, and two pairs of frontoparietal cirri.

PIGMENTATION.—Small preflexion larvae of *A. creaseri* are relatively lightly pigmented. They possess no melanistic pigmentation on either the head or the nape. Pigmentation over the dorsolateral surface of the gut is heavy and intense.

Melanophores are large, round, and closely packed together. One or 2 melanophores are present on the ventral surface of the gut lying just posterior to the cleithrum. Posterior to the anus, the sole pigmentation consists of a series of 7–11 large, rounded melanophores evenly spaced along the ventral midline, positioned approximately 1 to every three myomeres. This series originates under the third or fourth post-anal myomere and extends posteriorly toward the tail tip. The posteriormost 1 or 2 melanophores in this series lie on the ventral finfold and are notable: large and blotchlike.

Pigmentation increases markedly during larval development. Two melanophores form over the

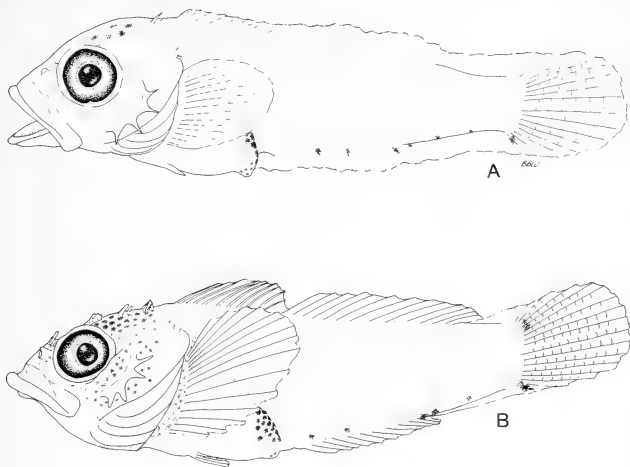


FIGURE 31. Larvae of *Artedius creaseri*: A) 9.1 mm SL, B) 13.0 mm SL.

midbrain in larvae >5.7 mm. During flexion, melanophores increase in number and extend anteriorly onto the forebrain. By ~ 8.0 mm, the dorsal surface of the head is entirely pigmented. Pigmentation extends dorsally along the anterior wall of the gut so that 3 or 4 large melanophores lie just posterior to the cleithrum. Several melanophores form at the posterior margin of the gut in larvae >6 mm, frequently forming a ring around the anus. The number of postanal ventral midline melanophores ranges from 6 to 12, and the 4th or 5th melanophore in the series increases markedly in size and extends below the body wall onto the ventral finfold. The posteriormost 2 melanophores in the series move up onto the base of the caudal finfold. One is positioned just posterior to the lower hypural plate and the other lies just below the tip of the notochord at the dorsal base of the upper hypural plate.

Transforming larvae (>10 mm) have melanophores extending ventrally along the preopercle and opercle and two to four melanophores

on the lower jaw. Pigment is also added on the pectoral fin.

MORPHOLOGY.—The smallest larval *A. creaseri* examined is 3.5 mm NL and recently hatched. Flexion of the notochord occurs between 5.7 and 7.9 mm NL. The largest planktonic specimen is 13 mm and beginning to develop juvenile pigmentation. The smallest benthic juvenile is 13.5 mm and still undergoing transformation. Thirty-two specimens ranging from 3.5 to 13.6 mm were measured for developmental morphology.

Artedius creaseri larvae are relatively deep-bodied with distinctively large heads and pointed snouts. Body depth at the pectoral fin base averages 26% in preflexion larvae and increases to 29% SL in postflexion larvae. Relative head length averages about 25% in preflexion and flexion larvae and increases to 33% SL in postflexion larvae. Snout length remains 30% HL during larval development.

FIN DEVELOPMENT.—Initiation of a thickening in the hypural region of the developing caudal

TABLE 7. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *ARTEDIUS CREASERI* AND *A. MEANYI*. Values are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

| Item | <i>Artedius creaseri</i> | <i>Artedius meanyi</i> |
|-------------------------------------|--------------------------|-------------------------|
| Head length/SL: | | |
| Preflexion | 24.4 ± 1.25 (22.9–26.5) | 18.6 ± 1.77 (17.9–21.3) |
| Flexion | 26.0 ± 2.46 (22.8–28.8) | 22.7 ± 3.53 (19.4–38.0) |
| Postflexion | 32.6 ± 3.80 (26.5–38.5) | 32.1 ± 4.68 (25.4–38.0) |
| Juvenile | 40.3 ± 2.97 (38.2–42.4) | – |
| Snout length/HL: | | |
| Preflexion | 29.7 ± 2.74 (25.0–33.0) | 27.5 ± 7.50 (15.1–31.0) |
| Flexion | 31.9 ± 3.58 (26.7–36.9) | 29.5 ± 5.01 (22.3–35.4) |
| Postflexion | 30.4 ± 2.95 (25.1–35.5) | 29.4 ± 4.34 (23.1–37.3) |
| Juvenile | 23.2 ± 1.20 (22.4–24.1) | – |
| Eye diameter/HL: | | |
| Preflexion | 42.0 ± 4.42 (34.7–47.3) | 44.0 ± 3.39 (35.0–47.7) |
| Flexion | 37.4 ± 3.11 (32.5–43.1) | 36.6 ± 4.93 (30.4–43.1) |
| Postflexion | 33.2 ± 4.01 (27.5–38.6) | 29.0 ± 3.31 (23.2–35.3) |
| Juvenile | 30.4 ± 1.20 (29.6–31.3) | – |
| Snout to anus length/SL: | | |
| Preflexion | 44.6 ± 3.01 (41.5–50.0) | 33.0 ± 2.86 (27.2–35.4) |
| Flexion | 43.5 ± 3.83 (39.7–50.0) | 39.6 ± 2.97 (36.1–44.3) |
| Postflexion | 51.5 ± 3.66 (44.6–55.8) | 48.3 ± 4.43 (38.0–55.2) |
| Juvenile | 54.4 ± 1.77 (53.2–55.7) | – |
| Snout to pelvic fin origin/SL: | | |
| Preflexion | – | – |
| Flexion | – | 23.0* |
| Postflexion | 29.5 ± 2.17 (27.0–33.1) | 29.1 ± 3.16 (21.9–33.6) |
| Juvenile | 32.0 ± 2.12 (30.5–33.5) | – |
| Pelvic fin origin to anus/SL: | | |
| Preflexion | – | – |
| Flexion | – | 20.1* |
| Postflexion | 24.6 ± 4.96 (17.5–33.9) | 19.4 ± 1.60 (15.7–22.1) |
| Juvenile | 22.4 ± 0.35 (22.2–22.7) | – |
| Body depth at pectoral fin base/SL: | | |
| Preflexion | 26.0 ± 2.54 (23.4–29.7) | 18.0 ± 1.64 (16.2–20.0) |
| Flexion | 26.0 ± 1.78 (22.7–28.1) | 19.9 ± 1.25 (17.7–22.2) |
| Postflexion | 28.8 ± 2.67 (25.3–33.8) | 24.6 ± 3.65 (17.2–30.1) |
| Juvenile | 24.8 ± 1.98 (23.4–26.2) | – |
| Body depth at anus/SL: | | |
| Preflexion | 21.8 ± 2.35 (19.4–26.0) | 15.2 ± 3.11 (11.9–19.1) |
| Flexion | 24.0 ± 3.08 (19.3–28.1) | 18.9 ± 1.55 (15.8–21.3) |
| Postflexion | 28.2 ± 3.07 (25.4–36.2) | 24.6 ± 2.73 (19.3–28.4) |
| Juvenile | 21.2 ± 2.19 (19.6–22.7) | – |
| Pectoral fin length/SL: | | |
| Preflexion | – | 8.4 ± 1.35 (6.4–9.1) |
| Flexion | 12.2 ± 1.97 (9.5–15.1) | 9.2 ± 1.77 (6.5–12.1) |
| Postflexion | 23.7 ± 6.11 (14.5–35.2) | 19.0 ± 6.21 (10.1–28.3) |
| Juvenile | 30.1 ± 1.34 (29.1–31.0) | – |

– = Not present at this stage.

* = Only one specimen available at this stage.

fin is first evident at 5.7 mm, coincident with the onset of notochord flexion. Caudal rays are present at 6.4 mm, but the adult complement of 6 +

6 principal caudal rays is not present until larvae reach ~8.0 mm.

Bases of the second dorsal (12–14) and anal

(9–11) fins are countable in larvae ~7–8 mm long, and fin rays are formed between 9 and 10 mm. The adult complement of dorsal fin spines (IX–X) is first countable at 9.7 mm. Pectoral fin rays begin forming at ~7–8 mm, and the adult complement is present at 8.6 mm. Pelvic buds begin to form at >8 mm; however, the adult complement of rays is not present until larvae are >11 mm.

SPINATION.—*Artedius creaseri* larvae develop prominent head spines. In contrast to *Artedius*, *Clinocottus*, and *Oligocottus* larvae which have multiple preopercular spines, *A. creaseri* larvae develop four equal-sized preopercular spines. Two spines develop first on the posterior margin of the preopercle at >5.7 mm. At a state of growth between ~6.4 and 7 mm, two additional spines develop, one dorsal and one ventral to the original two spines. The middle two spines remain slightly longer than the outer two throughout larval development. These spines persist through transformation and are present in juveniles. In larvae >10 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner shelf of the preopercle parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. Prominent spines also form in the parietal region of the head. A single parietal spine is first visible at 5.7 mm. By >9 mm, a second smaller parietal spine forms just posterior to the first. These spines are quite large and distinctive, and they are present in the largest planktonic larvae (>13 mm long).

When larvae reach ~8 mm, a spine forms in the supracleithral-posttemporal region. The supracleithral spine points dorsolaterally. A second supracleithral spine forms just ventral to the first and points dorsally. Larvae >9.5 mm form one posttemporal spine. These spines persist in the largest planktonic larvae (13.6 mm) but regress in young juveniles becoming incorporated into the developing lateral line canal system.

Artedius meanyi

(Figures 32, 33; Table 7)

LITERATURE.—Blackburn (1973) described a 4.3-mm larva resembling *A. meanyi*, which he called Cottid 3. Richardson (1977) and Richardson and Percy (1977) listed three larvae as *Ice-*

linus sp. 1. Richardson and Washington (1980) illustrated and described specimens 3.3, 8.6, 10.9, 12.5, 13.5, 15.2, 16.5, and 16.6 mm long as *Icelinus* spp.

IDENTIFICATION.—Larval *A. meanyi* were misidentified as *Icelinus* spp. by Richardson and Washington (1980) on the basis of meristics and the pelvic fin ray count of I,2, which is characteristic of *Icelinus*. Meristics also match those of *A. meanyi*, which possess I,3 (rarely I,2) pelvic fin rays (Rosenblatt and Wilkie 1963; Lea 1974). Recently, Howe and Richardson (1978) reexamined Lea's specimens of *A. meanyi* and reported that "... only one small specimen appeared to have two rays—all others had three rays." Lea's specimens were reexamined in this study. Cleared and stained specimens clearly have I,2 pelvic fin rays. The outermost ray is greatly thickened and branched at the tip in all specimens examined. All of the misidentified "*Icelinus*" larvae possess this distinctive, thickened outer ray.

In addition, during the present study, large transforming specimens of *A. meanyi* were obtained that possess scales on the dorsal surface of the head, the opercle, and in four or five rows on either side of the dorsal fins. Specimens also possessed preorbital cirri and distinctive postocular cirri with three tentacles arising from a single base. The combination of these morphological and meristic characters conclusively identifies these transforming larvae and juveniles as *A. meanyi*. The developmental series was linked together primarily on the basis of pigmentation and body shape.

DISTINGUISHING FEATURES.—Small preflexion larval *A. meanyi* are distinguished by their short, compact guts (snout to anus length averages 33% SL) and pointed snouts. Characteristic pigmentation includes a low number of ventral midline melanophores posterior to the anus (<13), several large melanophores situated anteriorly on the visceral mass at the base of the cleithrum, and two distinctive blotches of pigment on both the dorsal and anal finfolds.

Notochord flexion begins at a relatively large size, ~6.2 mm in *A. meanyi* larvae, and is complete by ~9.4 mm. Four large, evenly spaced spines form along the margin of the preopercle in postflexion larvae >9 mm. Two parietal spines develop at the posterior margin of each parietal in larvae >11 mm.

Postflexion and juvenile *A. meanyi* (13–18 mm

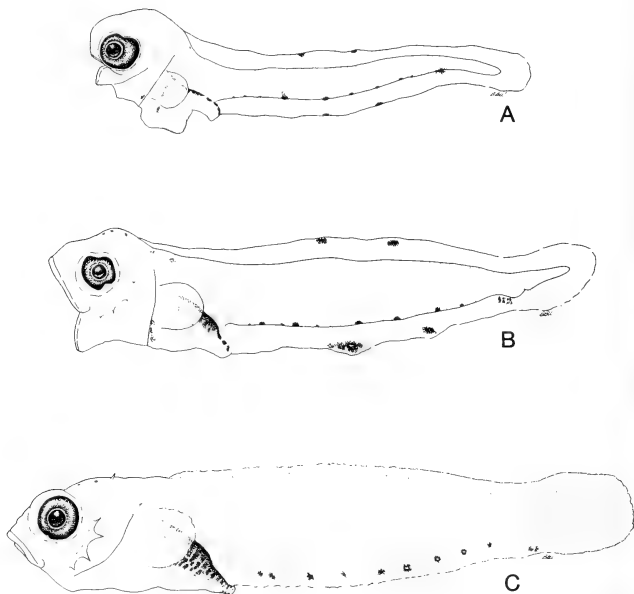


FIGURE 32. Larvae of *Artedius meanyi*: A) 3.3 mm NL, B) 8.6 mm NL, C) 10.9 mm NL (from Richardson and Washington 1980).

long) are distinguished by a low number of blotchy ventral midline melanophores posterior to the anus, a relatively pointed snout and large head (33% SL), a pelvic fin ray count of I,2 with the outermost ray thickened as if two rays are fused together, and other meristics. In addition, juvenile *A. meanyi* possess a single, slender preorbital cirrus, an eyeball cirrus, and a distinctive postorbital cirrus having three tentacles that arise from a single base. The largest specimens (16–18 mm) possess rows of prickle-like scales on the parietal, cheek, and opercular regions of the head and on the dorsal surface of the body and caudal peduncle.

PIGMENTATION.—Small *A. meanyi* larvae are relatively lightly pigmented. Melanistic pigmentation is absent on the head of preflexion larvae. Two to 5 round, external melanophores are clustered on the nape. The dorsolateral surface of the gut is lightly pigmented. Two or 3 large dendritic melanophores are embedded in the anterior musculature of the body cavity just posterior to the cleithrum. Posterior to the anus, a series of 7–13 large, blotch-like melanophores is positioned along the ventral midline originating under the second to fourth postanal myomere and extending toward the tail tip. These melanophores vary in size with the 3rd or 4th and the

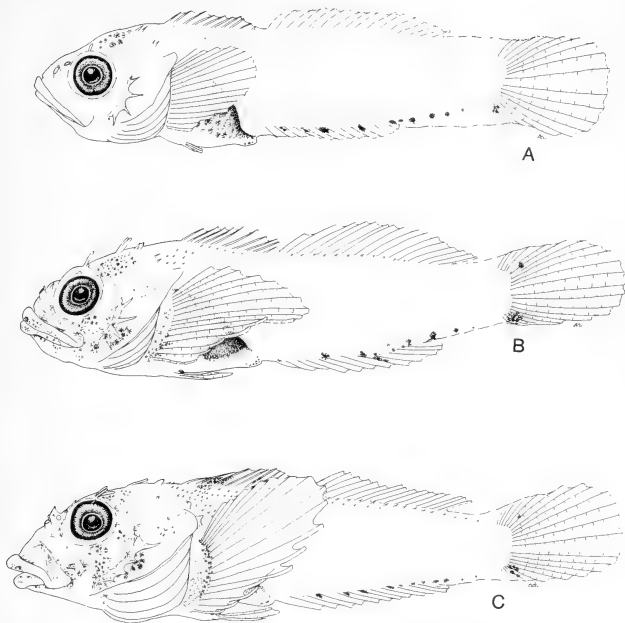


FIGURE 33. Young of *Arctidius meanyi*: A) 13.8 mm SL, B) 15.2 mm SL, C) 16.5 mm SL (from Richardson and Washington 1980).

posteriormost melanophores of the series being markedly larger and frequently extending onto the ventral finfold. Two large distinct pigment blotches are present on both the dorsal and ventral finfolds in small larvae. One specimen out of 45 examined possessed three pigment spots on both the dorsal and anal finfolds.

Melanistic pigmentation increases during larval development. Several melanophores are added over the brain in larvae between 7.4 and 8 mm. Melanophores in the nape region become embedded in larvae > 6 mm as body musculature develops. Pigmentation increases slightly over

the lateral surfaces of the gut. With the onset of notochord flexion and development of the caudal fin, the posteriormost melanophore of the ventral midline series is characteristically positioned at the ventral margin of the forming caudal fin. A second, large melanophore is frequently added at the dorsal margin of the caudal fin base dorsal to the notochord tip. The blotches of pigment on the dorsal and ventral finfolds disappear in larvae > 9 mm as fin rays begin to form.

During transformation, between 13 and 19 mm, head pigmentation increases markedly. Melanophores extend anteriorly over the interor-

bital region and onto the snout. Several melanophores are added just ventral to the orbit, between the eye and preopercle, and along the dorsal margin to the opercle. With development, melanophores are also added along the pectoral fin base, in a band across the dorsum, and on the dorsal fin around the first four dorsal spines. Melanophores are also added to the upper and lower lips, across the cheek, along the ventral margin of the opercle, and on the dorsal surface of the head.

MORPHOLOGY.—The smallest larval *A. meanyi* collected from plankton samples are ~3 mm NL long and appear recently hatched. Larvae undergo notochord flexion between 6.2 and 9.4 mm NL. Specimens as large as 18–19 mm were collected in plankton and neuston tows. Planktonic larvae >15 mm are beginning to undergo transformation indicated by the development of juvenile pigmentation and the formation of scales on the head and dorsum. The smallest benthic juveniles examined were 15–16 mm long and were fully transformed. Thirty specimens, ranging in size from 3.3 to 17.9 mm, were examined for morphometrics.

Small larval *A. meanyi* are relatively slender with a characteristic body shape. Body depth is constricted just posterior to the anus; the body bulges slightly in the midtail region and narrows again near the tail tip or caudal peduncle. This distinctive body shape remains apparent throughout larval development. The gut of *A. meanyi* is short and tightly coiled. Snout to anus length averages 33% SL in preflexion larvae increasing markedly to 48% in postflexion larvae. Prior to flexion of the notochord, body depth averages 18% at the pectoral fin base and 15% SL at the anus and increases to 25% SL at both the pectoral fin base and the anus in postflexion larvae and juveniles.

Artemis meanyi larvae have small heads with a distinctively pointed snout. Head length averages 19% in preflexion larvae, then increases dramatically to 33% SL in late postflexion larvae and juveniles. Snout length remains relatively constant throughout larval development, ranging from 28 to 30% HL.

FIN DEVELOPMENT.—The fins develop relatively late in *A. meanyi*. Initiation of notochord flexion begins at ~6.2 mm NL. Although caudal rays are first visible in larvae >7 mm long, principal caudal ray number (6 + 6) is not complete until after notochord flexion at ~11 mm. Dorsal

and anal soft rays begin to form in larvae 9.5–10 mm long. The full complement of fin rays is visible in larvae ~12 mm. Dorsal spines (IX–X) begin to form at ~11 mm and are all present by 12–13 mm. Pelvic fin buds form in larvae >9.5 mm; however, the adult complement of pelvic fin rays (I,2) is not complete until larvae reach ~12–13 mm.

SPINATION.—Preopercular spines form relatively late in the development of *A. meanyi* larvae. Two tiny spines are first visible along the central portion of the preopercle in larvae >6.2 mm with a third spine forming dorsal to these spines between 8 and 8.5 mm. By 9.4 mm, a fourth spine is added at the ventral margin of the preopercle. These four spines remain prominent and approximately equal-sized throughout larval development. In larvae >13 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner preopercular shelf parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. During transformation, between 15 and 17 mm, the dorsalmost preopercular spine becomes longer and stouter than the other spines; however, all four preopercular spines remain clearly visible on the largest pelagic juveniles examined (~19 mm long).

Spines also develop in the parietal and supra-cleithral-posttemporal regions of the head. A single tiny spine first forms at the posterior margin of the parietal in larvae >7 mm long. This spine gradually becomes longer, and in larvae between 12 and 13 mm a second, smaller nuchal spine forms immediately posterior to it.

A small spine forms on the dorsal margin of the posttemporal bone between 9 and 10 mm. A second, similarly sized spine is added ventrally on the posttemporal in larvae ~11 mm. At about the same time, a third spine forms posteroventrally to the two posttemporal spines on the dorsal portion of the supra-cleithrum. These three spines increase in size during transformation and eventually become associated with the junction of the cephalic and lateral line systems.

ADDENDUM

Since this study was accepted for publication, a subsequent review of cottid relationships has been published (Washington et al. 1984). Wash-

ington et al. (1984) presented a hypothesis of phylogenetic relationships of cottoids and briefly summarized characters that supported eight proposed monophyletic groups of cottid genera. Much of this work was based on an unpublished manuscript (Washington and Richardson n.d.) in which a hypothesis of cottid relationships based on osteological characters of early life history stages was presented. Results of Washington et al. (1984) support the proposed monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus* and the exclusion of *Artedius creaseri* and *A. meanyi* from this group. They listed five synapomorphic characters in addition to the multiple preopercular spines which support the monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus*. These characters include anterior neural arches enlarged and elevated, arms of the anterior neural arches open in a broad u-shape until late in the juvenile period, a greatly expanded cleithrum base, posterior extensions or bony plates at the cleithrum base which enclose the pelvic bones, and loss of ventral postcleithrum and reduction or loss of dorsal postcleithrum.

Washington et al. (1984) also placed *Artedius creaseri* and *A. meanyi* in a proposed monophyletic group of genera including *Icelinus* and *Myoxocephalus* as well as 10 other cottid genera. This placement gives additional evidence for the exclusion of *Artedius creaseri* and *A. meanyi* from the genus *Artedius* (sensu Bolin 1944) and supports their close relationship to *Icelinus* and *Myoxocephalus*. Further results of Washington et al. (1984) provide additional characters that strengthen the hypothesis of monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus*.

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- Note: Since this paper went to press, a phylogenetic study of the Cottoidea has been published that addresses relationships of 42 cottid genera including *Artedius*, *Clinocottus*, and *Oligocottus* (Yabe 1985). A discussion of Yabe's work will be included in a forthcoming paper (Washington and Richardson n.d.).
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May 6, 1986

BILATERAL ASYMMETRY IN PHALLOSTETHID FISHES
(ATHERINOMORPHA) WITH DESCRIPTION OF
A NEW SPECIES FROM SARAWAK

By

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ABSTRACT: *Phenacostethus trewavasae*, the first phallostethine from Borneo, is described from clay- and gravel-bottom freshwater streams of the Baram River, Sarawak. One of the distinguishing characteristics of *P. trewavasae* is a minute eye-lens. The subfamily Phallostethinae comprises *Phallostethus* Regan, known only from a single collection of one species; *P. dunckeri* Regan, from the mouth of the Muar River, in Johore on the Malay Peninsula; and *Phenacostethus* Myers, known previously from two species, *P. smithi* Myers and *P. posthon* Roberts, from coastal peninsular Malaysia and Thailand.

Male phallostethids are bilaterally asymmetric. The subcephalic copulatory organ, the priapium, is oriented so that the apical side of the body is either the left or right; hence, males are termed sinistral or dextral, respectively. Both *Phallostethus dunckeri* and *Phenacostethus smithi* have, in about equal numbers, males that are either sinistral or dextral. In *P. posthon*, all males are dextral, whereas, in *P. trewavasae*, all males are sinistral. One species of neostethine, *Mirophallus bikolanus* Herre, is known in which all males are dextral.

Bilateral asymmetry is compared among phallostethids to assess better the nature of this phenomenon, and its importance in determining the homology of priapial structures.

INTRODUCTION

Phallostethids are a group of some 20 known species of Indo-Australian atherinomorph fishes distinguished from all other teleosts by the presence in males of the priapium, a complex, subcephalic copulatory organ (Regan 1913, 1916). Phallostethids have been divided into two groups (and classified traditionally in two families, Phallostethidae and Neostethidae, as in Roberts 1971a, b) on the basis of gross differences in priapial morphology. Rosen and Parenti (1981) and Parenti (1984) treated the entire group as one family, the Phallostethidae sensu lato, and that convention is followed here; the two groups are referred to as the subfamilies Phallostethinae

and Neostethinae. The closest living relative of the freshwater, brackish, and occasionally salt-water phallostethids is hypothesized to be the monotypic western Pacific marine silverside (or hardyhead) *Dentatherina* Patten and Ivantsoff (Parenti 1984).

The subfamily Phallostethinae includes two genera: *Phallostethus* Regan with one species, *P. dunckeri* Regan, 1913, and *Phenacostethus* Myers, with three species, *P. smithi* Myers, 1928, *P. posthon* Roberts, 1971a, and *P. trewavasae*, described herein.

Phallostethids are found throughout coastal peninsular Malaysia, Thailand, Borneo, the Philippines, and Java. *Phallostethus* and *Phenacostethus* were known previously only from penin-

sular Malaysia and Thailand (see Roberts 1971a, fig. 1). The third species of *Phenacostethus*, *P. trewavasae*, was collected from the Baram River in Sarawak, Malaysian Borneo. Fowler (1937) described *Phenacostethus thai* from a series of nine specimens, four males and five females (Academy of Natural Sciences, Philadelphia, ANSP 51352–51360). Roberts (1971a) followed Herre (1942) in treating *Phenacostethus thai* as a synonym of *Phenacostethus smithi*, and I tentatively concur.

All Phallostethinae and Neostethinae males are bilaterally asymmetric with regard to orientation of the major supporting bones and other structures associated with the priapium. Most females are bilaterally symmetric; the anus is just anterior to the urogenital opening along the ventral midline, under the throat (see Regan 1913, fig. 2). In just one species of neostethine are bilaterally asymmetric females found (see Parenti, in press).

Bilateral asymmetry is well documented in fishes (see Hubbs and Hubbs 1945, and references therein, for a comprehensive review). Most phallostethid species have both sinistral and dextral males in more or less equal numbers. Roberts (1971a) described *Phenacostethus posthon*, the first known species in which males are exclusively dextral. *Phenacostethus trewavasae* males are exclusively sinistral. Both species are known from relatively large numbers of specimens, such that unique or fixed asymmetry can only be interpreted as a natural phenomenon in some phallostethids.

Phenacostethus trewavasae is also distinguished by a minute eye-lens. The structure and function of the retina and, hence, the quality of vision, is unknown.

MATERIALS AND METHODS

The material on which the description of *Phenacostethus trewavasae* is based was made available for study by Dr. E. J. Crossman, of the Royal Ontario Museum (ROM), where the holotype and majority of paratypes and additional specimens are deposited. Remaining paratypes have been deposited in the California Academy of Sciences (CAS), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), and the United States National Museum of Natural History (USNM), through the courtesy of Dr. Crossman.

Included in the comparative material are specimens of *Phallostethus dunckeri* Regan from the single known collection by G. Duncker from the Muar River, in Johore on the Malay Peninsula (Duncker 1904). Regan's (1913) description was based on seven specimens from this collection. Both Roberts (1971b) and Parenti (1984) believed that the only known specimens were the BMNH syntypes. However, additional specimens from the single collection by Duncker have been discovered in the Zoologisches Museum, Hamburg (ZMH) and have been made available for study through the courtesy of Prof. H. Wilkens. Some of the ZMH material was given lectotype and paralectotype status erroneously by Ladiges et al. (1958), who did not refer to the BMNH syntypes.

Osteological structures were examined in, and counts made on, material counterstained with alcian blue and alizarin red S following the procedure of Dingerkus and Uhler (1977), or solely alizarin stained. See text and Table 2 for catalog numbers of phallostethid material examined. Alcohol-preserved (USNM 230367, USNM 230181), solely alizarin-stained (USNM 230371, USNM 230366), and counterstained preparations (USNM 230374) of the western Pacific *Dentatherina merceri* were used for outgroup comparison. Additional comparative material was obtained on loan from the University of Michigan, Museum of Zoology (UMMZ) and the Museum of Comparative Zoology, Harvard University (MCZ).

A Zeiss SV8 stereomicroscope with drawing tube and photomicrography apparatus was used for dissection of specimens and recording of data.

Phenacostethus trewavasae, new species

(Figures 1–3, 4b)

HOLOTYPE.—ROM 41826, a mature, sinistral male, 14.1 mm standard length, collected 3 August 1981, by Dwight Watson, from Malaysia: Sarawak (Fourth Division), Baram River, Sungei Kejin Tugang, tributary of Sungei Kejin, depth to 1 m, clay- and gravel-bottom stream (03°41'30"N, 114°27'15"E).

PARATYPES.—ROM 44289 (8 sinistral males, 11 females); ROM CS 812 (2 sinistral males, 1 female, all cleared and stained with alizarin red S); ROM 41827 (1 adult female), taken with the holotype.

ROM 41829 (1 sinistral male); ROM 41830 (7 sinistral males, 6 females); CAS 55454 (3 sinistral males, 2 females); BMNH 1984.7.12:1–5 (3 sinistral males, 2 females); AMNH 55570 (3 sinistral males, 2 females); USNM 267266 (2 sinistral males, 3 females), all collected 11 February 1980, by Dwight Watson, from Malaysia: Sarawak (Fourth Division), Baram River, Sungei Kejin, station at confluence of Kejin Tugang and Kejin

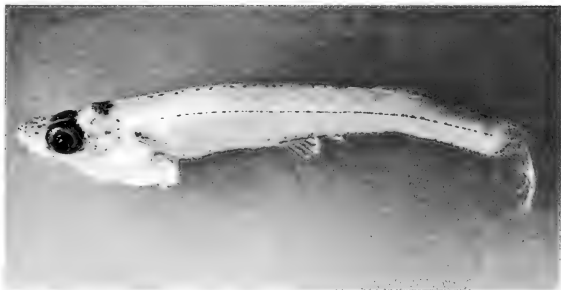


FIGURE 1. *Phenacostethus trewavasae*, 14.1-mm holotype (ROM 41826).

River, depth to 1 m, clay- and gravel-bottom stream, no vegetation (03°41'30"N, 114°27'15"E).

ADDITIONAL MATERIAL EXAMINED (no type status).—ROM 41828 (11 juveniles), collected 27–30 July 1981 from Malaysia: Sarawak (Fourth Division), Baram River, Loagan Titad.

ROM 44290 (9 sinistral males, 17 females, 3 juveniles or of undetermined gender, of which 2 sinistral males and 2 females have been counterstained with alcian blue and alizarin red S); ROM 44291 (24 sinistral males, 12 females, 14 juveniles or of undetermined gender) taken with the holotype.

DIAGNOSIS.—*Phenacostethus trewavasae* is distinguished from its sister species, *P. posthon*, by having only sinistral males, that is, with apbroctal side of body on the left. The hooklike

toxactinium arises on right side of head and curves very strongly under head towards left side of body. Males of *P. posthon* are exclusively dextral. Four characters distinguish the sister species from *Phenacostethus smithi*: distal portion of penis smooth; penial bone absent; ctenactinium small or absent; and stout and distinctly curved, hooklike toxactinium (see Fig. 5). Males of *P. smithi* are either sinistral or dextral and occur in about equal numbers (see Introduction, Relationships, Bilateral Asymmetry, and Table 2).

A second diagnostic character is a minute eye-lens (Fig. 4b), as compared with the relatively large eye-lens of *P. posthon* and *P. smithi* (Fig.

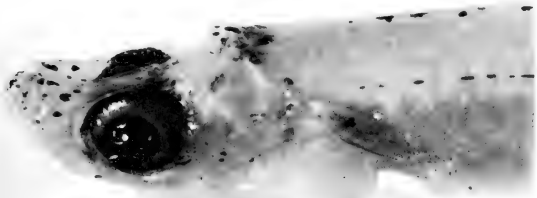


FIGURE 2. *Phenacostethus trewavasae*, left lateral view of head and anterior portion of body of 14.1-mm holotype (ROM 41826).

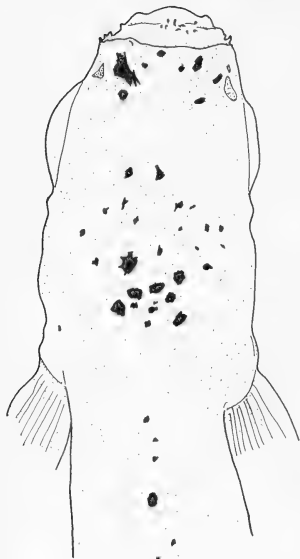


FIGURE 3. Diagrammatic representation of dorsal melanophore pattern, *Phenacostethus trewavasae*, male paratype (ROM 44289).

4a), more typical of that found in diminutive teleost fishes (see below).

DESCRIPTION.—Slender, laterally compressed diminutive phallostethid fish, distinguished by minute eye-lens and by males with sinistral priapium. *Phenacostethus trewavasae* like congeners in meristic data (Table 1). No vestigial pelvic fin rays or supports in females; males with pelvic and parts of pectoral fins modified into priapium that is invariably sinistral: prominent externalized subcephalic bone a toxactinium arising on right side of body, articulating with right axial bone, and curving strongly under head towards left side of body (Fig. 4b). Cartilaginous pulvinular pad lateral to and covering articulation point of, toxactinium and axial bone; small antepleural bone just posterior to point of articulation. Mi-

nute ctenactinium articulates with posterior base of right axial bone. Penis smooth not ruffled as in *P. smithi* (see Roberts 1971a). Pleural ribs of fifth? vertebra, each with a posterior flange, elongate dorsoventrally, meeting just dorsal to right axial bone (Fig. 4a). First pleural rib on fourth vertebra in females, fifth vertebra in males.

Skull, gill arches, and jaws like those illustrated for *Phallostethus dunckeri* Regan by Parenti (1984), with following qualifications. Frontals project above dorsal head profile (Fig. 1, 2, 4b). Three infraorbital bones: preorbital, second infraorbital, and dermosphenotic. Outer jaws with few unicuspid teeth; parodontary with cartilaginous core and slight perichondral ossification, no teeth. Lower jaw protrudes beyond anterior extent of upper jaw. Submaxillary element cartilaginous. Rostral cartilage pear-shaped, wider posteriorly. Two small accessory cartilages between medial ramus of maxilla and rostral cartilage (as in *Ceratostethus bicornis*, Roberts 1971b, fig. 5). Gill arch skeleton highly cartilaginous. Unicuspid teeth on fourth ceratobranchial and infra-pharyngobranchial toothplates. Three cartilaginous basibranchials posterior to cartilaginous basihyal.

Caudal skeleton with two epurals and autogenous parhypural. Caudal fin forked, dorsal and ventral rays forming incipient lobes. Pectoral fin narrow and elongate. Two dorsal fins, the first with a single spine or ray supported by single pterygiophore.

Ventral dermal keel extending from base of priapium in males or urogenital opening in females, to anal fin origin.

Scales on body small and deciduous, absent from dorsal surface of head. Color pattern in alcohol similar to that of congeners (as in Roberts, 1971a, confirmed by personal observation): melanophores scattered on dorsal surface of head and anterior portion of body (Fig. 3), along mid-lateral intermuscular septum, around orbit, on operculum and priapium, and along basal portion of anal fin, dorsal midline, and ventral midline. Ground coloration very pale yellow or light brownish in alcohol; coloration in life unknown, although *P. trewavasae* is probably nearly translucent in life, as are its congeners. Largest specimens reported by Roberts (1971a:13–14) of *P. posthon* and *P. smithi* with a bright orange yellow bar on caudal peduncle and a smaller orange yellow bar on the body “next to the anal fin origin.”

ETYMOLOGY.—*trewavasae*, in honor of Dr. Ethelwynn Trewavas, British Museum (Natural History), to express my deep appreciation of her continued contribution to the field of ichthyology.

EYE-LENS SIZE

The eye-lens is a nearly perfect sphere at the center of the eyeball (Fig. 4). In *P. trewavasae* (Fig. 4b), the eye-lens is minute compared with that of *P. smithi* (Fig. 4a). A minute eye-lens has been observed in all seven of the cleared and stained specimens of *P. trewavasae*. Four of these specimens were chosen at random from a lot of alcohol-preserved specimens for study: a mature male, an immature male, and two adult females (ROM 44290) that were counterstained for bone and cartilage. Three of the seven specimens—two mature males and one adult female (ROM CS 812)—stained solely with alizarin, were not prepared by me, but were probably chosen at random for preliminary identification at ROM. The presence of a minute eye-lens has been confirmed, by dissection, in alcohol-preserved specimens. Size of the eye-lens varies from minute to barely detectable with a dissecting microscope, so that the character of a minute eye-lens may represent a stage in a transition series from a small eye-lens to eye-lens absent.

The ratio of the distance between the center of the lens and the retina to the radius of the lens is nearly a constant in adult teleost fishes. This constant of 2.55, known as Matthiessen's ratio, has been demonstrated in numerous teleosts, and has been confirmed in the cichlid *Haplochromis elegans* Trewavas (Ott 1981). During growth of *H. elegans*, the ratio increases rapidly from about 2.2 to 2.8, then decreases slowly to about 2.5 before leveling off at about 2.55 in the adult (Ott 1981, fig. 15).

Matthiessen's ratio in *P. trewavasae* could not be measured directly as part of this study. However, a minute eye-lens at the center of the eyeball and a normal retina will not affect the distance from the center of the lens to the retina. But, obviously, Matthiessen's ratio will be greatly increased by a small eye-lens radius, and the distance from the center of the lens to the retina will be greater than the focal-length of the eye-lens.

Visual acuity at any given stage in ontogeny is a function of retinal structure as well as shape of

the eyeball (Ott 1981; Levine and MacNichol 1982; Fernald 1985). Growth of the eye-lens is probably retarded very early in ontogeny. Structure and function of the retina, as well as other accommodation made during ontogeny for a minute eye-lens, is unknown. Without such information, the quality of natural vision in *P. trewavasae* will remain open to speculation, but several statements can be made.

First, *P. trewavasae* may have poor visual acuity simply because of the optical properties of a minute eye-lens (Kirschfeld 1976). The short focal length of the eye-lens can be correlated with low resolving power, decreased ability to distinguish among wavelengths of light, and high chromatic aberration. In very small lenses, absolute aperture limits resolving power (Ott 1981:681).

Second, *P. trewavasae* lives in clay- and gravel-bottom, freshwater streams of the Baram River, Sarawak. The species is apparently omnivorous, with sample gut-contents including, for example, larval or juvenile *P. trewavasae* and adult dipterans. Field notes state that there was no vegetation at *P. trewavasae* collecting sites. If the minute eye-lens limits the visual acuity of *P. trewavasae*, then we may assume that the species does not seek out prey visually.

RELATIONSHIPS

Myers (1928) distinguished *Phenacostethus* from *Phallostethus* by a shorter anal fin (Table 1), a protruding lower jaw, and the absence in the female of a groove on the abdomen. Regan (1913, 1916) did not state whether *Phallostethus dunckeri* has a spinous first dorsal fin, and Myers (1928) and Roberts (1971a, b) could only speculate about its presence. The first dorsal fin is absent in the syntypes in the BMNH (Parenti 1984) and absent in the material in the ZMH.

Further, Myers (1928) said that *Phenacostethus* resembled *Phallostethus* and differed from *Neostethus* (and, in fact, from all Neostethinae) in having a priapium that has a prominent hook-like anterior element (the toxactinium) and a shieldlike pulvinular pad. Nevertheless, these elements, or their homologs, are present in most phallostethids. They are well developed and hence are the prominent priapial elements in *Phallostethus* and *Phenacostethus*.

Division of phallostethids into two groups emphasized gross differences between the types of priapia. However, no assessment of whether one

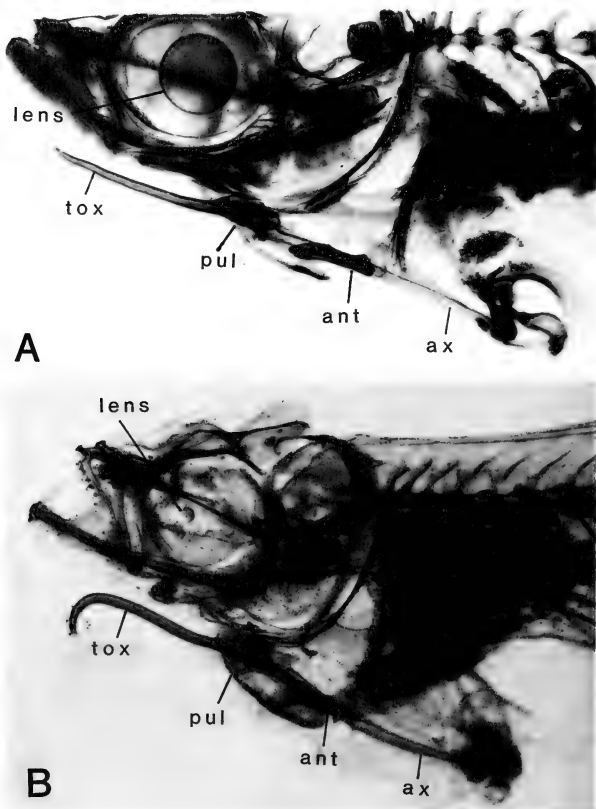


FIGURE 4. Left lateral view of head and anterior portion of body of cleared and stained preparations of male a. *Phenacostethus smithi* (MCZ 47299), and b. *Phenacostethus trewavasae* (ROM 44290), focused on eye-lens. Abbreviations: tox = toxactinium; pul = pulvinular pad; ant = antepleural; ax = axial bone.

or both represented a derived priapium has been incorporated into a classification. For example, Roberts's (1971b:396) branching diagram of phallostethid genera clearly indicates a paraphyletic Neostethinae. Furthermore, he interprets the neostethinae priapium as primitive (Roberts 1971b:395): "The priapium of Neostethinae, in which the only externalized elements are derived from pelvic spines and rays, is evidently more primitive than [the priapia of all other phallostethids]."

Phallostethus and *Phenacostethus* together can be defined as monophyletic by the following shared derived characters (some characters modified from Roberts 1971a:5–6; his numbering not followed):

1. Slender, elongate atherinomorph fishes, with deciduous scales; diminutive—maximum standard length recorded 17.0 mm (Roberts 1971a).

2. Body translucent or transparent, melanophores scattered on top of head (Fig. 3), middle of dorsum, midlateral intermuscular septum, priapium, and basal and distal portion of fin rays (Fig. 1, 2).

3. Dorsum of head with translucent, membranous dome (not as noticeable in alcohol-preserved specimens owing to dehydration).

4. Teeth on premaxilla, parodontary, and dentary small, fewer in number than in other phallostethids and atherinomorphs; no large outer teeth on lateral ramus of premaxilla.

5. Main externalized bone of priapium a toxactinium (Regan 1916; Myers 1928).

6. Large, oval, concave, cartilaginous pulvinular pad covering point of articulation of toxactinium with axial bone (Regan 1916; Myers 1928).

7. Coiled vas deferens terminates in fleshy genital pore or penis that projects from posterior section of priapium.

8. Pelvic spines or rays reduced or absent.

9. Vas deferens highly coiled, forming what has been termed an "epididymus" (Regan 1913, 1916).

Most of these characters represent reductions; that is, we might think of *Phallostethus* and *Phenacostethus* as diminutive phallostethids that, perhaps because of small size, have lost or reduced characters such as pelvic spines and fin rays, complete squamation and heavy pigmentation, and more complete, fuller outer dentition. However, the priapium of *Phallostethus* and *Phenacostethus* cannot be regarded as a reduced

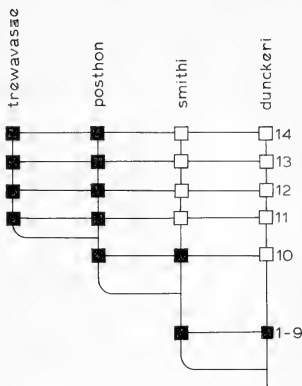


FIGURE 5. Cladogram of relationships among the four species of *Phallostethus* and *Phenacostethus*. Black squares represent one or more synapomorphies; open squares represent one or more symplesiomorphies. Character 1) slender, elongate, diminutive fishes with deciduous scales; 2) body translucent or transparent, melanophores scattered on top of head, middle of dorsum, midlateral intermuscular septum, priapium, and basal and distal portion of fin rays; 3) dorsum of head with translucent, membranous dome; 4) teeth on premaxilla, parodontary and dentary small; 5) main externalized bone of priapium a toxactinium; 6) large, oval, concave, cartilaginous pulvinular pad covering point of articulation of toxactinium with axial bone; 7) coiled vas deferens terminates in fleshy genital pore or penis; 8) pelvic spines or rays reduced or absent; 9) vas deferens highly coiled; 10) protruding lower jaw; 11) distal portion of penis smooth; 12) penial bone absent; 13) ctenactinium small or absent; 14) stout and distinctly curved hooklike toxactinium. See text for defining characters of each species.

character complex. Several elements, including the pulvinular and the externalized toxactinium (homologous with the internalized secondary pulvinular; Roberts 1971b), are more well developed than in other phallostethids. The fact that pelvic fin rays at the base of the priapium are absent in *Phallostethus* and *Phenacostethus*, whereas rudimentary rays are present in neostethines, is interpreted as a derived condition representing a further modification of the pelvic fin supports and rays.

Relationships among the four species of phallostethines are summarized in the cladogram in

TABLE 1. MERISTIC CHARACTERS OF *PHALLOSTETHUS* AND *PHENACOSTETHUS*

| | First dorsal rays | Second dorsal rays | Anal rays | Pectoral rays | Branchiostegal rays | Vertebrae |
|----------------------------------|-------------------|--------------------|-----------|---------------|---------------------|-----------|
| <i>Phallostethus dunckeri</i> | 0 | 8-10 | 26-28 | 9-10 | 4 | 40 |
| <i>Phenacostethus trewavasae</i> | 1 | 6 | 14-15 | 9-10 | 5 | 34 |
| <i>Phenacostethus posthon</i> | 1 | 5-6 | 14-15 | 9-10 | 4 | 34-35 |
| <i>Phenacostethus smithi</i> | 1 | 6-7 | 14-15 | 9-11 | 4-5 | 33-35 |

Figure 5. *Phallostethus* is readily defined by its extremely long anal fin, relatively high number of vertebrae (Table 1), serrated ctenactinium (Regan 1913), and absence of the first dorsal fin (Parenti 1984). The last two characters are also found in some neostethines.

Phenacostethus is defined as monophyletic by the protruding lower jaw (Myers 1928). Myer's additional character, absence of a groove on the abdomen of females, seems to be correlated with quality of preservation, and therefore is not used here.

Phallostethus and *Phenacostethus* are not synonymized here solely for reasons of tradition.

Phenacostethus trewavasae resembles *P. smithi* in that the first and second dorsal fins are separated by a relatively large distance, as opposed to being rather close together, as in *P. posthon* (see Roberts 1971a, fig. 2, 3). The distance between the first and second dorsal fin is a primitive character in *P. smithi* and *P. trewavasae*, and serves as a defining character of *P. posthon*.

Roberts (1971a) described *P. posthon* as reduced in a number of character states relative to *P. smithi*, then its only congener. Three character states that may be described as shared reductions in *P. posthon* and *P. trewavasae* are: (1) distal portion of penis smooth, as opposed to being

ruffled as in *P. smithi*; (2) penial bone absent; (3) ctenactinium, if present, small and barely detectable. These characters were illustrated in both *P. posthon* (Roberts 1971a, fig. 6) and *P. smithi* (Roberts 1971a, fig. 7). (Figures and captions were switched inadvertently when printed, as noted in a published erratum.)

These three reductions are considered synapomorphies of *P. posthon* and *P. trewavasae*. They are correlated with a stouter and more distinctly curved hooklike toxactinium (compare Fig. 4a and 4b). Thus, even though the two species have characters that can only be described as reductions, these characters are treated as synapomorphies in phylogenetic reconstruction because of their correlation with uniquely derived characters (Fig. 5).

BILATERAL ASYMMETRY

A. Anatomical Homology

Bilateral asymmetry is well documented in fishes (Hubbs and Hubbs 1945). The phenomenon usually concerns reproductive structures offset to, or more complex on, one side of the body; although, the well-known asymmetry of flatfishes (pleuronectiforms) is not necessarily associated with reproduction.

TABLE 2. BILATERAL ASYMMETRY IN FIVE SPECIES OF PHALLOSTETHIDAE (SENSU LATO)

| | Total | Dextral males | Sinistral males | Females | Juveniles or undetermined |
|--------------------------------------|-------|---------------|-----------------|---------|---------------------------|
| <i>Phallostethus dunckeri</i> (a) | 25 | 4 | 1 | 16 | 4 |
| <i>Phenacostethus trewavasae</i> (b) | 148 | 0 | 63 | 57 | 28 |
| <i>Phenacostethus posthon</i> (c) | 237 | 107 | 0 | 99 | 31 |
| <i>Phenacostethus smithi</i> (d) | 334 | 179 | 155 | 0 | 0 |
| (e) | 31 | 4 | 6 | 10 | 11 |
| <i>Mirophallus bikolanus</i> (f) | 300 | 173 | 0 | 108 | 19 |

(a) BMNH 1913.5.24:18-20,21,22, ZMH 193-195; (b) total of known specimens, catalog numbers in text; (c) MCZ 47300, 47301 A,B, USNM 229302; (d) Hubbs and Hubbs 1945:290, table XIX; (e) BMNH 1927.12.29:1-10; (f) AMNH 50592, CAS 50722, CAS 53165, UMMZ 211665.

Regan (1916:23) was the first to use the terms "sinistral" and "dextral" to refer to the orientation of the priapium: "In its asymmetry and in being either dextral or sinistral the priapium agrees with the copulatory organ of *Anableps*," a possibly bilaterally asymmetric killifish genus (see Hubbs and Hubbs 1945:289–291). According to the convention established by Regan, in a sinistral male, the anal opening is on the right, what he termed the "proctal side." Hence, the left side of a sinistral male is termed the "aproctal side." The opposite is true for a dextral male, which may be thought of as the mirror image of a sinistral conspecific male. All female phallostethines examined exhibit no bilateral asymmetry; the anus is just anterior to the urogenital opening along the ventral midline under the throat. (See Parenti in press for report of bilateral asymmetric females in one neostethine species.) Regan (1916:21) also pointed out marked differences between priapia of phallostethines and neostethines: "The approximate symmetry of the priapial ribs and cleithra in *Phallostethus*, as compared with their marked asymmetry in *Neostethus*, is no doubt due to the symmetrical attachment of the priapium in the former . . . and its asymmetrical attachment . . . in the latter."

Proportions of sinistral and dextral males of *Phenacostethus smithi* were shown to be equal (Hubbs and Hubbs 1945; Table 2, herein). It was assumed that, with sufficient sample sizes, phallostethid species would be represented by more or less equal numbers of sinistral and dextral males, until Roberts (1971a) described *Phenacostethus posthon*, an exclusively dextral species.

Roberts (1971a) termed *P. posthon* sinistral. However, it is more properly called dextral in keeping with homologies of priapia among all phallostethids. Confusion about whether to call a male sinistral (a left) or dextral (a right), may be traced to a casual statement by Myers (1928: 5): "The proctal side may be indifferently either the right or the left of the fish; in other words, the males are either 'rights' or 'lefts.'" In interpreting this statement strictly, one would assume Myers meant that a male with the proctal side on the right should be called a dextral, or a right. However, this is contrary to the terminology established by Regan and followed by most phallostethid systematists (e.g., Herre 1942; and Myers 1928 himself). Regan emphasized that the proctal side was away from the female during

copulation, and that the aproctal side, the side with the fleshy genital pore or penis, was the obviously functional side of the male with regard to internal fertilization (see also Villadolid and Manacop 1934).

Herre (1942:139) followed Regan's convention but was ambiguous when describing asymmetry: "The coiled, enlarged vas deferens lies within the posterior end of the priapium, from which its penis-like tip projects. The proctal side may be either side, so that males of the same species may be either 'rights' or 'lefts.'" Hubbs and Hubbs (1945:290, table XIX) followed Regan strictly and documented bilateral asymmetry by tabulating the "location, left (L) or right (R), of aproctal side of males of Phallostethidae *Phenacostethus smithi*."

Division of phallostethids into two families was based primarily on the type of prominent external priapial bones. Phallostethines have a hooklike toxactinium that articulates with the axial bone (Fig. 4), a homolog of the pelvic fin girdle (Bailey 1936; Aurich 1937), and curves underneath the head toward the aproctal side (Regan 1916; Herre 1942; Fig. 2, 4 herein). Hence, a male phallostethine with a toxactinium arising on the right side of the head and curving toward the left, aproctal side, is called sinistral because the aproctal side is the left. Such sinistral phallostethine males also have a rudimentary ctenactinium that articulates with the left, aproctal axial bone at its posterior extent.

The prominent externalized priapial bones of neostethines are the one or two ctenactinia that arise on the aproctal side of the body. Hence, a male neostethine with one or two ctenactinia arising on the left side of the body is termed sinistral not because of the position of these prominent priapial bones, but because the aproctal side is the left. This terminology should be adhered to strictly because of the consistency with the inferred homology of priapial structures. Furthermore, this convention for describing bilateral asymmetry of male phallostethids should be followed because the division between phallostethines and neostethines is not supported by unambiguous, derived characters.

Roberts (1971a:13), in describing *Phenacostethus posthon*, was explicit in describing bilateral asymmetry: "... the priapium is invariably sinistral (toxactinium arising on left side) in the material examined." It is clear, therefore, that

Roberts did not follow the convention established by Regan. Hence, I recommend that *P. posthon* be referred to as an exclusively dextral species, not sinistral as Roberts described it. This correction need not be made to Roberts's (1971b) discussion of the anatomy of *Ceratostethus bicornis* (Regan) because that species is a neostethine and the prominent external priapial bones are the ctenactinia, which arise on the aproctal side in every known example.

B. Unique or Fixed Asymmetry

Of the 148 known specimens of *Phenacostethus trewavasae*, 63 are sinistral males, 57 are females, and 28 are juveniles or of otherwise undetermined gender (see Diagnosis and Table 2). The collection of large samples of the exclusively sinistral *Phenacostethus trewavasae* allows us to conclude with certainty that unique or fixed asymmetry is a natural phenomenon in some phallostethids. In addition to the phallostethines *P. trewavasae* and *P. posthon*, the neostethine *Mirophallus bikolanus* Herre has males of fixed asymmetry (Tyson R. Roberts, personal communication). Three large lots of *M. bikolanus*, all collected from the Cabangan River, Albay Province in the Bicol (Bikol) region of Luzon, Philippine Islands, contain dextral males only. Of 300 specimens, 173 are dextral males, 108 are females, and 19 are juveniles or of undetermined gender (Table 2). The relatively high number of male and low number of juvenile or undetermined *M. bikolanus* is probably related to the fact that immature males are readily identifiable as such by the presence of a heavily pigmented anal region.

Unique or fixed asymmetry is a natural phenomenon in other atherinomorph fishes, as reviewed by Hubbs and Hubbs (1945). Females of the ricefish *Horaichthys setnai* Kulkarni may be considered sinistral in that the urogenital opening is to the left of the midline in a majority of females, and the right pelvic fin girde and rays are absent in females (Kulkarni 1940; Hubbs 1941). Males of *H. setnai* have an anal fin modified into an elaborate gonopodium that is not bilaterally asymmetric as far as known. The viviparous poeciliids, *Carluhubbia kidderi* (Hubbs) and *Xenodexia ctenolepis* Hubbs have a concavity on the right side of the gonopodium (Hubbs and Hubbs 1945). Males of the latter species also have a right pelvic fin modified into a so-called

"pectoral clasper" (Hubbs 1950), and a "... thickened fleshy ridge along the ventromesial edge of the proximal third of the outer ray of the right pelvic fin" (Rosen and Bailey 1963:143).

Phenacostethus posthon and *P. trewavasae* are sister species, the males of which are nearly mirror images of each other. Apart from type of bilateral asymmetry, they differ in several characteristics of priapial structure, placement of fins, and relative size of eye-lens (see Diagnosis, Description, and Relationships). One might assume that the common ancestor of these sister species, like most other phallostethids, contained both sinistral and dextral males (Fig. 5). One might assume further that it was the separation of the ancestral species into a sinistral and dextral population that precipitated (or, in fact, was) the speciation event. The problem with such a speciation hypothesis is that it presents a series of untestable statements, the first concerning states of the ancestral species, the second concerning isolation of sinistral and dextral subgroups.

Experimental data are needed to answer the questions: What is the genetic basis of bilateral asymmetry in phallostethids? Does a male phallostethid determine type of bilateral asymmetry of offspring? That is, does a sinistral male have only sinistral male offspring, and likewise, does a dextral male have only dextral male offspring? Breeding experiments to answer these questions, performed when live phallostethids are available for study, will further our understanding of the evolution of bilateral asymmetry, and the special case of fixed or unique asymmetry, in phallostethids.

CONCLUSIONS

Phenacostethus trewavasae new species, is described from the Baram River, Sarawak. It is the first phallostethine species known from Borneo. This subfamily had been reported previously from Thailand and peninsular Malaysia.

Two characters distinguish *P. trewavasae* from all other phallostethines: a minute eye-lens and males that are exclusively sinistral with regard to orientation of priapial structures. We may hypothesize reduced visual acuity in *P. trewavasae* because of the size of the eye-lens; however, a clear statement on vision awaits knowledge of structure of the retina.

All phallostethid males are bilaterally asymmetric, described by position of the anus: in si-

nistral males, the aprectal side is the left; in dextral males, the aprectal side is the right. Females exhibit no apparent asymmetry.

In most species, sinistral and dextral males are represented in more or less equal numbers. Sample sizes of the exclusively sinistral *Phenacostethus trewavasae* and the exclusively dextral *P. posthon* and *Miropallus bikolanus* allow us to conclude with certainty that unique or fixed asymmetry is a natural phenomenon in some phallostethids.

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Mr. Jim Patton, CAS Department of Photography, prepared the photographs in Figures 1 and 2.

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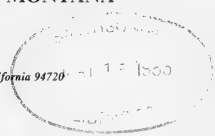
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LAND MOLLUSKS (GASTROPODA: PULMONATA) FROM
EARLY TERTIARY BOZEMAN GROUP, MONTANA

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ABSTRACT: The Bozeman Group consists of fluvial, eolian, and lacustrine rocks deposited in intermontane basins of western Montana after the Laramide Orogeny. In the Three Forks Quadrangle, three early Tertiary formations have yielded land mollusk fossils. The Milligan Creek Formation (of probable Eocene age) contains snails of the genera *Gastrocopta* (two species), *Radiocentrum*, and *Helminthoglypta*; the Climbing Arrow Formation (middle or late Eocene) contains *Gastrocopta* and *Polygyrella*; the Dunbar Creek Formation (latest Eocene or early Oligocene) contains *Gastrocopta* (two species), *Pupoides* (two species), *Radiocentrum*, and *Helminthoglypta*. Three species of *Gastrocopta*, one of *Pupoides* (*Ischnopupoides*), two of *Radiocentrum*, and one of *Helminthoglypta* are described as new. Two others (*Pupoides* and *Polygyrella*) are scarcely distinguishable from extant species.

No interregional correlations are suggested because the land mollusk faunas of the western interior are too spottily known at present. In the Bozeman Group, genera and species groups that are now allopatric occur together. The land mollusks indicate a change in terrain through time: from sparsely vegetated to forested and back again. Climates were temperate and, at least toward the end of the interval, seasonally variable.

Numerous land mollusk taxa in upper Cretaceous and Tertiary rocks of western North America occur outside the Holocene ranges of their families and genera. It is suggested that the evolutionary and biogeographic history of North American land mollusks through the Tertiary has involved (1) the sorting out of component taxa into different geographic/adaptive zones; (2) restriction of many forms to lower latitudes, concurrent with climatic cooling; and (3) eastward and westward displacements, probably related to availability of rainfall. For land mollusks, the late Eocene-early Oligocene was a time not so much of evolutionary innovation as of local extinction and biogeographic rearrangement.

INTRODUCTION

Land and freshwater mollusks from early Tertiary continental sediments of the Bozeman Group in the Three Forks Quadrangle, southwest Montana (Fig. 1), have been reported in checklists by Taylor (*in* Robinson 1963; Taylor 1975). The terrestrial gastropods were not figured or discussed taxonomically; many were not identified beyond family. However, the assemblage is an unusual one and bears strongly on the origins of present-day American land mollusk faunas. Preservation of the fossils ranges from fair to excellent. Seven species are represented by material good enough to permit description of them as new herein, and nearly all taxa can be char-

acterized in greater detail. Table 1 presents a summary of the fauna.

Robinson (1963) presented a detailed account of the geology of the Three Forks Quadrangle. He defined the Bozeman Group—which he anticipated would be recognizable on a regional scale—as the Tertiary fluvial, eolian, and lacustrine rocks that accumulated in the basins of western Montana after the Laramide Orogeny. In the Three Forks Quadrangle the group consists mainly of four formations (Fig. 2). The Sphinx Conglomerate, stratigraphically the lowest, is a limestone conglomerate probably originating as an alluvial apron; it is not fossiliferous.

Next lowest is the Milligan Creek Formation, consisting of light-colored, fine-grained, tuffa-

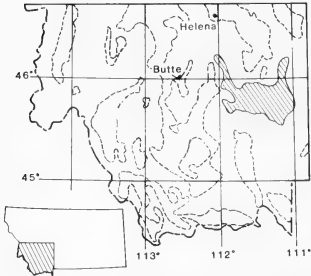


FIGURE 1. Index map of southwestern Montana. Three Forks Basin diagonally hatched; other intermontane basins stippled. After Robinson (1961).

ceous lake deposits that range from limestone to calcareous mudstone. Where it crops out, in the southwest part of the quadrangle, it produces whitish dissected benchlands. Its maximum

thickness is probably not much greater than 90 m. Fossils from the Milligan Creek Formation include five taxa of land snails, all from one locality (USGS 20007). Freshwater mollusks are evidently more widespread and are reported from five additional localities (Taylor 1975). The freshwater gastropod *Lymnaea* is also present at USGS 20007. Ostracods and charophyte remains occur in the formation. The age is probably Eocene but none of the fossils is age-diagnostic. The limestone and other fine-grained rocks of the Milligan Creek Formation were deposited in a perennial lake. Partly based on the snail here described as *Radiocentrum laevidomus*, Robinson (1963) inferred that the lake basin lay in mountainous terrain not much different from that of the present.

The Climbing Arrow Formation conformably overlies the Milligan Creek Formation in places but elsewhere may have formed contemporaneously with it. The Climbing Arrow is made up of olive, thick-bedded, sandy bentonitic clay and coarse sand, with subordinate light-colored siltstone, sandstone, conglomerate, and limestone.

TABLE 1. OCCURRENCE OF LAND MOLLUSKS IN EARLY TERTIARY BOZEMAN GROUP IN THREE FORKS QUADRANGLE, SOUTHWEST MONTANA. Locality numbers are those of U.S. Geological Survey Cenozoic Series.

| Taxon | Mil- ligan Creek Forma- tion | Climbing Arrow Formation | | Dunbar Creek Formation | | | | | | |
|---|--|--------------------------------|-------|------------------------|-------|-------|-------|-------|-------|-------|
| | 20007 | 20008 | 20009 | 20011 | 20012 | 20013 | 20014 | 20015 | 20016 | 20017 |
| Class Gastropoda | | | | | | | | | | |
| Subclass Pulmonata | | | | | | | | | | |
| Family Pupillidae | | | | | | | | | | |
| <i>Gastrocopta (Albinula) montana</i> n. sp. | X | — | — | — | cf. | cf. | — | — | — | cf. |
| <i>G. (A.) sp. a</i> | X | — | — | — | — | — | — | — | — | — |
| <i>G. (A.) sagittaria</i> n. sp. | — | — | X | — | — | — | — | — | — | — |
| <i>G. cordillerae</i> n. sp. | — | — | — | — | X | X | — | X | X | X |
| <i>Pupoides (Ischnopupoides) tephrodes</i> n. sp. | — | — | — | — | — | X | — | X | X | — |
| <i>P. (I.)</i> sp., cf. <i>P. (I.) hordaceus</i> (Gabb, 1866) | — | — | — | — | X | — | — | — | — | — |
| Family Oreohelicidae | | | | | | | | | | |
| <i>Radiocentrum taylori</i> n. sp. | — | — | — | — | — | X | X | X | X | X |
| <i>R. laevidomus</i> n. sp. | X | — | — | — | — | — | — | — | — | — |
| Family Ammonitellidae | | | | | | | | | | |
| <i>Polygyrella</i> sp., cf. <i>P. polygyrella</i> (Bland and Cooper, 1861) | — | X | X | — | — | — | — | — | — | — |
| Family Helminthoglyptidae | | | | | | | | | | |
| <i>Helminthoglypta bozemanensis</i> n. sp. | — | — | ? | X | — | — | — | cf. | cf. | — |

It is extensively exposed in the Three Forks Quadrangle and tends to form subdued topography of low, rounded hills separated by broad, smooth valleys. The formation is not less than 220 m thick, and may be fully twice that. Two fossil localities (USGS 20008, 20009) have yielded three taxa of land snails. Freshwater gastropods are also present in the formation, including one, *Physa?*, from USGS 20009 (Taylor 1975). The Climbing Arrow Formation ranges in age from middle or late Eocene to early Oligocene. A small assemblage of vertebrates from the lower part of the formation was assigned a probable Uintan age (middle to late, but not latest, Eocene) (G. E. Lewis in Robinson 1963). Pipestone Springs (late Eocene) and Chadronian (latest Eocene to early Oligocene) vertebrates are known from higher in the formation (Hough and Lewis in Robinson 1963). A single locality well down in the lowest stratigraphic unit of the Climbing Arrow has yielded the freshwater planorbid gastropod *Biomphalaria pseudammonius* (Schlot-heim), diagnostic of middle to late Eocene age and a tropical climate (McKenna et al. 1962; Taylor 1985). This locality is several hundred meters stratigraphically below the Uintan vertebrate locality. The terrestrial snail localities are probably in the Uintan rather than the Chadronian part of the formation. A diverse fossil microflora exists but has not been studied (Robinson 1963). The Climbing Arrow originated largely as the product of an aggrading stream system. The coarser sediments are stream-channel deposits; the finer-grained ones, evidently overflow deposits that accumulated on the flood-plains in short-lived ponds and lakes.

The Dunbar Creek Formation, stratigraphically the highest named formation of the group, consists of white to grayish yellow thick-bedded tuffaceous siltstone, partly lacustrine and partly eolian in origin, laced with fluvial sandstone and conglomerate; minor limestone and bentonitic clay are also present. The formation is 80–240 m thick in the Three Forks Quadrangle and forms a topography much like that of the Milligan Creek—white benchlands rising steplike from the floodplain, dissected by many steep-walled canyons. The constituent sediments were evidently deposited in a more or less enclosed local basin (part of the larger Three Forks structural basin) which, at least part of the time, contained standing water. Whether the ash of a particular stra-

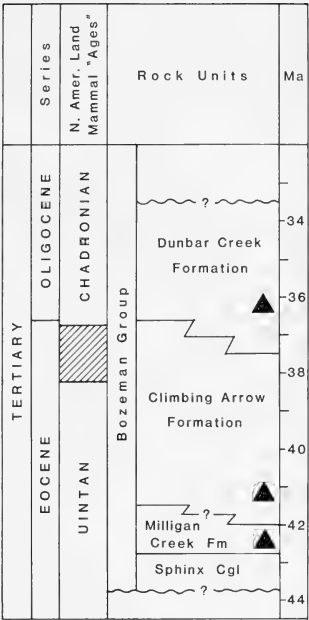


FIGURE 2. Stratigraphic and inferred temporal relations of early Tertiary formations of the Bozeman Group, Three Forks Basin, Montana. Filled triangles indicate sources of land mollusks reported in this study. Ma = millions of years before present.

tum fell in water or on dry land is not always easy to determine, but from the predominance of channeling by "sands and gravel derived from the neighboring highlands and containing little contemporaneous pyroclastic debris," Robinson (1963:80) concluded that if the bulk of the tuffaceous sediments were deposited in a lake, it must have been shallow and often dry. Seven sampling sites yielded a fauna of six species of terrestrial snails, while two other localities in the formation contain freshwater gastropods (Taylor

1975). Thin limestones in the Dunbar Creek Formation may be evaporites or possibly fossil caliche horizons, suggestive of bolson rather than lake conditions.

Based on the presence of brontothere and oreodont bones, Hough and Lewis (*in* Robinson 1963) assigned a Chadronian (latest Eocene to early Oligocene) age to the lower 80 m of the Dunbar Creek Formation. Vertebrate fossils and land snail remains are not recorded from identical localities, but the land snail localities are within this part of the formation. Other parts of the formation are of less certain age and regarded simply as Oligocene.

Remnant patches of middle and late Tertiary sands and gravels, too small and discontinuous to be mapped, also occur in the Three Forks Quadrangle. These are correlated with the Madison Valley beds of Douglass (1903), which elsewhere in the Three Forks Basin lie with angular unconformity on the Dunbar Creek Formation (Robinson 1961). They have yielded a variety of mammal bones, indicating Miocene and Pliocene ages, but as yet no molluscan fossils are recorded.

The unconformity within the Bozeman Group that divides lower, predominantly fine-grained, Eocene and Oligocene strata from upper, predominantly coarse-grained, Miocene and Pliocene strata is probably of regional extent. Kuenzi and Fields (1971, fig. 4) correlated similar rock sequences in the Ruby, Jefferson, Three Forks, Townsend, and Clarkston basins. A biota from the Douglass Creek Basin (Konizeski 1961) suggests time correlation with the Climbing Arrow Formation. Lillegraven and Tabrum (1983, fig. 2) presented an interbasinal correlation diagram including the Dunbar Creek and Climbing Arrow formations, but the placement of these units with reference to the radiometric time scale remains highly inferential.

LOCALITY DESCRIPTIONS

Locality numbers given are those of the U.S. Geological Survey Cenozoic series. Altitudes are given in feet as in the original locality register (with metric equivalents supplied) and are correct to ± 10 ft. All localities are in the Three Forks Quadrangle (USGS, Topographic, 1:62,500, edition of 1950), southwest Montana. Localities are plotted on map by Robinson (1963, pl. 2).

Milligan Creek Formation

20007. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 36, T 1 N, R 1 W; altitude 4,260 ft (1,300 m).

Climbing Arrow Formation

20008. SE $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 11, T 2 N, R 1 W; altitude 4,600 ft (1,400 m).

20009. NE $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 11, T 2 N, R 1 W; altitude 4,580 ft (1,400 m).

Dunbar Creek Formation

20011. SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 6, T 2 N, R 2 E; altitude 4,360 ft (1,330 m).

20012. NW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 5, T 2 N, R 2 E; altitude 4,350 ft (1,330 m).

20013. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,230 ft (1,290 m).

20014. Same location as USGS 20013 but 6 m stratigraphically higher.

20015. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,235 ft (1,290 m).

20016. S $\frac{1}{2}$ NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 19, T 3 N, R 1 E; altitude 4,450 ft (1,360 m).

20017. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,235 ft (1,290 m).

SYSTEMATIC PALEONTOLOGY

The following institutional abbreviations are used: CAS—Department of Invertebrate Zoology, California Academy of Sciences; USGS—United States Geological Survey; USNM—Division of Paleobiology, United States National Museum of Natural History, Smithsonian Institution.

Class GASTROPODA
Subclass PULMONATA
Order ORTHURETHRA
Family PUPILLIDAE

Gastrocopta Wollaston, 1878

TYPE-SPECIES: *Pupa acarus* Benson, 1856, by subsequent designation (Pilsbry 1916:18).

DIAGNOSIS.—Shell "rimate or perforate, cylindrical or ovate-conic, having the angular and parietal lamellae more or less completely united into one biramose, bifid, lobed or sinuous lamella (or rarely the angular is wanting). Columellar lamella present; palatal folds present . . . ; lip well expanded" (Pilsbry 1948:871).

REMARKS.—*Gastrocopta* is the most widely distributed genus of the Pupillidae, with a recorded stratigraphic range of Eocene to Recent (Pilsbry 1948; Zilch 1959; Preece 1982). Pilsbry distinguished two main geographic groups—a northern, and a tropical and southern continent series—each with several subgenera. The subgenus *Albinula* Sterki, 1892, is part of the northern group.

The “*Gastrocopta*? sp.” reported by La Rocque (1960) from the Flagstaff Formation, Paleocene of Utah, does not show sufficient detail for assignment to a subgenus. If correctly allocated to *Gastrocopta*, it is the oldest known member of the genus. Taylor (1975) reported an undescribed species of *Gastrocopta* (*Gastrocopta*) from the Tepee Trail (=Wagon Bed) Formation, upper Eocene of Wyoming, and other fossils questionably referred to *Gastrocopta* from the Wagon Bed and White River formations (lower Oligocene), Wyoming. Pilsbry (1916–18) noted that the Oligocene and Miocene species of Europe seem “a little too specialized” to have been ancestral to the American species. It is reasonable therefore to expect ancestral forms in Eocene, Paleocene, and perhaps upper Cretaceous strata in America and elsewhere.

(*Albinula*) Sterki, 1892

TYPE-SPECIES: *Pupa contracta* Say, 1822, by original designation.

DIAGNOSIS.—“Whitish-translucent gastropods having the inner end of the parietal lamella curved towards the periphery; angular lamella well developed, concrescent in varying degree with the parietal; the palatal folds stand upon a white palatal callus, and a suprapalatal fold is usually developed. Except in *G. armifera*, the columellar lamella is horizontal in front and curves toward the base within. The lip is thin and expanded” (Pilsbry 1948:874).

REMARKS.—*Albinula* occurs in the Eocene of England, the middle Oligocene through upper Miocene of Germany, the Miocene and Pliocene of France, and the Pliocene of Italy (Pilsbry 1916–18; Preece 1982). It is widespread at present in North America, although absent from the Pacific slope, but there are no other American fossil records earlier than Pliocene. The Three Forks Quadrangle is just within the western edge of the Holocene range of the subgenus. *Gastrocopta* (*Al-*

binula) *holzingeri* (Sterki, 1889) is reported to range west to Helena, Montana (Pilsbry 1948).

Several species of the subgenus, *G. armifera* (Say, 1821), *G. contracta* (Say, 1822), *G. holzingeri*, *G. falcis* Leonard, 1946, *G. proarmifera* Leonard, 1946, and *G. tridentata* (Leonard, 1946), occur in Pliocene and early Pleistocene faunas in Kansas (Franzen and Leonard 1947; Leonard 1950; Taylor 1960). *Gastrocopta armifera* also occurs in late Pleistocene deposits in Kansas and Arizona (Franzen and Leonard 1947; Bequaert and Miller 1973), and *G. contracta* occurs in Quaternary deposits in west Texas (Albritton and Bryan 1939).

Gastrocopta (*Albinula*) *montana* new species

(Figure 3)

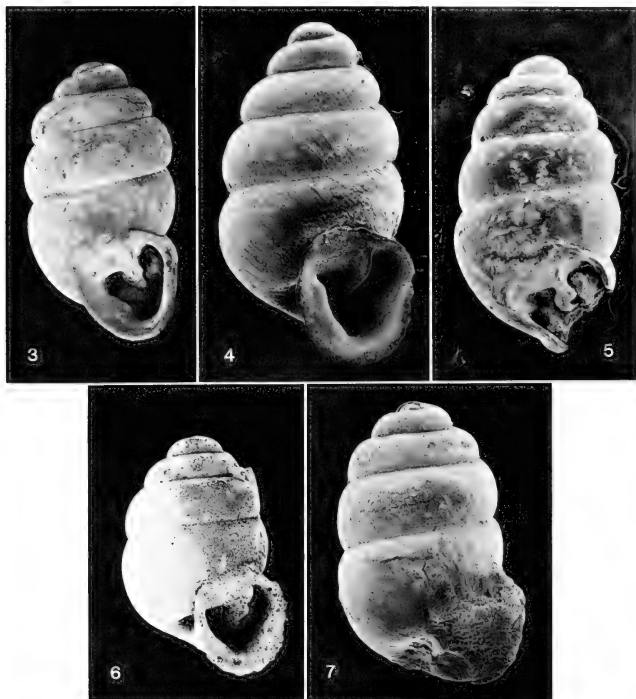
Pupillidae C. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206 (*non* p. 209).

Pupillidae D. D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:206.

DIAGNOSIS.—A cylindric-ovate *Gastrocopta* (*Albinula*) with sinuous, unbranched angular lamella, sulcate body whorl, strong crest, and low callus ridges inside inner and outer lips.

DESCRIPTION.—Shell dextral, umbilicate, cylindric-ovate, of about 5.25 whorls; suture lightly to moderately impressed, early whorls strongly convex, later ones less so. Nuclear whorls smooth; neanic sculpture of oblique growth lines, strongest just anterior to suture. Body whorl narrowly, roundly shouldered anterior to suture, compressed at periphery, attenuated toward base, sulcate behind aperture; last 0.3 whorl nearly straight in basal view, then angling toward umbilicus just behind peristome. Strong crest present behind aperture. Aperture rounded-triangular; peristome broadly reflected, thickened within by callus, limbs connected by thin callus film across face of body whorl. Outer lip sinuous, most produced medially, outer-posterior quadrant retractive. With prominent, sinuous, angular lamella, projecting not quite as far as plane of aperture, inner end thickened along axial side and deflected toward periphery. Low callus barriers present inside inner and outer lips, inner one bearing two faint denticles. Dimensions of holotype: height 2.0 mm, diameter 1.1 mm, whorls 5.2.

TYPE-MATERIAL.—Holotype: USNM 377373, from U.S. Geological Survey Cenozoic Locality 20007, Montana: Gallatin County: NW¼ SW¼ sec. 36, T 1 N, R 1 W, Three Forks



FIGURES 3-7: Figure 3. *Gastrocopta (Albinula) montana*, new species, holotype, USNM 377373; height 2.0 mm. Figure 4. *Gastrocopta (Albinula) contracta* (Say), CAS 046506; height 2.4 mm; Holocene, Lee County, Texas. Figure 5. *Gastrocopta (Albinula)* species a, USNM 377375; height 2.75 mm. Figure 6. *Gastrocopta (Albinula) sagittaria*, new species, holotype, USNM 377376; height 1.9 mm. Figure 7. *Gastrocopta cordillerae*, new species, holotype, USNM 377378; height 1.8 mm.

Quadrangle (1950) 1:62,500; altitude 4,260 ft (1,300 m). Miligan Creek Formation, Eocene (?). Two paratypes, USNM 377374, from same locality as holotype.

REFERRED MATERIAL (all, *Gastrocopta* sp., cf. *G. montana*).—Dunbar Creek Formation: USGS 20012, two specimens. USGS 20013, two specimens. USGS 20017, one specimen.

REMARKS.—The type-lot consists of well-pre-

served original shells filled with colorless calcite matrix. The holotype is an adult shell. One paratype is an adult shell with reflected peristome, height 2.1 mm, diameter 1.1 mm, with 5.3 whorls. The other paratype lacks the adult peristome; dimensions: height 2.1 mm, diameter 1.1 mm, with 5.0 whorls.

Gastrocopta montana is distinguished from *Gastrocopta* (*Albinula*) species *a*, next described, of the Milligan Creek Formation by its smaller size, more cylindrical shape, and low callus ridges thickening the inner and outer lips internally. The base of the body whorl of *Gastrocopta* (*Albinula*) species *a* is more strongly compressed, almost forming a keel around the umbilicus. *Gastrocopta sagittaria* of the Climbing Arrow Formation is more conic in shape, having a broad rather than narrowed anterior end.

Material from the Dunbar Creek Formation (USGS 20012, 20013, 20017) is provisionally referred to the species. Most of the shells are slightly more cylindrical than the type-lot of *G. montana*, but one of two specimens from USGS 20012 is as broadly ovate as the types. The specimens from USGS 20013 are internal molds of tuffaceous siltstone with very little shell remaining. They show the impressions of upper and lower palatal barriers a short distance behind the position of the crest. The lower barrier is larger and more deeply immersed than the upper. The better-preserved specimen from USGS 20012 consists of original shell, partly filled with recalcitrant siltstone matrix that obscures most of the apertural dentition, but a strong, unbranched angular lamella is present, projecting almost as far as the plane of the aperture. The peristome is everted; the outer lip is sinuous, most produced medially.

The Pliocene to Holocene *G. contracta* (Say, 1822) (Fig. 4), type-species of the subgenus *Albinula*, is the modern species most similar to *G. montana*, in its sinuous, unbranched angular lamella, strong crest, and callus ridges inside the inner and outer lips. *Gastrocopta contracta* is conic rather than cylindrical, with the penultimate whorl substantially broader than the antepenult; however, the basal configuration of the last whorl is quite similar. *Gastrocopta holzingeri* (Sterki, 1889), Pliocene to Holocene, is similar in shape to *G. montana* but has a forked, lambda-shaped angulo-parietal lamella. *Gastrocopta* (*Gastrocopta*) *cristata* (Pilsbry and Vanatta, 1900) is similar in shape and also has a distinct crest, but its angular lamella is smaller and does not turn to the right within; there is no toothed callus ridge paralleling the inner lip.

Along with English Eocene species (Preece 1982), this and the following species probably constitute the oldest known occurrence of the

subgenus *Albinula*, but as noted in the introduction the exact age of the Milligan Creek Formation is not well established.

Gastrocopta* (*Albinula*) species *a

(Figure 5)

Pupillidae A, D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:206.

Pupillidae B, D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206 (non p. 209).

DESCRIPTION.—Shell dextral, umbilicate, ovate to elongate-ovate, of 5.2–5.5 whorls, suture moderately to deeply impressed, spire profile convex, fourth and fifth whorls about equally broad. Sculpture of fine, oblique growth lines and a trace of puckering anterior to the suture. Body whorl compressed anteriorly, sulcate behind aperture, very much narrowed toward base; last 0.3 whorl nearly straight in basal view, cross section triangular, the anterior vertex slightly pinched off on either side. Umbilicus wide, excavated. Faint crest behind aperture. Aperture ovate-triangular; peristome everted, thin, continuous, appressed to body whorl. With prominent, strongly sinuous, angular lamella, projecting as far as plane of aperture, inner end thickened and deflected toward periphery. Columellar lamella horizontal. Peglike upper and lower palatal folds sometimes present inside aperture.

REFERRED MATERIAL.—Milligan Creek Formation: USGS 20007, five specimens.

REMARKS.—The specimens at hand, while not good enough for formal taxonomic description, demonstrate that a second species of *Gastrocopta* (*Albinula*), distinct from *G. montana*, occurs in the Milligan Creek Formation. The material consists of one adult shell, height 2.75 mm, diameter 1.6 mm, with 5.5 whorls (outer lip broken in manipulation); two other adults 2.3 mm in height and 1.4 mm in diameter with 5.2 whorls; an intact juvenile shell of four whorls, height 1.4 mm; and a fragment of spire (4+ whorls) about 2 mm in height. Original shell is present in all, showing fine surface incremental lines. The palatal folds present in the largest specimen are not borne on a palatal callus but arise separately within the aperture. No palatal folds are detectable on the two smaller adult shells. Otherwise the dentition is basically similar to the modern *G. contracta* (Say). The first bend in the angular lamella points toward the middle of the outer lip

at about the level of the upper palatal fold. Variation of 0.4–0.5 mm in height and 0.25–0.5 whorl in adult shells is not uncommon in modern species of *Gastrocopta* (Pilsbry 1948).

Gastrocopta montana of the Milligan Creek Formation is smaller, more cylindrical, with callus ridges thickening the inner and outer lips. *Gastrocopta sagittaria* of the Climbing Arrow Formation is also smaller and more conic in shape, having a broad rather than narrowed anterior end.

This species and *G. montana* both seem more closely related to *G. contracta* than to any other modern species; *G. contracta* may be the surviving member of a once more diversified lineage.

***Gastrocopta (Albinula) sagittaria* new species**
(Figure 6)

Pupillidae E, D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:208.

DIAGNOSIS.—A small, ovate-conic *Gastrocopta* with prominent, sinuous, unbranched angular lamella, broadly rounded, perforate base, and low, untoothed callus ridges inside inner and outer lips.

DESCRIPTION.—Shell small for the genus, dextral, umbilicate, ovate-conic, of 4.5–4.8 whorls; suture moderately impressed, spire profile convex, body whorl not much broader than penult. Sculpture of oblique growth lines. Body whorl either narrowly shouldered or compressed below suture, well rounded toward base; last 0.5 whorl nearly straight in basal view, laterally compressed and narrowed anteriorly into a triangular cross section. Moderately strong crest behind aperture. Aperture subquadrate; peristome everted, solid, continuous, appressed to body whorl; with low callus barriers inside inner and outer lips. With prominent, sinuous, angular lamella, projecting as far as plane of aperture, its inner end broadening to a flange extending toward periphery. Dimensions of holotype: height 1.9 mm, diameter 1.3 mm, whorls 4.8.

TYPE-MATERIAL.—Holotype: USNM 377376, from U.S. Geological Survey Cenozoic Locality 20009, Montana: Jefferson County: NE¼ NE¼ NE¼ sec. 11, T 2 N, R 1 W, Three Forks Quadrangle (1950) 1:62,500; altitude 4,580 ft (1,400 m), Climbing Arrow Formation, Eocene. Fourteen paratypes, USNM 377377, from same locality as holotype.

REMARKS.—The material consists of internal molds and thoroughly recrystallized shells, of pink to colorless calcite. Even in those specimens that

preserve the shape of the aperture and the prominent angular lamella, calcite fills the aperture to an extent that conceals the presence or absence of other lamellae or deep-seated folds. When specimens are immersed in toluene (refractive index 1.49693), it can be seen that the angular lamella first curves toward the outer lip, then recurves toward the axis. Its inner end broadens and bears a rounded flange extending toward the periphery, much as in *G. contracta* (Say).

The three most complete paratypes measure

| Locality | Height | Diameter | No. of whorls |
|------------|--------|----------|---------------|
| USGS 20009 | 1.9 mm | 1.3 mm | 4.7 |
| | 1.8 | 1.3 | 4.6 |
| | 1.8 | 1.3 | 4.5 |

Measurements include the expanded portion of the peristome.

Several younger species of *Albinula* have a similar, ovate-conic shape, including *Gastrocopta (Albinula) dupuyi* (Michaud, 1855), Pliocene of France, and the Pleistocene to Recent North American *G. contracta*. The broad, perforate base and the presence of fewer than five whorls distinguish this from any other species of *Gastrocopta* in the Bozeman Group.

The species is named for the Climbing Arrow (Latin, *sagitta*) Formation.

Subgenus indeterminate

***Gastrocopta cordillerae* new species**
(Figure 7)

Pupillidae B, D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (*non p.* 206).

Pupillidae F, D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

Pupillidae I, D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

Pupillidae indet., D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:209.

DIAGNOSIS.—An ovate-oblong *Gastrocopta* with short spire whorls but moderately tall body whorl, flattened or weakly sulcate behind aperture, narrowed base, small aperture, and strong to moderate crest.

DESCRIPTION.—Shell dextral, umbilicate, ovate-oblong with obtusely conic summit, of about 5.0–5.5 whorls; suture moderately impressed, whorls of spire short, convex. Nuclear whorls 1.4, smooth. First neanic whorl smooth; thereafter with sculpture of fine, markedly oblique growth lines, strongest just anterior to suture. Body whorl moderately tall, compressed, nar-

rowed toward base, flattened or weakly sulcate behind aperture, with a strong to moderate crest. Aperture small, rounded-triangular. Upper and lower palatal barriers present, discrete; rest of apertural dentition not known. Dimensions of holotype: height 1.8 mm, diameter 1.1 mm, whorls 5.1.

TYPE-MATERIAL.—Holotype: USNM 377378, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 ft (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Thirteen paratypes, USNM 377379, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20012, one specimen, juvenile. USGS 20013, three specimens. USGS 20016, one specimen, a calcitic internal mold with little shell remaining. USGS 20017, one specimen.

REMARKS.—The holotype and paratypes consist of moderately well preserved original shells filled with grayish yellow tuffaceous siltstone. No specimen in either the type-lot or the referred material shows fully the characteristics of the aperture, and for this reason it is not possible to assign the species to a subgenus. However, it is a characteristic species of the Dunbar Creek Formation, occurring at five out of the seven localities that yielded land snails, and is readily recognized by its ovate-oblong profile and the contrast between the short whorls of the spire and the relatively tall body whorl.

On the juvenile specimen from USGS 20012, axial ribs extend across the flat base but are much weaker than those above the peripheral angulation. The largest paratype is 2.4 mm long and 1.3 mm in diameter without having the complete aperture present. A referred specimen from USGS 20013 is 2.2 mm long, 1.3 mm in diameter, and ovate in outline, the base distinctly compressed; it shows a narrow angular lamella.

***Pupoides* Pfeiffer, 1854**

TYPE-SPECIES: *Bulimus nitidulus* Pfeiffer, 1839, by subsequent designation (Kobelt 1880 [1876–81]).

DIAGNOSIS.—Shell “about 3 to 6 mm long, rimate; long-ovate, turritid or rarely cylindric, with obtuse apex and few (generally 5–6) rather long whorls. Aperture ovate, toothless except for a small, tuberculiform angular lamella close to the insertion of the outer lip, or united with it, sometimes wanting; peristome expanded, reflected and usually thickened within. Internal axis slender, perforate” (Pilsbry 1948:920).

REMARKS.—*Pupoides* is mainly a tropical and subtropical genus, distributed on all continents except Europe; it is also absent from Southeast Asia and the East Indies. Pilsbry (1920–21) associated it with arid regions and relatively dry stations in humid areas.

Pilsbry (1922–26:249, 265) placed *Pupa incolata* White, 1876, from the Eocene of southwestern Wyoming, in *Pupoides*, but also included it in a list of Pupillidae of uncertain affinities. The figures by White (1883, pl. 29, fig. 15–17) show a conical shell with an externally thickened outer lip, doubtfully pupillid in my opinion.

(*Ischnopupoides*) Pilsbry, 1926

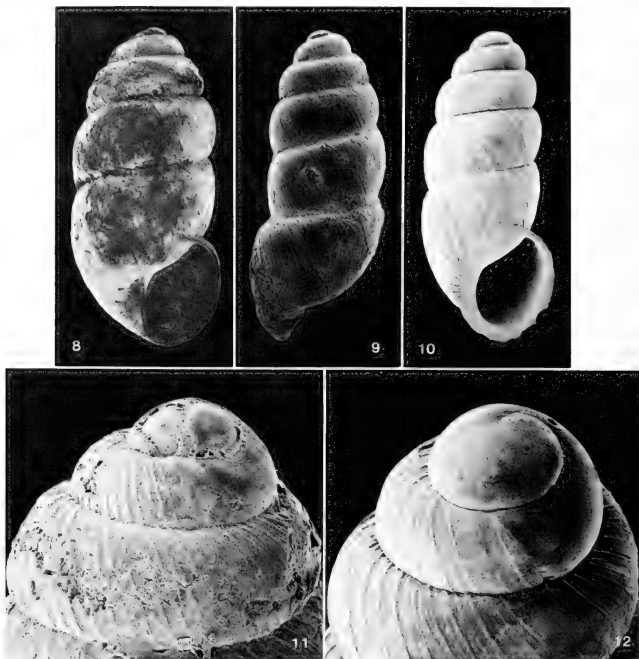
TYPE-SPECIES: *Pupa hordacea* Gabb, 1866, by original designation.

DIAGNOSIS.—“Shell cylindric or subcylindric; diameter decidedly less than half the length” (Pilsbry 1948:921).

REMARKS.—*Ischnopupoides* is a New World group with two closely related species living north of Mexico. *Pupoides* (*Ischnopupoides*) *hordacea* (Gabb, 1866) occurs today in Wyoming, Colorado, Kansas, Utah, Arizona, and New Mexico (Pilsbry 1948; Bequaert and Miller 1973). It is recorded from late Pleistocene or early Holocene deposits in Kansas, Texas, New Mexico, and Arizona (Bequaert and Miller 1973). *Pupoides* (*Ischnopupoides*) *inornatus* Vanatta, 1915, ranges from South Dakota to New Mexico, although as pointed out by Taylor (1960), it is documented to be living at only two localities; it also occurs in Blancan (late Pliocene and early Pleistocene) faunas in Nebraska, Kansas, and Texas. Other species referred to the subgenus occur in Mexico, Ecuador, Peru, Bolivia, Argentina, and Chile (Bequaert and Miller 1973). There are no previous records of *Ischnopupoides* in Montana.

Taylor (1975:430) reported an unnamed *Pupoides* (*Ischnopupoides*) species from the Tepee Trail (=Wagon Bed) Formation, upper Eocene of Wyoming, as follows: “one well-preserved internal mold shows the features of shape, size, apertural thickening, reflected peristome and lack of apertural lamellae. In diameter of shell and general proportions of aperture, the specimen agrees well with *P. (I.) inornatus* Vanatta, but its whorls are lower and hence total shell length is less in the fossil.”

In the following new species, *P. tephrodes*, diameter is approximately half the length (or height)



FIGURES 8-12: Figure 8. *Pupoides (Ischnopupoides) tephrodes*, new species, holotype, USNM 377380; height 3.0 mm. Figure 9. *Pupoides (Ischnopupoides) sp.*, cf. *P. (I.) hordaceus* (Gabb), USNM 377382; height 3.0 mm. Figure 10. *Pupoides (Ischnopupoides) hordaceus* (Gabb), CAS 046507; height 3.4 mm; Holocene, drift of Chaco River at Pueblo Bonito, Chaco Canyon National Monument, San Juan County, New Mexico. Figure 11. *Pupoides tephrodes* detail of apex of holotype showing transition from smooth nuclear to ribbed neanic whorls. Figure 12. *Pupoides hordaceus*, detail of apex of CAS 046507.

of the shell. This leaves little but the cylindric form, absence of apertural tubercles, and (in some species) the presence of fine axial riblets to distinguish the subgenus. Miller (*in* Bequaert and Miller 1973) found that the anatomy of *P. hordaceus* differed only in minor details from that of *Pupoides (Pupoides) albilabris* (C. B. Adams, 1841). Nevertheless, the presence in the Bozeman Group of *P. tephrodes* and another species hardly distinguishable from *P. hordaceus* points

to the existence in the eastern Cordillera of a lineage distinct from *Pupoides*, *sensu stricto*, since at least Oligocene time.

***Pupoides (Ischnopupoides) tephrodes* new species**
(Figures 8, 11)

Pupillidae C. D. W. Taylor *in* Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part) (*non* p. 206).

Pupillidae F. D. W. Taylor *in* Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

DIAGNOSIS.—A small, cylindric *Pupoides* (*Ischnopupoides*) with diameter equal to about half of height, sculpture of slender, well-spaced, retractive riblets, and peristome narrowly everted.

DESCRIPTION.—Shell dextral, narrowly umbilicate, cylindric with convexly low-conic summit, of about 5.2 tall whorls; suture moderately impressed, crenulated by axial riblets. Early whorls convex; fourth and fifth whorls roundly shouldered below suture, compressed at periphery and anteriorly. Nuclear whorls 1.5, smooth; neanic sculpture of slender, well-spaced, retractive riblets. Body whorl narrowly, slopingly shouldered, compressed at periphery, slightly attenuated toward base, rising gently on penult behind aperture. Aperture oblique, ovate; peristome narrowly everted, not thickened within; parietal margin oblique, covered by a thin callus. No angular tubercle present. Dimensions of holotype: height 3.0 mm, diameter 1.5 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377380, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 ft (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Two paratypes, USNM 377381, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20013, three specimens, internal molds. USGS 20016, three specimens, internal molds with some shell preserved, showing fine oblique riblets.

REMARKS.—The type-lot consists of moderately well preserved original shells filled with grayish yellow tuffaceous siltstone. The axial riblets are worn on all specimens so that in places they are visible only near the suture; similar wear occurs in Recent species of *Pupoides* (*Ischnopupoides*). One paratype measures: height 2.8 mm, diameter 1.3 mm, with 5.2 whorls. The other paratype measures: height 2.7 mm, diameter 1.2 mm, with 5.1 whorls. Diameter/height ratios for intact material range from 0.44–0.50, compared to a range of 0.40–0.45 for *P. hordaceus* and 0.44–0.46 for *P. inornatus* (calculated from dimensions given by Pilsbry [1948]).

The shells are smaller than in either *P. hordaceus* or *P. inornatus*, both of which may exceed 3.5 mm in length. The peristome is less sharply turned out. The rather tall, loosely coiled whorls (parietal wall encroaching little upon the aperture) and the cylindrical outline are wholly typical of the subgenus *Ischnopupoides*.

The name *tephrodes* combines the Greek *tephra*, ash, with the suffix *-odes*, denoting fullness.

Pupoides (Ischnopupoides) sp.,
cf. *P. (I.) hordaceus* (Gabb, 1866)

(Figure 9)

Pupillidae C. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part) (*non* p. 206).

DESCRIPTION.—Shell dextral, narrowly umbilicate, cylindric with convexly conic summit, of 5.1–5.5 tall whorls; suture not deeply impressed. Early whorls convex; fourth and fifth whorls roundly shouldered below suture, compressed at periphery and anteriorly. Nuclear whorls 1.4, smooth; neanic sculpture of faint, slender, irregularly spaced, retractive riblets. Body whorl elongate, smoothly rounding toward base, rising slightly on penult behind aperture. Aperture ovate; parietal margin sinuous, not strongly encroaching on aperture; peristome broken on all specimens at hand.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20012, five specimens.

REMARKS.—The material consists of recrystallized shells with filling of cream-colored tuffaceous siltstone. Although the peristome is not preserved in any of the specimens at hand, the shape of the shell is almost identical to Holocene *P. hordaceus* (Fig. 10, 12). The surface of the fossils is somewhat worn, so the original strength of the axial ribbing cannot be evaluated. The strongest riblets seem to have been more irregularly spaced than those of *P. hordaceus*. Better-preserved material would also show whether the ribbing was stronger than that of *P. inornatus* Vanatta.

The four most nearly intact specimens measure

| Locality | Height | Diameter | No. of whorls |
|------------|--------|----------|---------------|
| USGS 20012 | 3.2 mm | 1.2 mm* | 5.5 |
| | 3.1 | 1.3 | 5.4 |
| | 3.0 | 1.3 | 5.5 |
| | 3.0 | 1.4 | 5.1 |

* Broken.

These specimens differ from *P. tephrodes* in being slimmer and less distinctly ribbed, and in having a more steeply conical summit.

Order SIGMURETHRA
Family OREOHELICIDAE

Radiocentrum Pilsbry, 1905

TYPE-SPECIES: *Oreohelix chiricahuana* Pilsbry, 1905, by original designation.



FIGURES 13-15. *Radiocentrum hendersoni* (Russell), holotype, USNM 497659; diameter 7.8 mm.

DIAGNOSIS.—Oreohelicids with "embryonic shell of about $1\frac{1}{2}$ radially ribbed whorls; penis club-shaped, the walls of its cavity plain in the anterior part, having oblique ridges irregularly en chevron in the middle and posterior parts, wide and truncate at the end, epiphallus about as long as the penis, slender anteriorly, the penial retractor inserted on it a short distance from its entrance in the penis. Reproduction oviparous" (Pilsbry 1939:540). Babrakzai et al. (1975) found a large number of submetacentric chromosomes and a haploid chromosome number of 32 to be characteristic of *Radiocentrum*.

The few-whorled, radially costulate protoconch is the only paleontologically useful diagnostic character, but it is adequate for recognition of this group. The shells are otherwise much like *Oreohelix*, depressed-helicoid to lenticular in shape, the periphery ranging from rounded, through obtusely subangular, to distinctly carinate.

REMARKS.—The endemic North American pulmonate family Oreohelicidae consists of two genera: *Oreohelix* Pilsbry, 1905, and *Radiocentrum*, the latter originally proposed as a subgenus of the former.

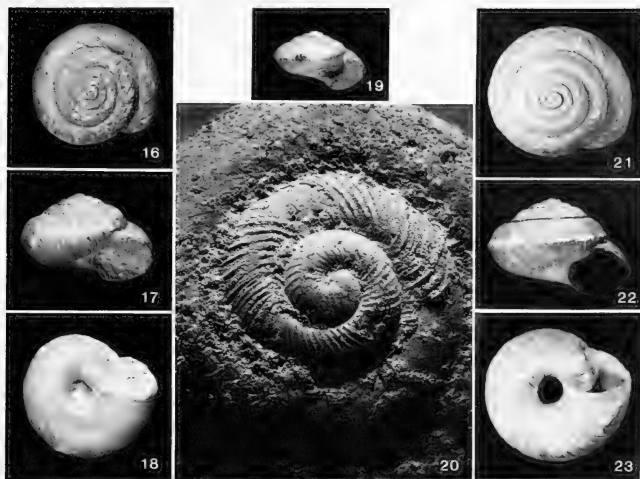
Conchologically, *Radiocentrum* has a distinctive, radially ribbed 1.5-whorled embryonic shell. Living *Radiocentrum* deposit eggs, whereas Recent *Oreohelix* are ovoviviparous. On reproductive characters and chromosome data, Babrakzai et al. (1975) elevated *Radiocentrum* to generic status.

The modern distribution of *Radiocentrum* includes southern New Mexico, southern Arizona, trans-Pecos Texas (late Pleistocene; Metcalf and Johnson 1971), northern Coahuila (probable late

Pleistocene; Metcalf 1980), Chihuahua, Baja California Sur (Miller 1973a; Christensen and Miller 1976), and Santa Catalina Island off the southern California (Hochberg et al., in press).

Tozer (1956) found *Oreohelix angulifera* (Whiteaves, 1885) from the St. Mary River and Edmonton formations, upper Cretaceous of western Alberta, and *Oreohelix thurstoni* (Russell, 1926) from the Paskapoo, Porcupine Hills, and Willow Creek formations, Paleocene of western Alberta, to have regular costae on the embryonic whorls, strongly suggestive of *Radiocentrum*. Additional fossil oreohelicids probably assignable to *Radiocentrum* include *R. grangeri* (Cockerell and Henderson, 1912) from the Eocene of Park County, Wyoming, and *R. hendersoni* (Russell, 1938) from the Oligocene of Colorado. The latter was originally described in the genus *Gonyodiscus* Fitzinger, 1833 (Discidae), but is here reassigned to *Radiocentrum* based upon examination of photographs of the holotype (USNM 497659) (Fig. 13-15), supplied by D. W. Taylor. Sculpture of the protoconch is not preserved, but the whorl diameter increases suddenly after 1.5 whorls, as it does at the beginning of neanic growth in many *Radiocentrum*. *Helix nacimentensis* White, 1886, from the Paleocene of New Mexico, assigned to *Radiocentrum* by Cockerell (1914), is probably not an oreohelcid snail and may belong to the Helminthoglyptidae (Taylor 1975).

Cretaceous and Tertiary species of *Radiocentrum* are all from north of the present range of the genus, along the eastern Cordillera. The genus has undergone a southward restriction or displacement of range since Paleogene time; the Pleistocene and Holocene range includes disjunctions probably related to the late Cenozoic



FIGURES 16-23: Figures 16-20. *Radiocentrum taylori*, new species. Figures 16-18, holotype, USNM 377383; diameter 12.4 mm. Figure 19, paratype, USNM 377384; diameter 8.1 mm. Figure 20, referred specimen, USNM 377386; detail of apical sculpture, $\times 35$. Figures 21-23. *Radiocentrum chiricahuanum obsoletum* (Pilsbry and Ferriss), CAS 046508; diameter 12.6 mm; Holocene, Whitetail Canyon, Chiricahua Mountains, Cochise County, Arizona. All specimens coated for photographing.

emergence of the Sonoran and Chihuahuan deserts as arid environments of regional extent (Hochberg et al., in press).

The type localities of the two new species of *Radiocentrum* described here are approximately 1,600 km north of the northernmost Holocene occurrences of the genus. The present distribution of *Radiocentrum* consists of scattered, highly local enclaves. Taken together, the fossil and Recent range data suggest restriction from a formerly more widespread and continuous range that included the northeastern Cordillera. *Radiocentrum* has been distinct from *Oreohelix* since at least the late Cretaceous; species of *Oreohelix* are known from upper Cretaceous, Paleocene, and Eocene strata from Alberta to Utah (Pilsbry 1939; Tozer 1956; La Rocque 1960). No other generic groups are recognized in the family. In contrast to the Helminthoglyptidae of the arid Southwest, which have responded to fragmen-

tation of range and isolation by a dramatic, evidently saltational, generic diversification (Miller 1973b, 1981a), the *Oreohelicidae* have been evolutionarily conservative.

***Radiocentrum taylori* new species**

(Figures 16-20)

Oreohelix n. sp., D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209.

DIAGNOSIS.—A small, solid, low-trochoid *Radiocentrum* of about 5.25 whorls; periphery angulate to obtusely keeled; protoconch strongly radially ribbed, ribs overhanging abaperturally; neanic sculpture of irregular ribs, lightly decussated on base by incised spirals.

DESCRIPTION.—Shell low-trochoid, solid, height about 0.65 times diameter, apical angle 124° . Whorls about 5.25; spire profile weakly convex; suture not deeply impressed. Body whorl

slightly shouldered, about equally convex above and below periphery, not markedly descending except immediately behind aperture. Periphery angulate to obtusely keeled (particularly on last 0.5 turn). Aperture circular, at about 40° angle to axis of coiling; limbs of peristome approaching closely, parietal wall with thin wash of callus; peristome not expanded but inner lip reflected toward umbilicus. Base well rounded, umbilicus contained about six times in diameter of shell. Protoconch consisting of 1.5 whorls, nuclear tip smooth, thereafter with prominent, elevated radial ribs, slightly convex-forward, overhanging on abapertural side, and almost as wide at the interspaces between. End of protoconch sometimes slightly thickened; onset of neanic growth marked by abrupt increase in whorl diameter and/or change in obliquity of radial ribs. Ribs of neanic shell at first upstanding and bladelikey, quickly becoming lower, more solid, and less regularly spaced. Ribbing on body whorl crude, slightly sinuous over periphery, and lightly decussated by fine spiral striae particularly evident on base and on shoulder of last 0.25 whorl. Dimensions of holotype: diameter 12.4 mm, height 7.9 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377383, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 feet (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Figured paratype, USNM 377384; 39 additional paratypes, USNM 377385, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20013, nine specimens—three external molds of spires (the largest 12.0 mm in diameter, with 5.0 whorls) with clear impressions of surface sculpture, one also having an internal mold counterpart; one internal mold with traces of exterior sculpture, diameter 12.1 mm, height 8.2 mm, with 5.5 whorls; four specimens with considerable shell remaining and very good preservation of protoconch sculpture (Fig. 20), diameter 4.6–9.7 mm, with 3.25–4 whorls. USGS 20014, two specimens—one a basal external mold 10.4 mm in diameter of an umbilicate shell with somewhat tumid base, low, forwardly concave, radial ribbing, and minor spiral rugosity; the other a shell 3.5 mm in diameter, in matrix, no sculpture preserved. USGS 20016, one external mold with internal mold counterpart, 9 mm in diameter, the matrix coarse but preserving radial riblets on the protoconch. USGS 20017, five specimens—one external and four internal molds, the largest 13.5 mm in diameter; three of the internal molds with some original shell remaining, showing angulate periphery, retractive axial ribbing, and fine, incised spiral lines on the shoulder; one with strongly ribbed protoconch well preserved.

REMARKS.—The type-lot consists of moderately well preserved to very well preserved origi-

inal shells and internal molds with matrix of cream-colored to yellowish gray, limy, tuffaceous siltstone. The paratypes range from 2.2 mm in diameter with 2.2 whorls to 11.4 mm in diameter with 5.3 whorls. Specimens of fewer than 4 whorls are acutely carinate, with the carina above the middle of the whorl, set off in some instances by faintly impressed grooves above and below. Some adult shells show minor spiral ribbing in addition to incised spiral striae on the last 0.25–0.5 whorl.

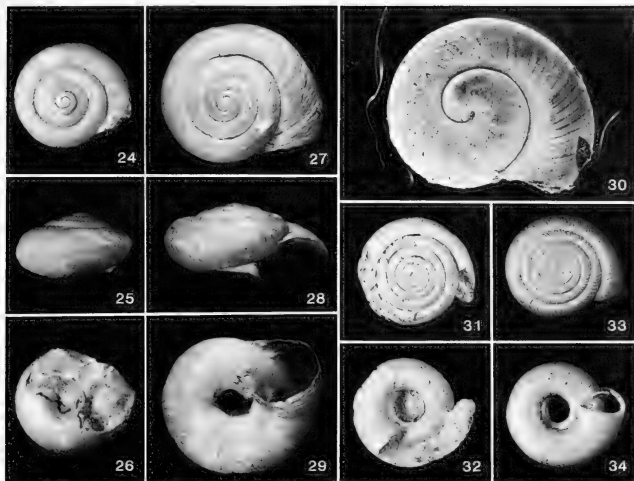
This is the most ubiquitous species in the Dunbar Creek Formation, occurring at five out of the seven localities that yielded land snails.

Radiocentrum taylori resembles the Holocene *R. chiricahuatum* (Pilsbry, 1905), another low-trochoid species with strong, irregular ribbing and an angulate to carinate periphery. The strongest resemblance is to the subspecies *R. c. obsoletum* (Pilsbry and Ferriss, 1910) (Fig. 21–23), in which the incised spiral sculpture is weak, the ribbing coarse and blunt, and the peripheral keel not especially prominent. The periphery of *R. taylori* is less carinate, most often acutely angular in subadult to adult shells, less commonly with spiral grooves setting off a peripheral keel. *Radiocentrum c. obsoletum* attains larger size, up to 15 mm diameter; *R. c. chiricahuatum*, at about 11 mm, is similar in size to *R. taylori*.

Radiocentrum taylori differs from *R. laevidomus*, next described, from the Milligan Creek Formation, in its coarser sculpture and higher-spired, trochoid shape. *Radiocentrum laevidomus* lacks the spiral sculpture of *R. taylori*; its protoconch has fine, simple ribs instead of the heavy, overhanging ribs of *R. taylori*.

Radiocentrum (?) *anguliferum* (Whiteaves, 1885) from the upper Cretaceous of Alberta differs in its very low spire and nearly involute mode of coiling. *Radiocentrum thurstoni* (Russell, 1926) from the Paleocene of Alberta has a subangular to rounded periphery and narrow umbilicus. It is also larger than any *R. taylori* specimens yet seen.

Radiocentrum hendersoni (Russell, 1938) from the Oligocene of Colorado is similar to *R. taylori* in its low-trochoid shape, prominent radial ribbing, and shouldered whorls. At 7.8 mm in diameter, with 4.5 whorls, the holotype of *R. hendersoni* (Fig. 13–15) may be immature. However, the last whorl descends below the peripheral angle, the shouldering of the whorl is intensified, and the inner lip expands toward the umbilicus,



FIGURES 24-34: Figures 24-26, 30. *Radiocentrum laevidomus*, new species. Figures 24-26, holotype, USNM 377387; diameter 10.1 mm. Figure 30. Paratype (hatching young), USNM 377388; diameter 1.6 mm. Figures 27-29. *Radiocentrum hachetanum* (Pilsbry), CAS 046509; diameter 14.2 mm; Holocene, summit of Hacheta Grande Mountain, Hidalgo County, New Mexico. Figures 31, 32. *Polygyrella* sp., cf. *P. polygyrella* (Bland and Cooper), USNM 377391; diameter 10.1 mm. Figures 33, 34. *Polygyrella polygyrella* (Bland and Cooper), CAS 046510; diameter 10.1 mm; Holocene, 2.4 km south of Selway Falls, Idaho County, Idaho. All specimens coated for photographing.

as in mature specimens of other oreohelicids. A 4.5-whorled paratype of *R. taylori* (Fig. 19) is 8.2 mm in diameter, lacks the incised spirals that decussate the ribs in *R. hendersoni*, and has a much less profoundly impressed suture.

I take pleasure in naming this species for Dwight W. Taylor, expert on freshwater Mollusca of western North America and author of the first reports on its occurrence.

***Radiocentrum laevidomus* new species**

(Figures 24-26, 30)

Oreohelix n. sp., D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206.

DIAGNOSIS.—A small, lenticular *Radiocentrum* of about 5 whorls; periphery angulate above middle of whorl; protoconch sculpture of fine,

low-standing, smooth radial riblets separated by wider interspaces; neanic sculpture of low, irregular radial striae; no spiral sculpture present.

DESCRIPTION.—Shell lenticular, apical angle 133°. Whorls about 5, enlarging rapidly; whorls of spire moderately convex, suture impressed. Body whorl expanding at about same rate as spire whorls, not descending behind aperture; periphery angulate above middle of whorl, becoming gently rounded on last 0.25 turn of 5-whorled specimen. Base rather deep, moderately inflated; umbilicus conical, its diameter contained three to four times in diameter of shell, with a hint of carination at its rim. Aperture simple, without thickening. Protoconch of 1.75 whorls, nuclear tip smooth, followed by smooth, regular, forwardly convex radial ribs separated by interspaces of greater width, increasing in strength

and distance to end of protoconch; ribs extending from suture to shoulder, weak to obsolete over periphery, then reappearing as a series of fine riblets spiraling inward around umbilicus of juvenile shells. Neanic whorls sculptured with low, irregular, forwardly convex radial striae. Striae strongest below suture, sometimes interrupted or deflected backward at peripheral angulation. Dimensions of holotype: diameter 10.1 mm, height 5.6 mm, whorls 4.6; of largest well-preserved paratype (USNM 377389): diameter 10.3 mm, height 6.5 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377387, from U.S. Geological Survey Cenozoic Locality 20007, Montana: Gallatin County: NW¼ SW¼ sec. 36, T 1 N, R 1 W, Three Forks Quadrangle (1950) 1:62,500; altitude 4,260 ft (1,300 m). Milligan Creek Formation, Eocene (?). Measured paratype, USNM 377389; figured paratype, USNM 377388; and 24 additional paratypes, USNM 377390, all from same locality as holotype.

REMARKS.—The type-lot consists of well-preserved original shells with matrix of solid to friable tan to cream-colored limestone. Color pattern is preserved on some specimens. The paratypes range from 1.5–5+ whorls. Sixteen of these are little more than hatchling young of 1.5–2.0 whorls (Fig. 30). The presence of such small juveniles free in the matrix indicates that the species was probably oviparous like modern *Radiocentrum*. In *Oreohelix*, the embryos are retained *in utero* to a stage of 2 whorls or more.

The spire of the holotype and of the largest well-preserved paratype are mottled with orange-brown blotches at intervals of 0.1–0.5 whorl. The blotches extend either inward or outward from the suture, in a few cases crossing an entire whorl, but do not pass from one whorl to the next. They are probably remnants of an original color pattern. Many specimens of the Holocene species *R. hachetanum* (Pilsbry, 1915) and *R. chiricahuenum* (Pilsbry, 1905) show similar mottling.

The species most similar to *R. laevidomus* in general shape and sculpture is the Holocene *R. hachetanum* (Fig. 27–29). The fine spiral lines in the intervals between protoconch ribs on *R. hachetanum* are not visible on *R. laevidomus*.

This species differs from *R. taylori* of the Dunbar Creek Formation in its finer, more delicate sculpture on both protoconch and neanic whorls, its lower spire, and lenticular rather than trochoid shape. The radial ribs on the protoconch of *R. taylori* are elevated, prominent, somewhat overhanging on the abapertural side, and nearly

as wide as their interspaces. Those of *R. laevidomus* are low-standing, evenly rounded, and distinctly narrower than their interspaces. Ribs on the very young paratypes, which could not have been subjected to much wear, have the same character (Fig. 30). *Radiocentrum laevidomus* shows no spiral sculpture like that present on *R. taylori*. Approximately the same characters differentiate *R. laevidomus* from *R. chiricahuenum*, which is very similar to *R. taylori* as noted above.

Radiocentrum(?) *anguliferum* (Whiteaves, 1885) from the upper Cretaceous of Alberta differs from *R. laevidomus* in its strongly angular periphery and nearly involute mode of coiling. *Radiocentrum hendersoni* (Russell, 1938) from the Oligocene of Colorado differs in its higher-spired, trochoid shell, strong radial ribbing, and very deeply impressed suture. *Radiocentrum thurstoni* (Russell, 1926) from the Paleocene of Alberta is another trochoid species, with a higher, more conical spire. According to Tozer (1956) the embryonic whorls of *Oreohelix obtusata* (Whiteaves, 1885), upper Cretaceous of Alberta, are apparently smooth, which would rule out assignment to *Radiocentrum*.

The name proposed combines the Latin *laevis*, smooth, with *domus*, house, in reference to the relatively faint sculpture of the shell.

Family AMMONITELLIDAE

Polygyrella Binney, 1863

TYPE-SPECIES.—*Helix polygyrella* Bland and Cooper, 1861, by monotypy.

DIAGNOSIS.—“The shell is widely umbilicate, discoidal with convex to nearly flat spire of narrow, closely coiled costulate whorls; base smooth, translucent. Aperture lunate-triangular, the unexpanded peristome somewhat thickened within, the ends connected by an erect, triangular parietal tooth. Within the last whorl there are one or two radial series of three teeth each. Jaw with flat plaits and fine vertical striae. Soft anatomy . . . about as in *Ammonitella*” (Pilsbry 1939: 555–556).

REMARKS.—*Polygyrella* is represented in the Holocene by one species, *Polygyrella polygyrella* (Bland and Cooper, 1861), with a range of northern Idaho, adjacent Montana, southeastern Washington, and northeastern Oregon. *Polygyrella* from the John Day Formation (late Oli-

gocene or early Miocene) of central Oregon are referred to the same species (Hanna 1920).

Taylor (1975) assigned specimens from the Eocene Kingsbury Conglomerate Member of the "Wasatch" Formation in the Powder River Basin, Wyoming, to *Polygyrella*. He further suggested that *Planorbis amplexus* Meek and Hayden, 1857 (upper Cretaceous, Judith River Formation, Montana), and *Anchistoma parvulum* Whiteaves, 1885 (upper Cretaceous, St. Mary River Formation, Alberta), are both species of *Polygyrella*. Based on its pattern of coiling, basal configuration, and parietal barrier, *Polygyra venerabilis* Russell, 1937, from the upper Cretaceous Belly River Formation, Alberta, seems to be another. Indeterminate species of *Polygyrella* are reported from upper Eocene strata in Glacier National Park, Montana (D. W. Taylor in Ross 1959), and (questionably) from an unnamed conglomeratic sequence of presumed early Tertiary age on Little Granite Creek, Hoback Basin, northwestern Wyoming (Taylor 1975).

Polygyrella* sp., cf. *P. polygyrella
(Bland and Cooper, 1861)

(Figures 31, 32)

Polygyrella, D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:208.

DESCRIPTION.—Shell subdiscoidal with broad umbilicus contained approximately three times in diameter. Spire flat to low-convex, suture lightly impressed. Whorls tightly coiled, sometimes with closely spaced, forwardly convex radial grooves extending outward from suture, not reaching shoulder of whorl. Body whorl with up to four shallow transverse constrictions. Last whorl not markedly descending except immediately behind aperture. Aperture oblique, peristome thickened and slightly expanded outward.

REFERRED MATERIAL.—Climbing Arrow Formation: USGS 20008, 5 specimens. USGS 20009, 14 specimens.

REMARKS.—The material from the Climbing Arrow Formation consists of internal molds (and some thoroughly recrystallized shells) shaped much like the modern *Polygyrella polygyrella* (Fig. 33, 34), with the subdiscoidal shape, flat to low-domed spire, tightly coiled whorls, and broad, circular umbilicus of that species. The fossils are composed in part of translucent, colorless to honey-colored, coarsely crystalline calcite, either replacing the shell or conforming to its interior,

and in part of pinkish tan, finely crystalline calcite probably representing a limy mud that partially filled the shells upon burial.

The peristome is moderately thickened in several specimens from locality USGS 20009; these are probably mature individuals. In them, the aperture slants at a 45° angle to the axis of coiling, the same as in *P. polygyrella*. Juvenile specimens of 4 whorls or less are planorboid, with much of the protoconch visible in the umbilicus.

Two distinctive shell features of *P. polygyrella* are not detectable: an erect parietal tooth and a radial series of barriers inside the last whorl. Careful preparation around the aperture of two specimens with mature, expanded peristomes revealed no parietal tooth. If completely recrystallized, such a tooth might not be distinguishable from other calcite filling the whorl; the same may be true for the series of barriers that would be expected about one-half whorl back of the aperture. One specimen from locality USGS 20009 shows radial grooves outboard of the suture on what is apparently the fourth whorl, corresponding to interspaces between radial costae on the spire of *P. polygyrella*.

The six largest specimens measure

| Locality | Diameter | No. of whorls |
|------------|----------|---------------|
| USGS 20008 | 10.2 mm | 7.1 |
| | 9.1 | 6.8 |
| | 8.6 | 6.7 |
| USGS 20009 | 9.0 | 6.2* |
| | 9.0 | 6.2* |
| | 8.0 | 5.9 |

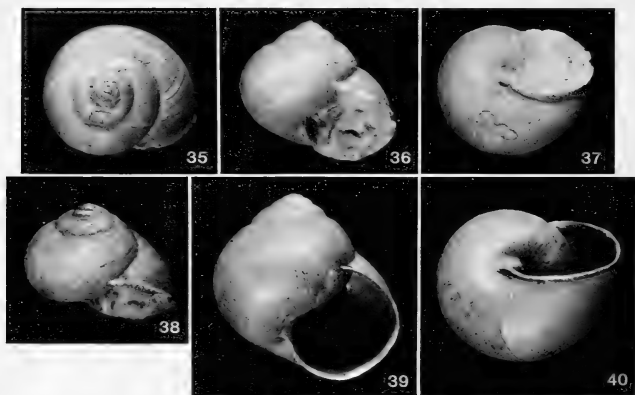
Asterisks denote specimens with mature expanded peristome.

Polygyrella parvula (Whiteaves, 1885) differs from *P. polygyrella* and the present specimens in its conoidal spire, sharply descending body whorl, and single slanting internal barrier. As illustrated (Meek 1876, pl. 42, fig. 16a–16e; Shimer and Shrock 1944, pl. 213, fig. 14, 15), *P. amplexa* (Meek and Hayden, 1857) is flat-spined or nearly so, with an umbilicus that is more conical than the steep-sided, pitlike umbilicus of *P. sp.*, cf. *P. polygyrella*. No information is available on the presence or configuration of internal barriers in *P. amplexa*, and the aperture is unknown.

Family HELMINTHOGLYPTIDAE

***Helminthoglypta* Ancey, 1887**

TYPE-SPECIES.—*Helix tudiculata* Binney, 1843, by original designation.



FIGURES 35–40: Figures 35–38. *Helminthoglypta bozemanensis*, new species, holotype, USNM 377392; diameter 16.6 mm. Figure 38, oblique view showing color banding. Figures 39, 40. *Helminthoglypta californiensis* (Lea). CAS 046511; diameter 19.3 mm; Holocene, Pacific Beach, north of Monterey, Monterey County, California. All specimens except Figure 38 coated for photographing.

DIAGNOSIS.—"Helices of moderate or large size, the shell globose or depressed with conic or low spire and open or covered umbilicus; periphery rounded at all stages of growth. Embryonic shell of $1\frac{1}{2}$ to $1\frac{3}{4}$ whorls; after the smooth tip and a few radial wrinkles it has sculpture of close, microscopic, waved, radial wrinkles, over which there are papillae in forwardly descending trends (often indistinct or practically absent). Adult sculpture of simple growth lines or with spiral engraved lines, malleation, papillae or granulation also. A dark band revolves above the periphery (sometimes absent). Peristome narrow, expanded outwardly, usually reflected at base, dilated at columellar insertion" (Pilsbry 1939: 63).

REMARKS.—The genus *Helminthoglypta* today is distributed from southeastern Oregon, through California west of the Cascade Range and the crest of the Sierra Nevada, into northern Baja California, Mexico. About 55 species are recognized. At the northern end of the range of the genus, *Helminthoglypta mailliardi* Pilsbry, 1927,

and *H. hertleini* Hanna and Smith, 1937, inhabit low elevations in the Klamath Mountains. At the southern end, *H. tudiculata* (Binney, 1843) and *H. traskii* (Newcomb, 1861) extend along the coast to the vicinity of San Antonio del Mar, Colonet, and *H. reederi* Miller, 1981, occurs in the Sierra San Pedro Mártir (Miller 1981b). One species, *Helminthoglypta alfi* Taylor, 1954, occurs in the Barstow Formation, upper Miocene of the Mojave Desert, California; it is similar to Recent Mojave Desert species. An undescribed species occurs in strata of probable Pliocene age in the Tehachapi Mountains, California (Roth, unpublished data). The Eocene species *Helminthoglypta obtusa* Anderson and Hanna, 1925, from the Tejon Formation, and *H. (?) stocki* Hanna, 1924, from the Sespe Formation, California, are probably incorrectly assigned to *Helminthoglypta*, but more material will have to be studied before a better allocation can be made. A land snail tentatively identified as *Helminthoglypta* is present in the Wiggins Formation (Oligocene), Wind River Basin, Wyoming (Taylor 1975).

***Helminthoglypta bozemanensis* new species**

(Figures 35–38)

Helminthoglyptidae n. gen., D. W. Taylor in Robinson 1963: 68, table 4.

Hemitrochus? Taylor 1975:208, 209.

DIAGNOSIS.—A small, globose-conic *Helminthoglypta* of about five whorls; body whorl weakly constricted behind reflected outer lip; umbilicus narrow, obliquely entering; sculpture of blunt incremental rugae and granulose vermiculation sometimes resolving into radial rows of granules; narrow dark peripheral band present, bordered above and below by wider light zones; less distinct dark zones on shoulder and just below suture.

DESCRIPTION.—Shell globose-conic, wider than tall, apical angle 107°. Whorls about 5, convex, rapidly expanding; suture impressed. Body whorl tumid, strongly descending for last 0.25 turn and more strongly for last 0.1 turn, weakly constricted behind outer lip. Aperture subcircular; parietal wall shallowly sigmoid, with thin wash of callus; peristome reflected and narrowly expanded, smooth at edge, more strongly reflected and thickened in umbilical region. Base well-rounded; umbilicus very narrow, scarcely perforate, obliquely entering behind inner lip. Protoconch smooth, probably consisting of about 1.8 whorls. Neanic whorls sculptured with (a) moderately strong, blunt, oblique incremental rugae, most irregularly spaced but some rhythmically spaced at intervals of about 1.0 mm, strongest on whorl shoulder but continuing over base, and (b) low granulose vermiculation, strongest between rugae and generally trending parallel to them. Vermiculation weaker on base and behind outer lip, where it generally appears as radial rows of blunt, axially elongate granules. Body whorl with narrow (0.8 mm-wide) brown suprapерipheral band, bordered above and below by slightly wider (1.2 mm) zones lighter than ground color of shell, and less distinct dark zones on midshoulder and just below suture. Dimensions of holotype: diameter (exclusive of expanded lip) 16.6 mm, height 13.3 mm, whorls 4.8; dimensions of paratype: diameter (slightly distorted) 15.4 mm, height 13.9 mm, whorls 5.2.

TYPE-MATERIAL.—Holotype: USNM 377392, from U.S. Geological Survey Cenozoic locality 20011, Montana: Broadwater County: SE¼ NW¼ sec. 6, T 2 N, R 2 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,360 ft (1,330 m). Dun-

bar Creek Formation, Eocene or Oligocene. Paratype: USNM 377393, from same locality as holotype.

REFERRED MATERIAL.—Four additional specimens from the USGS collection are referable, with differing degrees of confidence, to *Helminthoglypta* and *H. bozemanensis*. Climbing Arrow Formation: USGS 20009, one specimen, a fragment of smooth apical whorls and partial spire, 5 mm in greatest diameter, probably assignable to *Helminthoglypta*. Dunbar Creek Formation: USGS 20015, two specimens, internal molds, (1) diameter 7.4 mm, height 5.6 mm, whorls 3.4, and (2) diameter 9.8 mm, height 8.9 mm, whorls 3.8; small amount of shell material remaining on latter shows spaced incremental rugae oriented as on holotype, surface detail not preserved; raised line on internal mold in position of suprapерipheral band: =*Helminthoglypta* sp., cf. *H. bozemanensis*. USGS 20016, one specimen, internal mold, diameter 13.0 mm, height 10.5 mm, whorls 4.1, =*Helminthoglypta* sp., cf. *H. bozemanensis*.

REMARKS.—The holotype (Fig. 35–38) is a very well preserved specimen with almost all the original shell remaining and clear indication of the former position of color bands. The paratype is an internal mold with little shell remaining, the spire somewhat collapsed into the body whorl.

This species is assigned to *Helminthoglypta* because of the distinct suprapерipheral band, shape, sculpture, and reflected peristome. There are particularly strong similarities to the Recent *Helminthoglypta californiensis* (Lea, 1838) (Fig. 39, 40) of the central California coast. The weak constriction of the body whorl immediately behind the evenly expanded outer lip, and the extent to which the last quarter-whorl descends are identical in both species. The fine sculpture of *H. californiensis* consists of rows of axially elongated granules paralleling the incremental lines. In many specimens, the granules correspond rather loosely from one row to the next. In other specimens, and in other members of the "*Helminthoglypta nickliniana* series" (Pilsbry 1939), to which *H. californiensis* belongs, the granules may line up quite precisely in diagonal rows, producing a distinctive clothlike pattern. In *H. bozemanensis*, where the granulose vermiculation most clearly resolves into rows of discrete granules (mainly on the base and behind the outer lip), the sculpture strongly resembles that of *H. californiensis*.

Taylor (1975) ruled out assignment to *Helminthoglypta* because of the multiple color bands, not otherwise known in the genus, and questionably referred these specimens to *Hemitrochus* Swainson, 1840 (type-species, *Hemitrochus hoemastomus* Swainson, 1840 [= *Helix varians* Menke, 1829], by monotypy). *Hemitrochus* con-

sists of about 25 Recent species distributed in southern Florida and the Antilles (Pilsbry 1889–90, 1893–95; Turner 1958).

The dim bands at the shoulder and suture of *Helminthoglypta bozemanensis* are located where the margins of the dark shoulder zone occur in modern *Helminthoglypta*. Several instances exist, in Helminthoglyptidae and other families, of vacant-centered bands as a polymorphism of banded shells (Roth 1981a, *Monadenia*; Roth and Bogan 1984, *Liguus*). The upper and lower shell bands in the helminthoglyptid genus *Humboldtiana* Ihering, 1892, for which Pilsbry (1939) could not suggest a homology, may have originated in this way, as the emphasized edges of two now-vanished broad zones. The central band in *Humboldtiana* is probably homologous with the supraproperipheral band of most other Helminthoglyptidae. The upper and lower bands bracket the central band about as evenly as the dark zones top and bottom on a *Helminthoglypta* shell. The strengths of the upper and the lower band are strongly correlated, but apparently independent of the strength of the central band, suggesting a different derivation.

Because of the apparent ease of the transformation from solid to vacant-centered band, I do not think that the banding pattern of *H. bozemanensis* precludes assignment to *Helminthoglypta*. Other similarities to *Hemitrochus* do exist, however. They include the smooth protoconch, obliquely entering umbilicus, and spaced incremental rugae. In no Recent species of *Hemitrochus* do the whorls enlarge as rapidly; in globose-conic species, the spire makes up more of the shell. The base is typically shorter, tending to be flattish rather than tumid, and the strongest color band is usually at or below the periphery. The extent to which the lip turns out at maturity varies with the species, but often there is additional thickening inside the edge of the aperture, which is not present in *Helminthoglypta bozemanensis*.

Taylor (1975) also reported shells that he assigned to *Hemitrochus*? from the White River Formation (Oligocene), Beaver Divide area, central Wyoming. La Rocque (1960) noted the similarity of "*Helix*" *riparia* White, 1876, from the Flagstaff Formation, Paleocene and Eocene of Utah, to *Hemitrochus* but declined to make a firm generic assignment for the species.

Of the other helminthoglyptid genera that might be compared, *Leptarionta* Fischer and

Crosse, 1872, has a glossy or silky shell with growth lines hardly evident in relief. *Xerarionta* Pilsbry, 1913, and *Plesarionta* Pilsbry, 1939, both have incised spiral sculpture that is not present in *Helminthoglypta bozemanensis*. *Humboldtiana* has compound sculpture consisting of incremental rugae and blunt granulation (sometimes, as in *H. palmeri* Clench and Rehder, 1930, partly fusing into an irregular vermiculation). The possible homology of *Humboldtiana*'s three bands with the pattern of *Helminthoglypta bozemanensis* has already been mentioned. However, no Recent *Humboldtiana* has the globose-conic shape of *H. bozemanensis*; in *Humboldtiana* the protoconch is finely pustulose, its juncture with the teleoconch well marked; the outer lip is barely reflected, and there is no constriction behind the aperture. *Lysinoe* Adams and Adams, 1855, has, in addition to growth rugae, regularly spaced, discrete papillae (corresponding to the bases of periostracal bristles) in diagonal series. Nothing similar is present in *H. bozemanensis*.

Because of the supraproperipheral band (a form of disruptive coloration), it is assumed that the periostracum of *H. bozemanensis* was transparent, although vestigial banding occurs under an opaque periostracum in *Monadenia* (Roth 1981b).

FAUNAL COMPOSITION AND PALEOECOLOGY

MILLIGAN CREEK FORMATION.—The faunule from the Milligan Creek Formation consists of two species of *Gastrocopta* (*Albinula*) and one species of *Radiocentrum*. The only species that may have a stratigraphic record outside the formation is *G. montana*, which is provisionally recognized in the Dunbar Creek Formation.

The two *Gastrocopta* species seem to be most closely related to *Gastrocopta* (*Albinula*) *contracta*, which I regard as a plausible ecological analog. *Gastrocopta contracta* ranges over much of eastern North America, as far west as South Dakota, Oklahoma, and western Texas (Pilsbry 1948; Cheatum and Fullington 1973). It extends farther west in Mexico, reaching southern Sonora (Arroyo San Rafael, San Bernardo) and northern Sinaloa (San Blas) (Pilsbry 1953). In the United States its western limit coincides approximately with the 16-inch [41-cm] normal annual isohyet (U.S. Department of Commerce 1968). *Gastrocopta contracta* does not occur in western Montana but *Albinula* in the broad sense is present in the form of *G. holzingeri*.

The modern habitat of *Gastrocopta contracta* is on shaded slopes along watercourses, under dead wood, leafmold, and grass (Franzen and Leonard 1947, referring to Kansas). It is recorded from dense vegetation in mixed mesophytic forest in Kentucky (Branson and Batch 1970). No ecological notes on its Mexican occurrences are available. Other species of *Albinula* occur on wooded slopes, either near or away from streams, under dead wood, bark, stones, and in moist grass around seepages (Franzen and Leonard 1947; Taylor 1960).

Radiocentrum does not now range north of Santa Catalina Island, California, southern Arizona and New Mexico, and trans-Pecos Texas. Its habitat is generally in mountainous terrain, among cliffs and rockslides, usually where vegetation is sparse. It is not an inhabitant of forests. At least two species are reported to be restricted to limestone (Pilsbry 1939), but others occur on shale or among lava rockslides (Pilsbry 1939; Miller 1973a). On Santa Catalina Island, *R. avalonense* (Pilsbry, 1905) occurs on steep slopes of talus where the country rock is granitic, around the roots of black sage (*Salvia mellifera*) shrubs (Hochberg et al., in press). Modern disjunctions within the range of *Radiocentrum* are closely linked to zones of extreme aridity—the Sonoran and Chihuahuan deserts (Hochberg et al., in press). The southern Arizona and New Mexico occurrences are in isolated areas receiving at least 41 cm annual precipitation, at least half of it in the summer months (U.S. Dept. Commerce 1968).

Radiocentrum and *G. contracta* are not known to be sympatric anywhere at present; the two groups come closest in western Texas—*Radiocentrum* in El Paso County (Metcalf and Johnson 1971) and *G. contracta* in Culberson, Jeff Davis, and Presidio counties (Cheatum and Fullington 1973). However, the range of *Radiocentrum* is apparently contracting, with several peripheral occurrences known only from empty shells, and there may have been limited sympatry within the recent past in either the southwestern United States or northern Mexico.

The *G. contracta*-like species in the Milligan Creek Formation imply somewhat more mesic conditions (possibly at the microhabitat level) than does *Radiocentrum*. Robinson (1961, 1963) concluded that the limestone and other fine-grained rocks of the Milligan Creek Formation were deposited in a perennial lake lying in moun-

tainous terrain. The habitat of the *Gastrocopta* species may have been in leafmold along wooded watercourses feeding the lake. *Radiocentrum laevidomus* may have lived in more sparsely vegetated habitats nearby. Its source area was probably not remote, however, as it is the numerically dominant species in the USGS sample. The indicated climate is warm-temperate to subtropical. A minimum of 40 cm annual precipitation is suggested, much of it in the summer months. The land snails do not indicate a frost-free climate; within the southern Arizona–New Mexico range of *Radiocentrum* there is a period of generally less than 200 days between the last freeze of spring and the first freeze of autumn. Over much of the eastern range of *Gastrocopta contracta* the frost-free period is even shorter (U.S. Dept. Commerce 1968).

CLIMBING ARROW FORMATION.—The faunule from the Climbing Arrow Formation consists of *Gastrocopta* (*Albinula*) *sagittaria*, *Polygyrella* sp., cf. *P. polygyrella*, and a fragment of apical whorls and incomplete spire probably assignable to *Helminthoglypta*. The *Gastrocopta* is not known to occur outside the formation. The present material does not allow a determination whether the *Helminthoglypta*(?) is the same as *H. bozemanensis* of the Dunbar Creek Formation. The *Polygyrella* species, although not adequately preserved, does not seem to differ in any significant way from *Polygyrella polygyrella*, which ranges from late Oligocene or early Miocene (Hanna 1920) to Holocene.

As already noted, *Gastrocopta* (*Albinula*) is basically an eastern group at present, with one species entering western Montana. The only modern species of *Polygyrella*, *P. polygyrella*, ranges through northern Idaho and adjacent parts of Montana, southeastern Washington, and northeastern Oregon (Pilsbry 1939; Smith 1943). There are no records from as far east as the Three Forks Quadrangle. The original locality for *P. polygyrella* was on the eastern slope of the Coeur d'Alene Mountains, in moss and decaying wood in damp spruce forest. At Cataldo, Idaho, it was found in schist rockslides near the base of east-facing slopes near the Coeur d'Alene River; on lava rock, as at Stites, Idaho, it buries itself in the black, coarsely granular soil beneath the rockslides (Pilsbry 1939). Smith (1943) found it in lava rockslides and reported it to be common at lower elevations in the Clearwater Mountains of Idaho. The main part of its range is in a moun-

tainous region that receives ~50–75 cm annual precipitation; just eastward in the rain shadow of the Continental Divide the precipitation falls off sharply to half or a third of this total (U.S. Dept. Commerce 1968). A large proportion of this precipitation falls as rain in the months of April, May, and June.

The indicated environment is temperate, cooler and wetter than that of the Milligan Creek Formation. Both *Polygyrella* and the *Gastrocopta* are suggestive of wooded conditions, perhaps mature forest with plenty of wood on the ground. Shaded rockslides adjoining wooded streambanks are another possibility. The fine-grained, bentonitic sediments of the Climbing Arrow Formation suggest low relief in the immediate area, so perhaps humid forest is the more plausible environment. It is compatible with the flood plain deposition inferred by Robinson (1963). The Three Forks Basin may have drained eastward (Robinson 1961), but it was undoubtedly not in a Cordilleran rain shadow as at the present time.

The ecological significance of *Helminthoglypta* is discussed more fully below under the Dunbar Creek Formation. It is consistent with an equable, mesic climate, although *Helminthoglypta* and *Polygyrella* are strictly allopatric at present.

The presence of the tropical freshwater snail *Biomphalaria pseudammonius* contradicts the temperate climatic inferences based on the land snails. According to Taylor (1985), *B. pseudammonius* is doubtfully distinct from the living *B. glabrata*, which has an optimum reproductive temperature of 25°C and fails to reproduce at 20°C. The *Biomphalaria* is from a different locality (USGS 20010) than the land snails, in an adjoining section, 50–55 m topographically lower. It seems unlikely that there was enough local relief to throw temperate (i.e., as from higher-altitude) and tropical faunal elements into juxtaposition.

Konizski (1961) described the paleoecology and inferred climate of a biota (including *Biomphalaria* cf. *B. pseudammonius*) from the Douglass Creek Basin, Montana, approximately 150 km northwest of the Three Forks Basin. The vertebrate fauna is similar to the Pipestone Springs fossil assemblage, correlative with the upper part of the Climbing Arrow Formation but probably somewhat younger than the beds yielding the land gastropods. Plant remains, determined by Axelrod, indicate that the climate was temperate "but whether it was warm temperate . . . is not

now known. Rainfall was distributed in summer and winter and was not less than 30 to 35 inches. Winters appear to have been comparatively mild, but the frequency of frost or snow cannot be determined from the material at hand" (D. I. Axelrod in Konizski 1961:1639). Konizski concluded that the climate was temperate and probably varied seasonally; winters were mild compared to the present. Plant associations were stratified by altitude. The vertebrate assemblage suggests montane woodland rather than a savannah or open plains environment. The sedimentology indicates a basin profile of low relief with erosion a function of chemical as well as mechanical weathering.

Robinson (1963) suggested that part of the Climbing Arrow Formation may have been deposited contemporaneously with the Milligan Creek Formation, but the environments inferred from *Polygyrella*, on the one hand, and *Radiocentrum* on the other, are so distinct that facies difference seems an inadequate explanation.

Taylor (1975:204) remarked that the molluscan collections from the Climbing Arrow Formation are of special interest "because they provide a stratigraphic tie with late Eocene and early Oligocene fossil vertebrates in this area." It is unfortunate therefore that the *Polygyrella* may be a stratigraphically long-ranging species and that the *helminthoglyptid* is not represented by better material. *Gastrocopta sagittaria*, with its distinctive, ovate-conic shape, may prove to have biostratigraphic utility.

DUNBAR CREEK FORMATION.—The faunule from the Dunbar Creek Formation consists of two species of *Gastrocopta*, two of *Pupoides* (*Ischnopupoides*), *Radiocentrum taylori*, and *Helminthoglypta bozemanensis*. *Gastrocopta cordillerae*, *Pupoides tephrodes*, and *Radiocentrum taylori* are known only from this formation. *Gastrocopta* sp. cf. *G. montana* may be the same species present in the Milligan Creek Formation. *Helminthoglypta bozemanensis* is questionably present in the Climbing Arrow Formation.

The phylogenetic affinities of *G. cordillerae* are not known, so it adds no ecological or geographic information to that derivable from *G. sp. cf. G. montana*, discussed above under the Milligan Creek Formation. The same comments made above for *Radiocentrum laevidomus* also apply to *R. taylori*.

Pupoides (*Ischnopupoides*) is indicative of dry conditions. Today, *P. hordaceus* is "a species of

the arid plateaus and foothills [of Colorado, Utah, New Mexico, and Arizona], not found in the humid upper zone of the mountains" (Pilsbry 1948:925). Bequaert and Miller (1973) report it from northern Arizona, living in litter of an arid biotope, under shrubs and low trees, near the top of a steep rocky bluff at an elevation of 5,800 ft [1,800 m]. Both *P. hordaceus* and *P. inornatus* are found only as empty shells in many more localities than they are known living. This suggests that, like *Radiocentrum*, the subgenus is now undergoing local extinction in many parts of its range. The known distribution is not obviously linked to any thermal or precipitation gradient on a regional scale.

Helminthoglypta is now basically a Californian genus, with a few species extending into Oregon and Baja California. It occurs over a wide range of habitats from equable, maritime situations along the coast to highly arid conditions in the Mojave Desert. There is some indication of correlation between shell form and climate. The globose-conic species and subspecies of *Helminthoglypta*—*H. californiensis* (Lea); *H. mailliardi* Pilsbry; *H. fieldi* Pilsbry, 1930; *H. nickliniana awania* (Bartsch, 1919)—are all coastal forms, living in temperate climates with few extremes of temperature. Inland forms on the whole tend to be flatter and more tightly coiled, the extremes being the "Mojave Desert series" (Pilsbry 1939) consisting of small, almost planispiral, widely umbilicate shells with the whorls increasing slowly in size. An exception is *Helminthoglypta berryi* Hanna, 1929, from the foothills of the Sierra Nevada and Tehachapi ranges, an aberrant form that is the most highly fossorial species of the genus. The presence of a strong color pattern in *H. bozemanensis* does not suggest a fossorial mode of life, so that *H. berryi* is probably not as good a modern analog as *H. mailliardi* or *H. californiensis*. To the extent that shell shape in *Helminthoglypta* is correlated with environment, *H. bozemanensis* suggests an equable climate with a mean annual range of temperature of less than 13°C (data from Wolfe 1979). For the coastal species mentioned above the total annual rainfall varies from over 200 cm in the range of *H. mailliardi* to less than 30 cm in the range of *H. fieldi*. The precipitation is concentrated in the winter months, with practically none between May and October (U.S. Dept. Commerce 1968).

Helminthoglypta today is nowhere sympatric

with the other genera; its closest approach to any is on the mainland of Los Angeles County, opposite Santa Catalina Island where *Radiocentrum avalonense* occurs. Without postulating different climatic tolerances for one or more of these genera in the Paleogene, it is hard to reconcile their joint occurrence in the Dunbar Creek Formation. About the only inferences one can draw about the Dunbar Creek environment are that it was probably drier than that of the Climbing Arrow Formation, with sparser vegetation (possibly scrub, savannah, or open woodland), and moderate seasonal variation in temperature and precipitation. Presumed caliche horizons in the Dunbar Creek Formation suggest deposition in a seasonally dry basin or bolson (Robinson 1963) and are compatible with this interpretation.

GENERAL TRENDS.—The land mollusk fauna of the Bozeman Group shows three salient characteristics: (1) the occurrence of several genera well outside their modern ranges; (2) the seemingly paradoxical co-occurrence of genera now widely separated geographically and environmentally; and (3) change through time from sparsely vegetated to forested terrain and back again.

Tropical to subtropical climates extended to high latitudes during the early Tertiary (Durham 1950; Savin et al. 1975; Savin 1977; Wolfe 1978; Lillegraven 1979). Not all taxa in the Bozeman Group, however, show the simple southward shift of range that one would expect if temperature tolerance were the sole determining factor. *Polygyrella* still occupies the same general region. *Helminthoglypta* now lives along the Pacific Coast, extending from cool-mesic to warm and arid environments. *Radiocentrum* has undergone a southward shift to the American southwest, where it lives in rocky habitats but is apparently excluded from regions of extreme aridity. *Gastrocopta* is absent from the west coast but widely distributed in the eastern states; the subgenus *Albinula* approaches but does not overlap the range of *Radiocentrum*.

The present range limitations of *Radiocentrum* may involve interactions between genera as well as simple environmental tolerances. The ovoviviparous *Oreohelix* is now the dominant genus of large land snails throughout much of the Cretaceous-early Tertiary range of *Radiocentrum* (Bequaert and Miller 1973, fig. 4). Except for some work on the agonistic behavior of slugs (Rollo and Wellington 1977, 1979), little

is known about molluscan interactions that could lead to competitive exclusion. However, it is possible that in a climatic context of increasing summer drought and seasonal temperature variation the ovoviviparous mode might have permitted larger and more stable populations of *Oreohelix* to exist, which then outcompeted *Radiocentrum* for limiting resources such as shelter sites.

A mixture of diverse present-day biogeographic elements also existed in the British Isles during the Paleogene, among plants and insects as well as land mollusks (Preece 1982 and references cited therein). Daley (1972) argued that those apparently paradoxical associations represent a climate that has no close modern analog: seasonal but frostless, with high rainfall, and temperatures elevated but not as high as those of tropical rain forest areas today.

Table 2 lists land mollusks from western North America (the western Great Plains to the Pacific Coast) that have a Tertiary or late Cretaceous fossil record outside the Holocene ranges of their families or genera. Many fossil land snails are difficult to assign taxonomically (there is even debate over whether certain species are prosobranchs or pulmonates), hence a number of the generic assignments are provisional. Major differences of interpretation are annotated. It is beyond the scope of this paper to resolve some of the more difficult taxonomic problems involving these species, but in most cases the biogeographic and paleoenvironmental conclusions are not radically affected. Taxa that are wholly problematic because of inadequate type material (e.g., "*Eucalodium*" *eophilum* Cockerell, 1915) or without any convincing modern analogs (Grangerellidae) are excluded.

From this table it is apparent that families and genera now distributed in many other parts of the world were present in western North America in the late Cretaceous and early Tertiary. The largest block of taxa now exists in the American tropics, but almost as many groups now occur in tropical regions of Africa, Asia, and the Pacific Islands as well as in a Pacific coastal belt extending from Alaska to northern Baja California. Another large group now lives in warm-temperate to subtropical parts of the southern United States and Mexico. Others show minor displacement within the western interior. None of the taxa are now restricted to far northern America or Eurasia; those are young molluscan faunas, derived as species from middle latitudes colonized deglaciated regions in Pleistocene to Ho-

locene time. Lower-latitude Tertiary fossil localities (such as those of the lower Miocene of Florida) contain no land snail genera now restricted to higher latitudes.

The main bulk of local extinction seems to have taken place by the end of the Oligocene, but to some extent the evidence is negative: Miocene and Pliocene deposits yielding land mollusks are few. However, Miocene and Pliocene faunas are overwhelmingly composed of genera still extant in the region.

The extinction of many genera of land mollusks over parts of their west North American range may represent the sorting out of formerly sympatric groups into different ecologic/geographic zones. A similar scenario was proposed for the subgenera of *Monadenia* in the Pacific states (Roth 1981a), and a comparable pattern is evidently involved in the origin and development of coniferous forests in the west (Axelrod 1976). It is also possible that if the climatic parameters in the microhabitats of snails were better known, the former association of genera now geographically separated would seem less paradoxical—and the lack of congruence in their modern ranges more attributable to the operations of chance. The answer awaits a closer study of the ecology of living land mollusks.

How much of the environmental change shown by Bozeman Group mollusks is the result of secular climatic change, and how much due to local factors such as tectonism? Radiometric dates associated with faunas of the Chadronian North American Land Mammal "age" range between 37.4 ± 1.2 Ma and 32.3 ± 0.7 Ma (Evernden et al. 1964; Prothero, Dunham, and Farmer 1982). The transition from Uintan to Chadronian faunas occurs within the Climbing Arrow Formation (Robinson 1963). The Eocene-Oligocene boundary, placed at 36.6 Ma (Palmer 1983), probably also occurs within the Climbing Arrow or Dunbar Creek Formation (Fig. 2). (See also correlation by Lillegraven and Tabrum [1983, fig. 2], except that they place the Eocene-Oligocene boundary at 38 Ma.)

Lillegraven summarized the evidence for a late Eocene climatic deterioration, beginning perhaps 5–7 million years before the advent of the Oligocene. He concluded that "the late Eocene and early Oligocene was represented by a world-wide pulse of increased continentality, oceanic cooling, and a significant compression of tropical zones with dilation of temperate conditions. The time was marked by increased rates of extinc-

TABLE 2. TERTIARY AND UPPER CRETACEOUS LAND MOLLUSK TAXA FROM WESTERN NORTH AMERICA (WESTERN GREAT PLAINS TO THE PACIFIC COAST) THAT OCCUR OUTSIDE THE HOLOCENE RANGES OF THEIR FAMILIES OR GENERA

| Taxon | Fossil occurrence | Holocene range |
|---|--|---|
| Subclass Prosobranchia | | |
| Family Helicinidae | | Helicinid snails with apertural barriers: Greater Antilles, Mexico, Venezuela, Ecuador, Peru, Bolivia, Brazil (Boss and Jacobson 1975); Laos, Szechuan (Wenz 1938; Bishop 1980) |
| <i>Eohipptychia eohippina</i> (Cockerell, 1915) | Eocene, Wyoming | |
| <i>Hendersonia evanstonensis</i> (White, 1878) | Paleocene and Eocene, Wyoming | <i>Hendersonia</i> : E North America (Solem 1979) |
| <i>H. oregona</i> (Hanna, 1920) | Oligocene or Miocene, Oregon | |
| <i>Lucidella</i> (?) <i>buttsi</i> (Russell, 1955) | Eocene or Oligocene, British Colum- bia; Oligocene, Montana | <i>Lucidella</i> : Antilles, Central America (Wenz 1938) |
| <i>Tozerpina mokowanensis</i> (Tozer, 1956) | Upper Cretaceous, Alberta | Note 1 |
| <i>T. douglasi</i> (Tozer, 1956) | Paleocene, Alberta | Note 1 |
| <i>T. rutherfordi</i> (Russell, 1929) | Paleocene, Alberta | Note 1 |
| " <i>Helicina</i> " <i>cretacea</i> Yen, 1954 | Upper Cretaceous, Wyoming | |
| " <i>H.</i> " <i>cokevillensis</i> Yen, 1954 | Upper Cretaceous, Wyoming | |
| " <i>H.</i> " <i>vokesi</i> Hanna, 1936 | Eocene, California | |
| Family Cyclophoridae | | Cyclophoridae (sensu lato): American tropics, Andes; E and SE Asia: Poly- nesia; E Africa, Malagasy Is. (Solem 1979) |
| <i>Paleocyclotus</i> ? sp. (Yen 1952) | Upper Cretaceous, Wyoming | |
| <i>Pseudarinia convexa</i> Yen, 1952 | Upper Cretaceous, Wyoming | |
| <i>P. pupilla</i> Yen, 1952 | Upper Cretaceous, Wyoming | |
| <i>P. uniplica</i> Yen, 1954 | Upper Cretaceous, Wyoming | |
| <i>Rhiostoma americana</i> Hanna, 1920 | Oligocene, Oregon | <i>Rhiostoma</i> : SE Asia (Wenz 1938) |
| Subclass Pulmonata | | |
| Family Ellobiidae | | |
| <i>Carychium</i> sp. (La Rocque 1960; Taylor 1975) | Eocene, Wyoming, Utah | <i>Carychium</i> : North America except NE Cordillera; American tropics; Eu- rope, Asia, Philippines, Indonesia (Pilsbry 1948; Zilch 1959) |
| Family Tornatellinidae | | Tornatellinidae: Polynesia and Juan Fernandez Is. (Solem 1979) |
| <i>Protornatellina isoclina</i> (White, 1895) | Upper Cretaceous, Wyoming | |
| Family Pupillidae | | |
| <i>Gastrocopta</i> (<i>Gastrocopta</i>) sp. (Taylor 1975) | Eocene, central Wyoming | Subgenus <i>Gastrocopta</i> : South Dakota to SW U.S.; American tropics; Afri- ca, Mascarene Is., Ceylon, Philip- pines (Pilsbry 1948) |
| <i>Pupoides</i> (<i>Ischnopupoides</i>) sp. (Taylor 1975) | Eocene, central Wyoming | <i>Ischnopupoides</i> : South Dakota to Ari- zona (no Montana or central Wyo- ming records); Mexico to Argentina, Chile (this paper) |
| <i>P. (I.) tephrodes</i> n. sp. | Eocene or Oligocene, Montana | |
| <i>P. (I.)</i> sp., cf. <i>P. (I.) hordaceus</i> (Gabb, 1866) (this paper) | Eocene or Oligocene, Montana | <i>P. (I.) hordaceus</i> : SE Wyoming to New Mexico (Bequaert and Miller 1973) |
| Family Strobilopsidae | | Strobilopsidae, <i>Strobilops</i> : E North America; American tropics; E Asia (Pilsbry 1948); Baja California (Mil- ler and Christensen 1980) |

TABLE 2. CONTINUED.

| Taxon | Fossil occurrence | Holocene range |
|---|---|--|
| <i>Strobilops</i> sp. (Taylor 1975) | Early Tertiary, Wyoming | |
| Family Clausiliidae | | Clausiliidae: Eurasia; Andes; 2 spp. in Greater Antilles (Solem 1979) |
| Genus and sp. indet. (Taylor 1975) | Eocene, Wyoming | |
| Family Subulinidae | | Subulinidae: Tropics except Polynesia and Micronesia; S Africa; Mediterranean region; high diversity in Africa and tropical South America (Zilch 1959) |
| <i>Pseudocolumna spitzia</i> Tozer, 1956 | Upper Cretaceous, Alberta | |
| <i>P. vermicula</i> (Meek and Hayden, 1857) | Paleocene, North Dakota | Note 2 |
| <i>P. haydeniana</i> (Cockerell, 1906) | Paleocene, Alberta, North Dakota; Eocene, Wyoming | Note 2 |
| <i>P.</i> spp. (Taylor 1975) | Paleocene and Eocene, Wyoming | |
| Family Urocoptidae | | Urocoptidae: southern U.S.; American tropics (Zilch 1960) |
| <i>Holospira dyeri</i> Tozer, 1956 | Upper Cretaceous, Alberta | <i>Holospira</i> : Texas, New Mexico, Arizona; Mexico (Bequaert and Miller 1973) |
| <i>H. grangeri</i> Cockerell, 1914 | Paleocene, New Mexico | Note 3 |
| <i>H.</i> (?) sp. (La Rocque 1960; McKenna, Robinson, and Taylor 1962; Dorr 1969) | Paleocene and Eocene(?), Utah; Eocene, Wyoming | |
| <i>H. leidy</i> (Meek, 1873) | Eocene, Wyoming | |
| <i>H.</i> (?) <i>adventicia</i> Russell, 1955 | Eocene or Oligocene, British Columbia | |
| Genus and sp. indet. (Taylor 1975) | Eocene, Montana, Wyoming | |
| Family Bulimulidae | | Bulimulidae: In North America, only one species north of southern tier of states (Pilsbry 1946); Central and South America; Australasia |
| <i>Bulimulus</i> (?) sp. (La Rocque 1960) | Eocene, Utah | <i>Bulimulus</i> (sensu lato): southern U.S.; Mexico to South America (Zilch 1960) |
| <i>Oreoconus jepseni</i> (Russell, 1931) | Eocene, Wyoming | |
| <i>O. planispira</i> Taylor, 1962 | Eocene, Wyoming | |
| <i>O.</i> spp. (Oriol 1962; Taylor 1975) | Eocene and Oligocene, Wyoming; Eocene, Utah | |
| Family Charopidae | | Charopidae: Australia, New Zealand, New Caledonia; South Africa; Central and South America; Idaho to Arizona (Solem 1979) |
| aff. <i>Charopa</i> (Taylor 1975) | Paleocene, Wyoming | |
| Family Discidae | | |
| <i>Anguispira russelli</i> Tozer, 1956 | Paleocene, Alberta | <i>Anguispira</i> : North America, mainly S of U.S.-Canadian border; questionably, Alberta (La Rocque 1953); no Wyoming records |
| <i>A. holroydensis</i> Russell, 1956 | Miocene, Wyoming | |
| Family Arionidae | | |

TABLE 2. CONTINUED.

| Taxon | Fossil occurrence | Holocene range |
|---|--|--|
| <i>Binneya antiqua</i> Russell, 1955 | Eocene or Oligocene, British Columbia | <i>Binneya</i> : California Channel Is.; Isla de Guadalupe, Baja California (Pilsbry 1948) |
| <i>Craterarion pachyostrakon</i> Taylor, 1954 | Miocene, southern California | <i>Craterarion</i> : possibly Holocene of central California (Taylor and Roth, MS) |
| Family Zonitidae | | |
| " <i>Gastrodonta</i> " <i>coryphodontis</i> Cockerell, 1914 | Eocene, Wyoming | Note 4 |
| " <i>G.</i> " <i>imperfecta</i> Hanna, 1920 | Oligocene or Miocene, Oregon | Note 4 |
| " <i>Omphalina</i> " <i>laminarum</i> Cockerell, 1906 | Oligocene, Colorado | Note 4 |
| " <i>O.</i> " <i>oreodontis</i> Cockerell and Henderson, 1912 | Oligocene, Colorado | Note 4 |
| <i>Ventridens(?) lens</i> (Gabb, 1864) | Upper Cretaceous, California | Note 5. <i>Ventridens</i> : E North America (Pilsbry 1946) |
| <i>V.(?)</i> sp. (Russell 1955) | Eocene or Oligocene, British Columbia | |
| Family Polygyridae | | |
| <i>Polygyra(?) petrochlora</i> Cockerell, 1914 | Eocene, New Mexico | <i>Polygyra</i> (including <i>Daedalochila</i>): SE North America, Mexico, Antilles, Bermuda (Pilsbry 1940) |
| <i>P.(?)</i> sp. (Taylor 1975) | Eocene, Wyoming | |
| " <i>P.</i> " <i>veternior</i> (Cockerell, 1915) | Eocene, Wyoming | |
| " <i>P.</i> " <i>expansa</i> Hanna, 1920 | Oligocene or Miocene, Oregon | Note 6 |
| " <i>P.</i> " <i>martini</i> Hanna, 1920 | Oligocene or Miocene, Oregon | Note 6 |
| <i>Triodopsis(?)</i> spp. (Taylor 1975) | Eocene and Oligocene, Wyoming | <i>Triodopsis</i> : Washington, Oregon, Idaho; E and midwestern U.S. (Vagvolgyi 1968) |
| <i>Vespericola(?) dalli</i> (Stearns, 1885) | Oligocene or Miocene, central Oregon | <i>Vespericola</i> : Alaska to California; in Oregon, west of Cascade crest (Pilsbry 1940) |
| Family Oleacinidae | | |
| | | Oleacinidae: SE North America to Texas; American tropics; Mediterranean region (Pilsbry 1948; Zilch 1960) |
| Genus and sp. indet. (Taylor 1975) | Eocene, Wyoming | |
| Family Camaenidae | | |
| | | Camaenidae: India to Australia and Solomon Is.; Costa Rica to Peru; Antilles (Solem 1978) |
| <i>Caracolus aquilonaris</i> Bishop, 1979 | Oligocene, Nebraska | <i>Caracolus</i> : Greater Antilles (Bishop 1979) |
| <i>Hodopoeus crassus</i> Pilsbry and Cockerell, 1945 | Paleocene(?), SW U.S. | Note 7 |
| <i>H. hesperarche</i> (Cockerell, 1914) | Paleocene(?), Texas | Note 7 |
| <i>Kanabohelix kanabensis</i> (White, 1876) | Upper Cretaceous, Utah | Note 8 |
| <i>Pleurodonte</i> (<i>Pleurodonte</i>) <i>wilsoni</i> Roth, 1984 | Eocene and Oligocene, W Texas | Subgenus <i>Pleurodonte</i> : Lesser Antilles (Roth 1984) |
| <i>P. (Dentellaria)(?)</i> sp. (Roth 1984) | Eocene, W Texas | Subgenus <i>Dentellaria</i> : Jamaica (Roth 1984) |
| " <i>Helix</i> " <i>spatiosa</i> Meek and Hayden, 1861 | Paleocene, Alberta, North Dakota; Paleocene and Eocene, Wyoming; Eocene, Texas | Note 9 |
| " <i>Oreohelix</i> " <i>steini</i> Cockerell, 1914 | Paleocene, New Mexico | Note 9 |
| Genus and sp. indet. (Roth 1984) | Eocene, W Texas | |

TABLE 2. CONTINUED.

| Taxon | Fossil occurrence | Holocene range |
|--|--------------------------------------|--|
| Family Ammonitellidae | | |
| <i>Ammonitella lunata</i> (Conrad, 1871) | Oligocene or Miocene, Oregon | <i>Ammonitella</i> : Sierra Nevada, California (Pilsbry 1939) |
| <i>Polygyrella amplexa</i> (Meek and Hayden, 1857) | Upper Cretaceous, Montana | <i>Polygyrella</i> : NE Oregon to W Montana (Pilsbry 1939) |
| <i>P. parvula</i> (Whiteaves, 1885) | Upper Cretaceous, Alberta | |
| <i>P. venerabilis</i> (Russell, 1937) | Upper Cretaceous, Alberta | |
| <i>P. sp.</i> , cf. <i>P. polygyrella</i> (this paper) | Eocene, Montana | |
| <i>P. sp.</i> (Ross 1959; Taylor 1975) | Eocene, Montana, Wyoming | |
| <i>P. polygyrella</i> (Bland and Cooper, 1861) | Oligocene or Miocene, central Oregon | <i>P. polygyrella</i> : NE Oregon to W Montana (Pilsbry 1939) |
| Family Oreohelicidae | | |
| <i>Radiocentrum</i> (?) <i>anguliferum</i> (Whiteaves, 1885) | Upper Cretaceous, Alberta | <i>Radiocentrum</i> : SW U.S. and N Mexico; Baja California Sur (this paper) |
| <i>R. thurstoni</i> (Russell, 1926) | Paleocene, Alberta | |
| <i>R. grangeri</i> (Cockerell and Henderson, 1912) | Eocene, Wyoming | |
| <i>R. laevidomus</i> n. sp. | Eocene(?), Montana | |
| <i>R. taylori</i> n. sp. | Eocene or Oligocene, Montana | |
| <i>R. hendersoni</i> (Russell, 1938) | Oligocene, Colorado | |
| Family Helminthoglyptidae | | |
| | | Helminthoglyptidae: Alaska to California; SW U.S.; Mexico, Central America, Florida Keys, Antilles; Andes from Ecuador to W Argentina (Pilsbry 1939) |
| <i>Glypterpes rotundatus</i> (Russell, 1931) | Paleocene, Alberta | |
| <i>G. veternus</i> (Meek and Hayden, 1861) | Eocene, Wyoming | |
| <i>Helminthoglypta bozemanensis</i> n. sp. | Eocene or Oligocene, Montana | <i>Helminthoglypta</i> : S Oregon to N Baja California (this paper) |
| <i>H.</i> (?) sp. (Taylor 1975) | Oligocene, Wyoming | |
| <i>Hemitrochus</i> (?) sp. (Taylor 1975) | Oligocene, Wyoming | <i>Hemitrochus</i> : S Florida, Antilles (Turner 1958) |
| <i>Lysinoe breedlovei</i> Roth, 1984 | Eocene and Oligocene, W Texas | <i>Lysinoe</i> : Chiapas, Mexico; Central America (Roth 1984) |
| <i>Mesoglypterpes sagensis</i> Yen, 1952 | Upper Cretaceous, Wyoming | |
| <i>Monadenia antedecens</i> (Stearns, 1900) | Oligocene or Miocene, central Oregon | <i>Monadenia</i> : Alaska to California; in Oregon, W of Cascade crest (Roth 1981b) |
| <i>M. dubiosa</i> (Stearns, 1902) | Oligocene or Miocene, central Oregon | |
| <i>M. (Shastelix?) marginicola</i> (Conrad, 1871) | Oligocene or Miocene, central Oregon | <i>Shastelix</i> : Klamath Mountains, N California (Roth 1981b) |
| <i>Polymita texana</i> Roth, 1984 | Eocene, W Texas | <i>Polymita</i> : Oriente Province, Cuba (Zilch 1960) |
| <i>Xerarionta waltmilleri</i> Roth, 1984 | Oligocene, W Texas | <i>Xerarionta</i> : S California to Baja California (Roth 1984) |
| " <i>Helix</i> " <i>adapis</i> White, 1886 | Paleocene, New Mexico | Note 10 |
| " <i>H.</i> " <i>nacimientensis</i> White, 1886 | Paleocene, New Mexico | Note 10 |
| Undescribed genus and sp. (Taylor 1975) | Eocene, Wyoming | |

Notes

1. Solem (1979) suggested relationship to West Indian Camaenidae; now shown to belong to one (Bishop 1980) or more (Solem in press) genera of Helicinidae.

tions and faunal replacements in many groups of organisms beyond that evident in the first two-thirds of the Eocene. Continental aridity increased in interior regions of North America and general world-wide climatic equability decreased" (Lillegraven 1979:344). Axelrod (1981, table 1) noted that the period around 40 million years before present was one of spreading dry climate in southwestern North America.

As a generalization (admittedly much simplified), organisms in the western interior of North America that were most sensitive to cooling temperatures should have undergone southward displacement: the general trend of isotherms is latitudinal. Organisms most sensitive to drought (annual or seasonal) should have been displaced to east or west: away from the complex topography of the Great Basin and Rocky Mountains, the general trend of isohyets is longitudinal (U.S. Dept. Commerce 1968). What one in fact sees is a mixture of displacements, both among Bozeman Group taxa and among North American land mollusk groups in general (Table 2).

At the family level, the late Eocene and early Oligocene was the time of greatest modernization of the worldwide land mammal fauna, archaic kinds generally adapted to warmer climates giving way to modern varieties more tolerant of the temperate climate of the late Cenozoic (Lillegraven 1979). For North American land mollusks, at least, the time seems not to have been one of evolutionary innovation so much as local extinction and biogeographic rearrangement.

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2. These *Pseudocolumna* "can be interpreted as smooth-shelled bulimulids equivalent in shape and size to South American *Bostryx* (*Peroneus*) rather than to any African subulinids" (Solem 1979:281).

3. The Paleocene *Holospira* sites in New Mexico are about 370 km north of the modern range of the genus (Bequaert and Miller 1973).

4. Genus of original proposal almost certainly incorrect; allocation uncertain, possibly helicoid (Pilsbry 1946; Solem 1979).

5. Pilsbry (in Stewart 1926) assigned this species to *Ventridens* but later (1946:436) expressed reservations about the assignment.

6. "Not . . . certainly referable to any recent West Coast genera of Polygyridae" (Pilsbry 1940:893).

7. Solem (1978, 1979) noted resemblance between *Hodopocus* and the extant South American camaenid genus *Isomeria*.

8. Regarded as helicoid by Bishop (1980) but shown by Solem (in press) to be stylommatophoran; possibly camaenid (Solem 1978, 1979).

9. New genus of Camaenidae (D. W. Taylor, personal communication). Related Paleogene species occur in New Mexico and southern California.

10. Allocation uncertain, possibly helminthoglyptid (Solem 1979, *H. adapis*; Taylor 1975, *H. nacimientensis*).

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LATE CENOZOIC MARINE MOLLUSKS FROM TUFF
CONES IN THE GALÁPAGOS ISLANDS

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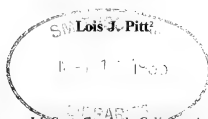
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ABSTRACT: Palagonite tuff cones on Isla Santa Cruz in the Galápagos Archipelago have yielded fossil marine mollusks, preserved both as individual shells with tuff infillings and as larger fossiliferous limestone inclusions. Twenty species (19 gastropods and 1 bivalve) are reported from the Cerro Gallina tuff cone, and representative specimens are illustrated. Two of the nominal species are known only as fossils from the Galápagos; the remaining nominal species are living today, although not necessarily in the archipelago. The two modes of preservation in Galápagos tuff cones reflect two different age relationships between the fossils and the enclosing pyroclastic rock: the individual fossils are more or less contemporaneous with the tuff matrix, while the larger fossiliferous inclusions are incorporated from an older limestone formation. The subaqueously formed and subsequently uplifted tuff cones represent an earlier phase of Galápagos volcanism than the younger Bruhnes-age volcanoes and subaerial flows that dominate the emergent surfaces of the islands today, although geologic evidence suggests that they may have formed no earlier than about 3 million years ago.

INTRODUCTION

Igneous rocks seldom contain fossils, and oceanic islands of volcanic origin seldom pre-

serve fossil records of their contemporaneous biotas. Although the geologic history of the Galápagos Archipelago is dominated by volcanic activity, there are at least five distinctive sedimentary settings in which remains of marine organisms have been preserved (Lipps and Hickman 1982; Hickman and Lipps 1985). In

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addition, there is one volcanic setting that has preserved marine fossils in an unusual manner: palagonite tuff cones, massive topographic structures formed from the products of submarine pyroclastic volcanism but incorporating occasional isolated shells and larger fossiliferous limestone inclusions. In this paper we provide the first systematic documentation and illustration of tuff cone faunas in the Galápagos, along with a brief discussion of their occurrence, distribution, and mode of fossilization.

This report (contribution number 366 of the Charles Darwin Foundation) is based on a paleontological reconnaissance expedition to the Galápagos during February 1982, organized by the senior author and including the remaining authors as participants (see also Pitt and James 1983; Pitt 1984). We thank the Galápagos National Park Service, the Charles Darwin Research Station and its former directors, D. C. Duffy and F. Koster, and Ecuadorian military officials for their cooperation and assistance. We are grateful to A. and J. DeRoi for calling our attention to the presence of marine shells in the tuff cone at Cerro Gallina. Our research has been supported in part by the Committees on Research, University of California, Berkeley and Davis, and the Museum of Paleontology, University of California, Berkeley.

GEOLOGIC SETTING

There are six major tuff cones and tuff cone complexes ringing Isla Santa Cruz, a large, low island near the center of the young, active volcanic archipelago (Fig. 1). The cones are primarily of submarine origin and represent an earlier, subsequently uplifted phase of Galápagos volcanism than the younger cinder cones, volcanoes, and subaerial flows (McBirney and Williams 1969; Bow 1979). The uplifted cones are now deeply eroded and dissected, emerging as islands from more recent subaerial basalt flows. Although one of the cones is now situated 1 km inland from the modern shoreline (Bow 1979), the others have conspicuous wave-cut exposures and stand out as landmarks along the coast.

The absolute age and contemporaneity of the tuff cones on Santa Cruz have not been demonstrated. These cones occur below Bruhnes paleomagnetic-age flows of the late Pleistocene and Recent and may represent Matuyama-age volcanism. However, the oldest radiometric date

that has been obtained in the archipelago is a potassium-argon date of 4.8 ± 1.87 mybp on the palagonite tuff on South Plazas, part of the Cerro Colorado cone complex (Cox and Dalrymple 1966; Cox 1983). Examination of fossiliferous inclusions in the tuff and consideration of Matuyama-age dates associated with the inferred source of the inclusions (Cox and Dalrymple 1966; Cox 1983) lead us to reject the Plazas date (which is inherently questionable in its large standard deviation).

We examined and collected fossils from two of the tuff cones, Cerro Gallina and Cerro Colorado. The more abundant and diverse material was from Cerro Gallina, and it is this fauna that is treated systematically and illustrated below.

The geology of Cerro Colorado is more complicated. Here we also observed and collected fossil mollusks from a prominent, richly fossiliferous limestone bed, originally reported by Durham (1965), that crops out north of and in faulted contact with the main tuff cone complex (see Hickman and Lipps 1985). The faunas of the fossiliferous limestone and tuffaceous sandstone beds on Santa Cruz and Isla Baltra merit separate consideration and are not treated in this report. Earlier California Academy of Sciences collections from these settings on Baltra and Santa Cruz were described by Dall (1924), Dall and Ochsner (1928), Hertlein and Strong (1939), and Hertlein (1972); Durham (1979) described a new species of *Haliotis* from the limestone at Cerro Colorado. Durham's collections are housed in the Museum of Paleontology, University of California, Berkeley.

CERRO GALLINA.—Cerro Gallina stands out as a dissected red hill of bedded lapilli tuffs rising approximately 100 m above sea level on the southwest coast of Isla Santa Cruz ($00^{\circ}42'50''S$; $90^{\circ}29'50''W$). Fossils occur as isolated whole shells within the tuff from the base of the exposed cone at sea level to its eroded summit. A fauna of 20 species (19 gastropods and 1 bivalve) was collected.

CERRO COLORADO.—Cerro Colorado (Fig. 2), a reddish brown eroded tuff cone remnant, is a conspicuous landmark on the eastern coastline of Santa Cruz ($00^{\circ}34'30''S$; $90^{\circ}10'20''W$). It is part of a larger tuff cone complex that includes at least two distinct vents (Bow 1979). The Island of South Plazas is an offshore remnant of this complex. Although fossils are less abundant in the tuff at Cerro Colorado than at Cerro Gallina,

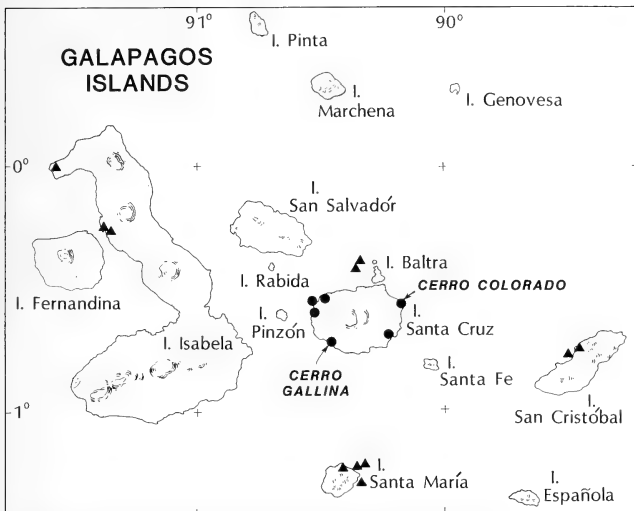


FIGURE 1. Map of the Galápagos Islands showing locations of palagonite tuff cones (dots) on Isla Santa Cruz, including Cerro Gallina and Cerro Colorado. Some additional tuff cones on other islands are also shown (triangles).

their distribution and mode of preservation is more interesting. In some of the well-sorted facies more distal to the main Cerro Colorado vent (Fig. 3), we found individual fossil shells, although the proximal tuff on the mainland is largely unfossiliferous. On South Plazas, in poorly sorted facies proximal to the second vent, fossils also occur as isolated individual shells (Fig. 4), but they are more prominent as large fossiliferous limestone inclusions (Fig. 5) that have been incorporated from an older fossiliferous limestone that is lithologically and faunally similar to limestone cropping out in the cliffs immediately north of Cerro Colorado.

OTHER FOSSILIFEROUS TUFF CONES.—More detailed examination of tuff cones in the Galápagos may expand the fauna reported here. Bow (1979) studied several of the tuff cones on Santa Cruz that we did not visit and reported incor-

poration of exotic blocks of limestone coquina up to several meters across. Although Darwin apparently did not personally observe or collect fossil material from tuff cones in the Galápagos, he reported (1844) receiving shell fragments imbedded in tuff from an officer who collected them "several hundred feet" above sea level on San Cristóbal. Darwin did, however, study the tuffs from the San Cristóbal cones as well as those on Santiago and Isabela, and was the first geologist to recognize that they had formed subaqueously (Darwin 1844). Fossils have not been reported from the tuff cones on Isla Isabela, and we saw no trace of shell material in our exploration of the Tagus cone complex.

FOSSILIZATION IN VOLCANIC ROCKS

Because volcanic rocks form from molten material, they do not normally contain fossils, al-

though there are scattered reports of fossils preserved in predominantly igneous settings.

There are peculiar tectonic environments in which marine mollusks have been preserved within thick sequences of oceanic basalt, notably in Oregon and Washington where Tertiary volcanic sequences have been accreted to the North American continent over a subduction zone (Hickman and Lindberg 1984). Hickman (1976) described two new species of *Pleurotomaria* from the Siletz River Volcanics in Oregon and figured fragments of two additional species from the Crescent Formation, a thick (at least 5,000 m) Eocene volcanic sequence in northwestern Washington. Individual fossils are not, however, encased in basalt, but occur characteristically in thin limestone lenses or tuffaceous agglomerates within the basalt. Snavely and Baldwin (1948) reported marine mollusks from tuffaceous interbeds in the Siletz River Volcanics; tuffaceous agglomerates in the Crescent Formation also preserve foraminifera (Berthiaume 1938) and corals (Durham 1942), as well as marine mollusks.

Direct incorporation of organic remains into volcanogenic rocks is more difficult and less common. Subaerial ash falls provide one mechanism for rapidly burying organisms in a medium that has cooled sufficiently to be nondestructive. Pompeii and Herculaneum are modern examples of the same process that enveloped successive forests of tree trunks in the Eocene of Yellowstone National Park.

Closer to the molten state, tree trunks do occasionally leave molds in rapidly cooling basalt flows, where total destruction of volatile organic matter is not complete until the lava is sufficiently chilled to preserve the empty space as a hollow tube. There is also the famous mold of a bloated rhinoceros in Miocene Columbia River Basalts in eastern Washington (Beck 1937; Chappell et al. 1949, 1951). Again, this fossil was preserved under very special circumstances involving rapid chilling of the lava.

Finally, there are several accounts of fossils preserved in volcanic rocks as inclusions. Late Quaternary fossiliferous xenoliths in the subaerially deposited tephra of Surtsey have been discussed in a series of reports dealing with this historic volcanic event (Alexandersson 1970, 1972; Simonarson 1974). Fossiliferous inclusions also occur on adjacent Heimaey in the older Vestmann Islands (Jakobsson 1968; Simonarson

1982), and were apparently carried upward in the hot magma to be ejected to their current elevation as these volcanoes emerged from the sea.

The individual fossil shells and the fossiliferous limestone inclusions in the subaqueously formed Galápagos tuff cones represent yet another mode of preservation of organic remains in a volcanic setting. Our knowledge of the physical and chemical process by which basaltic magmas are palagonitized and subaqueous tuff cones formed is based primarily on studies in the Galápagos (McBirney and Williams 1969; Simkin 1984). It is therefore appropriate to consider the organic component of these otherwise well-known volcanic structures.

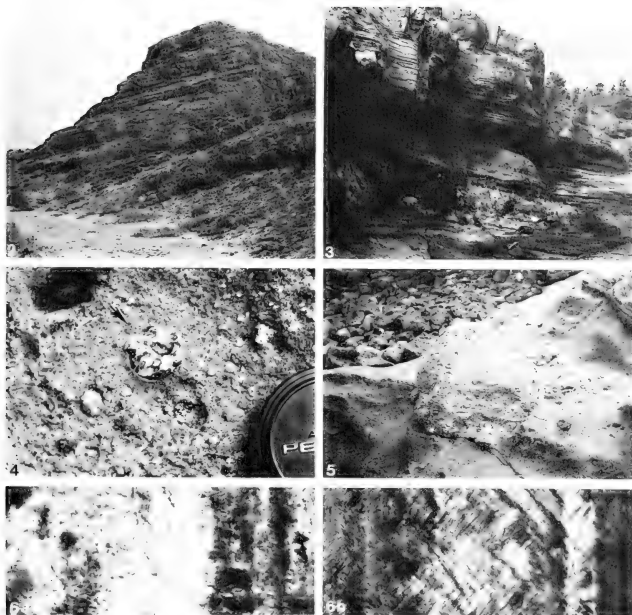
GALÁPAGOS TUFF CONE FORMATION AND INCORPORATION OF SHELLS AND FOSSILS

Explosive submarine volcanism of the type that produced the Galápagos tuff cones is atypical of the current eruptive mode in the archipelago, being more typical of convergent plate boundaries than of spreading centers and hot spots (see Simkin 1984, for a review of eruptive styles and products in the Galápagos). On Santa Cruz we observed two main types of fragmental deposits resulting from explosive volcanism: relatively young, steep-sided, cinder cones that formed subaerially; and older, consolidated, tuff deposits with more subdued, broader profiles that formed subaqueously when gaseous magma erupted from shallow submarine vents.

There are two different ways that molluscan shells have become incorporated into the Galápagos tuffs: (1) as living or recently dead individuals that were on the surface or in unconsolidated sediment adjacent to the vent at the time of eruption, or (2) as blocks of older fossiliferous rock that were incorporated into the tuff as it formed.

At Cerro Gallina, fossils occur as isolated shells with infillings of palagonite tuff. These shells were therefore empty at the time of eruption and were infilled and incorporated into the cones during the episodes of cold-water quenching, volumetric expansions and fragmentation, chemical alteration, and cone building.

The palagonite tuffs associated with both vents in the Cerro Colorado tuff cone complex contain isolated infilled shells similar to those at Cerro Gallina. Examination of a thin section of one of



FIGURES 2–6. Galápagos tuff cones and mode of occurrence and preservation of fossil material. Figure 2. Cerro Colorado, eroded tuff cone remnant on the east coast of Isla Santa Cruz. Figure 3. Seachiff exposure of well-bedded distal facies of a portion of the eroded tuff cone at Cerro Colorado. Figure 4. Individual fossil shell in tuff matrix (at arrow) on South Plazas, Cerro Colorado tuff cone complex. Figure 5. Fossiliferous limestone inclusion in tuff on South Plazas. Figure 6. Thin section of fossil strombid gastropod from the Cerro Colorado tuff cone. a. Outer shell layers showing loss of original microstructure. b. Inner shell layers showing well-preserved crossed-lamellar microstructure. Scale bar = 160 μ m.

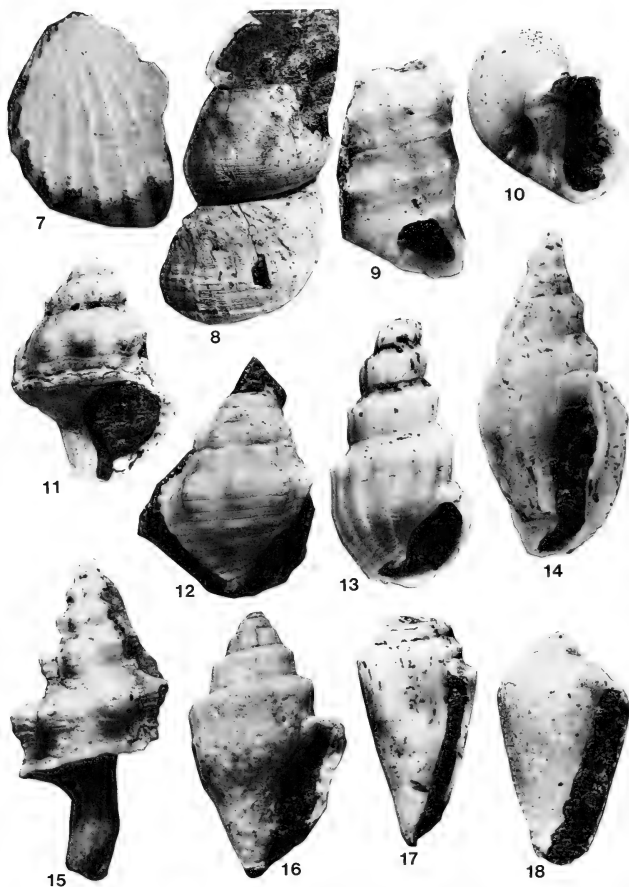
these shells (Fig. 6) shows alteration of both the innermost and outermost layers where they are in contact with the tuff matrix. The alteration consists of a loss of shell microstructure (Fig. 6a) in contrast to the well-preserved original crossed-lamellar structure of the interior layers (Fig. 6b).

In addition to isolated shells (Fig. 4), which are most evident in the better-sorted and better-bedded distal facies at Cerro Colorado, there are older xenoliths in the form of fossiliferous lime-

stone boulders (Fig. 5). The boulders were incorporated into the tuff as the magma erupted through older rocks, and they are analogous to those found on Surtsey except that they were incorporated subaqueously rather than blown out subaerially.

PALEOECOLOGY AND TAPHONOMY

The tuff cone mollusks are primarily assigned to species that are alive today and restricted to



FIGURES 7-18. Fossil mollusks from Cerro Gallina, Isla Santa Cruz. Figure 7. *Trigonocardia?* sp. CAS Geology 61411, CAS Loc. 61227, length 11.5 mm. Figure 8. *Turritella broderipiana marmorata* Kiener, 1843, CAS Geology 61412, CAS Loc. 61226, length 61.4 mm. Figure 9. *Turritella rubescens* Reeve, 1849, CAS Geology 61413, CAS Loc. 61233, length 11.4 mm. Figure

depths of less than 100 meters. Many of the shells in the Cerro Gallina tuff show signs of post-mortem infestation by boring organisms (Fig. 7–9, 11–13, 16), suggesting that they were exposed for a period of time prior to burial. Most of the shells are entire, and we did not encounter fragmented shell debris suggestive of extensive exposure and transportation. The fauna is, however, dominated by relatively thick-shelled species with morphologies resistant to post-mortem destruction.

SYSTEMATIC PALEONTOLOGY

The specimens upon which this study is based are deposited in the Department of Geology, California Academy of Sciences (CAS). Voucher specimen numbers are assigned only to figured specimens. All specimens bear Academy locality numbers, and complete locality descriptions are provided in the Appendix and in the locality register maintained in the Department of Invertebrates and Geology. Representative fossil specimens from the tuff cones will also be deposited in the reference collection at the Charles Darwin Research Station, Isla Santa Cruz, Galápagos. Comparative discussion of taxa treated below is based on examination of material in Academy collections.

Class PELECYPODA
Subclass HETERODONTA
Order VENEROIDA
Superfamily CARDIACEA
Family CARDIIDAE
Subfamily FRAGINAE
Genus *Trigonocardia* Dall, 1900

Trigonocardia sp.

(Figure 7)

DISCUSSION.—This taxon is represented by a single worn partial valve. Sculpture consists of flattened, scaled ribs with narrow, finely cross-

threaded interspaces as in *Trigonocardia biangulata* (Broderip and Sowerby, 1829). This specimen is not as convex as in typical *Trigonocardia* and lacks all of the hinge region, making positive generic and specific allocation impossible without additional material.

DISTRIBUTION.—Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene.

LOCALITY.—CAS Loc. 61227.

FIGURED SPECIMEN (incomplete).—CAS Geology No. 61411. Length 11.5 mm; width 8.6 mm.

Class GASTROPODA
Order MESOGASTROPODA
Superfamily TURRITELLACEA
Family TURRITELLIDAE
Subfamily TURRITELLINAE
Genus *Turritella* Lamarck, 1799

Turritella broderipiana marmorata Kiener, 1843 (Figure 8)

Turritella broderipiana Orbigny, 1840:388.

Turritella marmorata Kiener, 1843:23, pl. 8, fig. 1.

Turritella broderipiana marmorata Kiener. Hertlein 1972:41–42, fig. 26–28.

DISCUSSION.—*Turritella broderipiana* was originally described but not illustrated, leading to difficulties recognizing the taxon and assessing its relationship to the subsequently described *T. marmorata* on one hand and *T. gonostoma* Valenciennes, 1832 on the other. Our fossil specimens from the Galápagos are most similar to Kiener's (1843) illustrations of *T. marmorata*, but the above synonymy does not resolve all the problems attending use of the three available names. We summarize these problems below.

Reeve (1849, species 6, pl. 2, fig. 6A, B) figured specimens that he assigned to *Turritella broderipiana* and *T. marmorata* and placed Kiener's name in synonymy with *T. broderipiana*. Keen (1958:290, fig. 183, and 1971:392, fig. 438) figured the holotype of *T. broderipiana* and came to a conclusion counter to that of Reeve: that *T. marmorata* was a synonym of the more northern

10. *Polinices uber* (Valenciennes, 1832). CAS Geology 61414, CAS Loc. 61235, length 19.9 mm. Figure 11. *Bursa caelata* (Broderip, 1833). CAS Geology 61415, CAS Loc. 61225, length 45.1 mm. Figure 12. *Cantharus sanguinolentus* (Duclos, 1833). CAS Geology 61416, CAS Loc. 61225, length 30.3 mm. Figure 13. *Phos laevigatus* (A. Adams, 1851). CAS Geology 61417, CAS Loc. 61235, length 30.0 mm. Figure 14. *Strombina lanceolata* (Sowerby, 1832). CAS Geology 61406, CAS Loc. 61225, length 17.4 mm. Figure 15. *Latirus centrifugus* (Dall, 1915). CAS Geology 61407, CAS Loc. 61225, length 29.2 mm. Figure 16. *Columbella castanea* Sowerby, 1832, CAS Geology 61408, CAS Loc. 61225, length 24.1 mm. Figure 17. *Conus (Asprella) arcuatus* Broderip and Sowerby, 1829. CAS Geology 61409, CAS Loc. 61235, length 25.3 mm. Figure 18. *Conus (Cylindrus) lucidus* Wood, 1828, CAS Geology 61410, CAS Loc. 61225, length 25.2 mm.

species *T. gonostoma* rather than the southern *T. broderipiana*.

Hertlein (1972) elected another alternative when he recognized the subspecies *Turritella broderipiana marmorata* for specimens from Peru as well as specimens from Late Cenozoic deposits on Isla Baltra, Galápagos Islands. We have followed Hertlein in our identification of specimens from Cerro Gallina because they compare most closely with Hertlein's material from the adjacent Isla Baltra as well as with CAS specimens from Peru.

Both *Turritella broderipiana* and *T. gonostoma* have been characterized as highly variable (Merriam 1941:9), and evaluation of the species complex is beyond the scope of this paper. In Recent populations, color pattern has been used to separate the two species. The taxonomic significance of pigmentation has not been evaluated, however, and cannot be used to distinguish fossil specimens. Additional material from mainland Ecuador and Peru, where the geographic ranges of the two color-forms overlap, may eventually help resolve this problem.

DISTRIBUTION.—Ecuador to Peru, living and fossil.

GEOLOGIC OCCURRENCE.—Miocene(?)–Recent.

LOCALITIES.—CAS Locs. 61225, 61226, 61238.

MATERIAL COLLECTED.—Five specimens.

FIGURED SPECIMEN.—CAS Geology No. 61412 (Loc. 61226).
Length 61.4 mm; width 32.8 mm.

***Turritella rubescens* Reeve, 1849**

(Figure 9)

Turritella rubescens Reeve, 1849, vol. 5, pl. 11, sp. 63; Keen 1958:290, fig. 187, as synonym of *T. nodulosa* King and Broderip 1832; Keen 1971:394, fig. 445.

DISCUSSION.—Specimens from Cerro Gallina match the original figure of Reeve (1849) and the lower figure of Keen (1971), which illustrates a syntype from the British Museum (Natural History). The four figures of Keen (1971:445) indicate the variability of this species.

DISTRIBUTION.—Gulf of California to Colombia, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61233.

MATERIAL COLLECTED.—Three specimens.

FIGURED SPECIMEN.—CAS Geology No. 61413 (Loc. 61233).
Length 11.4 mm; width 6.8 mm.

Superfamily NATICACEA

Family NATICIDAE

Genus *Polinices* Montfort, 1810

Subgenus *Polinices* sensu stricto

Polinices (*Polinices*) *uber* (Valenciennes, 1832)

(Figure 10)

Natica uber Valenciennes, 1832:266.

Polinices uber (Valenciennes, 1832). Carpenter 1857:452–453; Dall and Ochsner 1928:96–97; Hertlein and Strong 1939:370.

Polinices (*Polinices*) *uber* (Valenciennes, 1832). Keen 1958:323, fig. 272; Keen 1971:480, fig. 882.

DISCUSSION.—Two incomplete specimens of this species were collected from Cerro Gallina. On one specimen the spire is low, the body whorl globose and smooth, the columellar callus thin, and the umbilicus deep. This specimen does not have a funicle, and the outer lip is missing. Marinovich (1977) discussed the complex relationships of *P. uber*, *P. intemeratus* (Philippi, 1853) and *P. unimaculatus* (Reeve, 1855).

DISTRIBUTION.—Cedros Island, western Baja California, throughout the Gulf of California, and south to the Galápagos and Paita, Peru, living; Imperial Formation of California and Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pliocene–Recent.

LOCALITIES.—CAS Locs. 61235, 61238.

MATERIAL COLLECTED.—Two specimens.

FIGURED SPECIMEN.—CAS Geology No. 61414 (Loc. 61235).
Length 19.9 mm; width 17.2 mm.

Superfamily CYMATIACEA

Family BURSIDAE

Genus *Bursa* Röding, 1798

Bursa caelata Broderip, 1833

(Figure 11)

Ranella caelata Broderip, 1833:179.

Bursa caelata (Broderip, 1833). Keen 1958:347, fig. 327; Keen 1971:508, fig. 964.

DISCUSSION.—Four incomplete fossil specimens from the Cerro Gallina tuff cone are most similar morphologically to specimens of the Recent *Bursa caelata* (Broderip, 1833). The fossils have three nodes between varices, four on some of the earlier whorls. Spiral sculpture is worn, but there are indications of possible secondary nodes. Varices are too worn to show sculpture pattern. The typical Recent specimen of *B. caelata* has numerous primary nodes at the shoulder, with rows of secondary nodes above and below the shoulder, and several rows below the shoulder on the body whorl. Some specimens in lots from Panama and Costa Rica have only three nodes between varices and have few secondary spirals and nodes. The fossil specimens are not complete enough to obtain accurate measurements. However, proportions are very close to

those of Recent conspecific specimens in the CAS collections.

DISTRIBUTION.—Gulf of California to Peru, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61234.

MATERIAL COLLECTED.—Five specimens.

FIGURED SPECIMEN.—CAS Geology No. 61415 (Loc. 61225). Length 45.1 mm; width 31.8 mm.

Superfamily BUCCINACEA

Family BUCCINIDAE

Genus *Cantharus* Röding, 1798

Subgenus *Gemophos* Olsson and Harbison, 1953

Cantharus (*Gemophos*) *sanguinolentus* (Duclos, 1833)

(Figure 12)

Purpura sanguinolentus Duclos, 1833, pl. 22, fig. 1.

Cantharus sanguinolentus (Duclos, 1833). Keen 1958:400, fig. 539; Keen 1971:561, fig. 1115.

DISCUSSION.—The single specimen collected at Cerro Gallina is incomplete, lacking the early whorls, outer lip, and anterior canal. A comparison was made between our specimen and *Cantharus janellii* (Kiener, 1835–36). Our specimen has low elongated nodes at the shoulder, while *C. janellii* has more pronounced and rounder nodes. The spiral sculpture is variable and should not be considered a diagnostic feature. Differences between these two species are in the node at the shoulder, the columellar markings, and the color (*C. sanguinolentus* has columellar pustules while *C. janellii* has columellar plications). Also, *C. sanguinolentus* has a pink columella whereas *C. janellii* has a black columella.

DISTRIBUTION.—Outer coast of Baja California through the southern part of the Gulf of California to Guaymas, Mexico, and south to the Ecuadorian mainland, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 61225.

FIGURED SPECIMEN.—CAS Geology No. 61416. Length 30.3 mm; width 21.5 mm.

Genus *Engina* Gray, 1839

Engina pyrostoma (Sowerby, 1832)

(Not figured)

Columbella pyrostoma Sowerby, 1832:116–117 (not illustrated).

Engina pyrostoma (Sowerby, 1832). Keen 1971:565, fig. 1128; Hertlein 1972:29.

DISCUSSION.—The single specimen collected at Cerro Gallina is worn and incomplete. Never-

theless, it exhibits sufficient morphological similarity to Recent specimens of *Engina pyrostoma* to warrant recognizing it as a fossil representative of this endemic Galápagos taxon.

DISTRIBUTION.—Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pliocene–Recent.

LOCALITY.—CAS Loc. 61236.

Genus *Phos* Montfort, 1810

Subgenus *Metaphos* Olsson, 1964

Phos (*Metaphos*) *laevigatus* A. Adams, 1851

(Figure 13)

Phos laevigatus Adams, 1851:155 (not figured, but see Emerson 1967, for discussion of subsequent figuring of the type specimen).

Phos chelonina Dall, 1917:578. Strong and Lowe 1936:310, pl. 22, fig. 3 (holotype).

Metaphos laevigatus (Adams, 1851). Emerson 1967:99–102, pl. 13, figs. 1–8.

Phos (*Metaphos*) *laevigatus* (Adams, 1851). Keen 1971:569, fig. 1145.

DISCUSSION.—The single specimen from Cerro Gallina lacks early whorls and the anterior canal, and fine shell sculpture details are worn. When whole, it had approximately eight whorls, 14 rounded axials, and a weakly tabulate shoulder sloping to the suture giving the effect of being slightly noded; spirals numerous, whorls straight-sided, body whorl tapering on anterior one-third.

DISTRIBUTION.—Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 61235.

FIGURED SPECIMEN.—CAS Geology No. 61417. Length 30.0 mm; width 15.5 mm.

Family COLUMBELLIDAE

Genus *Columbella* Lamarck, 1799

Columbella cf. *C. strombiformis* Lamarck, 1822

(Not figured)

DISCUSSION.—The single specimen from Cerro Gallina is missing about one-quarter turn from the outer lip and part of the anterior canal. In general outline, the specimen resembles *Columbella strombiformis*. Aperture shape is also similar to that of *C. strombiformis* when the missing portion of the shell is taken into consideration.

DISTRIBUTION.—Galápagos Islands.

GEOLOGIC OCCURRENCE.—Pleistocene.

LOCALITY.—CAS Loc. 61225.

Columbella castanea Sowerby, 1832

(Figure 16)

Columbella castanea Sowerby, 1832:118; Keen 1971:574, fig. 1154.

DISCUSSION.—*Columbella castanea* differs from other Panamic columbellids in its turreted whorl profile. The single specimen from Cerro Gallina has a second slight angulation at the suture that is more pronounced than on living specimens. *Columbella major* Sowerby, 1832, which we also collected as a Pleistocene fossil in terrace deposits on Isla Santa Fe, is distinguished by its rounder periphery and straighter-sided spire profile.

DISTRIBUTION.—Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 61225.

FIGURED SPECIMEN.—CAS Geology No. 61408. Length 24.1 mm; width 14.2 mm.

Genus Anachis H. and A. Adams, 1853**Anachis?** sp. indet.

(Not figured)

DISCUSSION.—An incomplete specimen, tentatively assigned to the genus *Anachis*, was collected from Cerro Gallina. The specimen has 14 low, axial ribs that become obsolete below the periphery, where they are replaced by numerous fine, raised spirals. The columella is smooth with a light callus, the aperture is narrow with a rather deep posterior notch, and the outer lip is lirate within.

DISTRIBUTION.—Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene.

LOCALITY.—CAS Loc. 61225.

Genus Strombina Mörch, 1852**Subgenus Strombina** sensu stricto**Strombina (Strombina) lanceolata** Sowerby, 1832

(Figure 14)

Columbella lanceolata Sowerby, 1832:116 (not illustrated).*Strombina lanceolata* (Sowerby, 1832). Keen 1958:394.*Strombina (Strombina) lanceolata* (Sowerby, 1832). Keen 1971:601, fig. 1275.*Strombina recurva* Sowerby, Dall and Ochsner (1928:96) [not *Strombina recurva* (Sowerby, 1832)].*Strombina gibberula* Sowerby, Hertlein (1972:29) [not *Strombina gibberula* (Sowerby, 1832)].

DISCUSSION.—This is one of the most abundant species in the fauna at Cerro Gallina. Specimens compare favorably both with modern rep-

resentatives of the species and with specimens from Isla Baltra that were originally assigned by Dall and Ochsner (1928) and Hertlein (1972) to other species of *Strombina* (see synonymy).

DISTRIBUTION.—Ecuadorian mainland to Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pliocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61234, 61235, 61236, 61237.

MATERIAL COLLECTED.—Eighteen specimens.

FIGURED SPECIMEN.—CAS Geology No. 61406. Length 17.4 mm; width 8.1 mm.

Family NASSARIIDAE**Genus Nassarius** Duméril, 1806**Nassarius caelolineatus** Nesbitt and Pitt, 1986

(Not figured)

Nassarius caelolineatus Nesbitt and Pitt, 1986:294–295, fig. 1, 2, 17a.

DISCUSSION.—Abundant specimens of a nassariid gastropod at Cerro Gallina compare favorably with both living and fossil specimens from the Galápagos that have been assigned to *Nassarius nodocinctus* (A. Adams, 1852). Material from the Galápagos does represent an endemic taxon, but a new name was required because specimens conspecific with the syntypes of *N. nodocinctus* have never been collected in the archipelago.

DISTRIBUTION.—Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pliocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61234, 61236.

MATERIAL COLLECTED.—Twenty-five specimens.

Family FASCIOLARIIDAE**Subfamily FASCIOLARIINAE****Genus Latirus** Montfort, 1810**Latirus centrifugus** (Dall, 1915)

(Figure 15)

Fusinus centrifugus Dall, 1915:56 (not figured).*Latirus centrifugus* (Dall). Keen 1971:613, fig. 1327.

DISCUSSION.—Two fasciolariid specimens collected from different parts of the Cerro Gallina tuff cone have the proportions and characteristic ornamentation of *Latirus centrifugus*. This is the first report of this species as a fossil in the Galápagos. Fasciolarids described by Dall and Ochsner (1928) under *Latirus* from the older Pliocene limestone bed north of Cerro Colorado have shorter anterior canals and different ornamentation.

DISTRIBUTION.—Galápagos Islands, living and fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61234.

MATERIAL COLLECTED.—Two specimens.

FIGURED SPECIMEN.—CAS Geology No. 61407 (Loc. 61225).

Length 29.2 mm; width 14.9 mm.

Superfamily CONACEA

Family CONIDAE

Genus *Conus* Linnaeus, 1758

Subgenus *Asprella* Schauffuss, 1869

Conus (Asprella) arcuatus Broderip and Sowerby, 1829

(Figure 17)

Conus arcuatus Broderip and Sowerby, 1829:379.

Conus (Lithoconus) arcuatus Broderip and Sowerby. Keen 1958: 458, fig. 936.

Conus (Asprella) arcuatus Broderip and Sowerby. Keen 1971: 663, fig. 1496.

DISCUSSION.—Specimens collected over a range of 40 m elevation in the Cerro Gallina tuff cone preserve the slender profile and turreted, faintly nodulose spire diagnostic of this species.

DISTRIBUTION.—Gulf of California to Panama, living; Costa Rica to Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITIES.—CAS Locs. 61225, 61234, 61235.

MATERIAL COLLECTED.—Three specimens.

FIGURED SPECIMEN.—CAS Geology No. 61409 (Loc. 61235).

Length 25.3 mm; width 12.8 mm.

Subgenus *Chelyconus* Mörch, 1852

Conus (Chelyconus) orion Broderip, 1833

(Not figured)

Conus orion Broderip, 1833:55; Keen 1958:483 (as a synonym of *Conus vittatus* Bruguière, 1792).

Conus (Chelyconus) orion Broderip, 1833. Keen 1971:664, fig. 1499.

DISCUSSION.—The single specimen from Cerro Gallina is worn but retains the characteristic profile and features of this species.

DISTRIBUTION.—Mexico to Ecuador, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 16237.

Subgenus *Cylindrus* Deshayes, 1824

Conus (Cylindrus) lucidus Wood, 1828

(Figure 18)

Conus lucidus Wood, 1828:8, pl. 3, fig. 4; Hanna 1963:56–58, pl. 6, fig. 1.

Conus loomisi Dall and Ochsner, 1928:103, pl. 2, fig. 6.

Conus (Cylindrus) lucidus Wood, 1828. Keen 1958:484, fig. 933; Keen 1971:664, fig. 1503.

DISCUSSION.—*Conus loomisi* Dall and Ochsner, from Pleistocene terrace deposits on Isla Isabela, is here considered a synonym of *C. (C.) lucidus* because fossil specimens in the CAS collections clearly show the color pattern of living *C. (C.) lucidus*. Although the fossil specimens from Cerro Gallina do not preserve color patterns, the raised spiral threads distinguish it from cones of similar profile, such as *Conus vittatus*. For complete synonymy and discussion, see Hanna (1963:56–58).

DISTRIBUTION.—Baja California, Mexico, to mainland Ecuador and the Galápagos Islands, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITIES.—CAS Locs. 61224, 61225, 61234, 61235, 61237.

MATERIAL COLLECTED.—Seven specimens.

FIGURED SPECIMEN.—CAS Geology No. 61410 (Loc. 61225).

Length 25.2 mm; width 14.3 mm.

Family TEREBRIDAE

Genus *Terebra* Bruguière, 1789

Terebra armillata Hinds, 1844

(Not figured)

Terebra armillata Hinds, 1844:154; Keen 1958:490, fig. 956; Keen 1971:672, fig. 1522; Bratcher and Burch 1971:556–557, fig. 27.

DISCUSSION.—Two fragmentary terebrid specimens from Cerro Gallina, each consisting of approximately two whorls, have proportions and sculpture that place them within the range of variation that Bratcher and Burch (1971) described for this species.

DISTRIBUTION.—Baja California, Mexico, to Peru and the Galápagos Islands, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 61225.

Terebra plicata Gray, 1834

(Not figured)

Terebra plicata Gray, 1834:61; Keen 1971:682, fig. 1556.

DISCUSSION.—This species is represented in our collections by a single specimen consisting of one whorl. The sculpture, although worn, is sufficiently distinctive to place it within the range of variation in CAS specimens of living representatives of the species.

DISTRIBUTION.—Central America to the Galápagos Islands, living; Galápagos Islands, fossil.

GEOLOGIC OCCURRENCE.—Pleistocene–Recent.

LOCALITY.—CAS Loc. 61236.

Family TURRIDAE?

(Not figured)

DISCUSSION.—Two poorly preserved specimens from Cerro Gallina are tentatively referred to the Turridae.

LOCALITY.—CAS Loc. 61236.

APPENDIX

Locality Data

CERRO GALLINA, ISLA SANTA CRUZ (00°42'50"S; 90°29'50"W)

CAS 61224. Low tuff cliff just above beach level, west side of small cove on west side of Cerro Gallina. (Field no. G-1-82.) Collected by W. D. Pitt and J. H. Lipps, 2 Feb. 1982.

CAS 61225. Southeast side of Cerro Gallina at beach on east side of small cove bounded by tuff cliffs, including all exposures along sea cliff from gully running into head of cove eastward to last accessible cliffs (about 30 m). Fossils occur as isolated shells in tuff. (Field no. G-4-82.) Collected by W. D. Pitt, L. J. Pitt, C. S. Hickman, J. H. Lipps, M. J. James, 2 Feb. 1982.

CAS 61226. Stratified, water-worked unit in massive tuff, at head of beach in tuff beds gently sloping across top of beach immediately east of gully entering head of cove. (Field no. G-5-82.) Collected by C. S. Hickman and W. D. Pitt, 2 Feb. 1982.

CAS 61227. Small ridge trending south toward beach, just above sea cliff on east side of cove and just above CAS 61226 (Field no. G-5-82). No field number. Collected by J. H. Lipps, 2 Feb. 1982.

CAS 61233. Approximately 12 m above sea level on second ridge north of beach in gully entering head of cove. (Field no. G-9-82.) Collected by C. S. Hickman, 2 Feb. 1982.

CAS 61234. Halfway up gentle ridge to sharp break in slope leading up to peak of Cerro Gallina; ridge is third one north of beach in gully and causes a bend in the gully where it intersects it. Approximately 20 m above sea level. (Field no. G-6-82.) Collected by J. H. Lipps, 2 Feb. 1982.

CAS 61235. Massive outcrop of tuff approximately 40 m above sea level on same ridge described in CAS 61234. (Field no. G-6-82.) Collected by J. H. Lipps and C. S. Hickman, 2 Feb. 1982.

CAS 61236. On same ridge as CAS 61234 (Field no. G-6-82) in massive tuff above principal break is slope leading to top of Cerro Gallina. (Field no. G-8-82.) Collected by J. H. Lipps and C. S. Hickman, 2 Feb. 1982.

CAS 61237. On ridge trending south from top of Cerro Gallina, approximately 20 m below summit. (Field no. G-10-82.) Collected by J. H. Lipps and C. S. Hickman, 2 Feb. 1982.

CAS 61238. Tuff cliff on southeast side of Cerro Gallina, on northwest side of sandy beach approximately 1½ m up sea cliff. (Field no. G-3-82.) Collected by C. S. Hickman and W. D. Pitt, 2 Feb. 1982.

CERRO COLORADO, ISLA SANTA CRUZ (00°34'30"S; 90°10'20"W)

CAS 61228. Red tuff hill opposite South Plazas Island, northeastern coast of Santa Cruz. Isolated fossils collected on north and west slopes of cone. (Field no. G-56-82.) Collected by W. D. Pitt, C. S. Hickman, J. H. Lipps, 11 Feb. 1982.

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THE CERAMBYCIDAE, OR LONGHORNED BEETLES, OF
SOUTHERN TEXAS: A FAUNAL SURVEY (COLEOPTERA)

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ABSTRACT: An annotated species list of the longhorned wood-boring beetles (Coleoptera: Cerambycidae) is presented for southern Texas. The area surveyed roughly corresponds to the Texas portions of the Matamorán and Nuecían districts of the Tamaulipan Biotic Province, including all of the lower Río Grande valley. Data given for the 178 species include original author citation, range, adult activity period, confirmed larval hosts, and anecdotal collecting and locality information. We propose no taxonomic changes, and nomenclature corresponds to the most recent literature. The species list is ordered according to the monographic revision of the family Cerambycidae (Linsley 1962a, b, 1963a, 1964; Linsley and Chemsak 1976, 1985), excepting that portion of the subfamily Lamiinae not yet treated by those authors, which is ordered according to the checklist of the Cerambycidae (Chemsak and Linsley 1982). Brief accounts of the biological, ecological, and historical aspects of the fauna are discussed. Prior literature on southern Texas Cerambycidae is summarized and collated.

Species reared from selected native plants are listed by host, with an updated account of species known to infest *Citrus* in southern Texas.

The origins and phyletic relationships of the fauna are briefly discussed, with a summary of some of the taxonomic limitations complicating faunal analyses of Neotropical Cerambycidae. Literature cited includes all original species descriptions.

INTRODUCTION

Adult Cerambycidae are characteristically elongate, subcylindrical beetles with long antennae, fully developed hind wings (numerous species, however, are flightless), and five-segmented tarsi with the fourth segment greatly

reduced in size. Variation within the family is extreme; North American genera range in average length from 3 mm (*Cyrtinus*) to over 70 mm (*Derobrachus*) and vary in appearance from obscure, drab ground-dwelling forms to brightly colored, contrastingly patterned insect jewels, capable of swift flight. They are equally diverse

ecologically and behaviorally, occupying thousands of forest ecosystem microhabitats and niches, and partitioning resources to permit common use of limited amounts of suitable host plant material. Gosling (1981) documented the presence of active populations of over 100 species of cerambycids in an 80-ha woodlot in Michigan, and the number of species and population densities are even greater in Neotropical forest ecosystems. Chemsak and Linsley (1970) reported collecting 55 species of cerambycids at a light one August evening in the thorn forest north of Mazatlán, Sinaloa, Mexico. This figure represents no more than one-third of the total longhorned beetle fauna at that locality, since it does not include species taken other nights, nonphototropic species, species not active during that particular season, or any of the numerous diurnal species known to occur there.

Cerambycids are phytophagous, and as a family they utilize their host plants from rootlets to buds. Adult beetles may feed upon flowers, leaves, pine cones and needles, fruit, sap, fungi, or bark; while larval Cerambycidae feed externally upon roots, or bore within living, dying, or dead trunks, branches, stems, bark, floral stalks, or roots of both herbaceous and woody plants. Most species utilize existing suitable host materials for larval development, but a few genera create a larval habitat by girdling (either externally as adults, or internally as larvae) portions of living plants. No cerambycids are known to be truly predaceous, but adults of certain mimetic species of *Elytroleptus* have been observed feeding upon their lycid beetle models. The larval habits of this genus are unrecorded, but adults of two species have been taken from pupal cells in dead twigs, and the larvae probably feed upon dead wood (see Eisner et al. 1962, for a discussion of *Elytroleptus* predation upon Lycidae). The only other account of Cerambycidae as predators, by Bitenfeld (1948), shows adult *Aromia moschata* (Linnaeus) eating young spiders, but it is generally regarded with suspicion due to its lack of detailed observations and the absence of any subsequent corroboration.

Cerambycid larvae are whitish or yellowish, elongate, cylindrical or subquadrate in cross-section, with rounded heads and powerful chewing mouthparts. Growth and development may be quite rapid, with several generations maturing annually, or very slow, extending over several years. Larval feeding may be confined to a spe-

cific part of the host, particularly in species utilizing living plants, or the larvae may tunnel throughout the woody portions of the host, carving galleries several meters long.

A few genera degrade or destroy large volumes of harvested timber; others attack and weaken shade, fruit, and forest trees. Most species of Cerambycidae, however, breed in shrubs and trees of little current economic importance. Overall, longhorned beetles are essential to forest decomposition, recycling vast amounts of dead plant material. Larval feeding activities may alter a considerable volume of dead host material; Hovore and Penrose (1982) found that larval workings resulted in a wood-mass reduction of up to 70% in dead *Leucaena* in Texas. Additionally, larval galleries and adult emergence holes permit access into the wood for water, fungus, and soft-bodied insects such as termites and ants. Many adult cerambycids feed upon pollen and other portions of flowers, thereby serving as pollinators for many plant species. And both adult and immature life stages are a major food source for a broad spectrum of arthropod and vertebrate predators.

Based upon extant study material, the Neotropical Cerambycidae are both the most evolutionarily diversified and least-studied portion of the world longhorned beetle fauna. Over 5,000 Neotropical species have already been characterized, with many more thousands awaiting description or discovery. Unfortunately, the New World tropics are rapidly disappearing before the onslaught of unregulated land and resource usage; in many regions little remains of the original tropical forests. At this writing the estimated extinction rate for tropical organisms is one per day, with forests being cut at a rate of between 25 and 100 ha per minute (Wiley 1982). As forest tree species become extinct, their obligate faunas also disappear, altering or destroying many long-established interrelationships and trophic patterns. By virtue of the inseparable and often narrowly circumscribed relationships between Cerambycidae and their host plants, the population dynamics of these insects may well reflect the general health, or decline, of an overall forest ecosystem.

In North America, the forest habitats in greatest jeopardy are those combining small geographical size with accessible or economically desirable resources, climates, or soils. Thus, the semitropical regions of southern Florida and

southern Texas are North America's most critically threatened major ecosystems, with only fractional remnants of the original biota persisting in either area.

HISTORICAL ACCOUNTS FROM LITERATURE

Although primarily confined to remnant habitats in the extreme southern portion of Texas, the Neotropical cerambycid fauna is remarkable for its species diversity and abundance. The lower Rio Grande valley (Lower Valley) has received considerable entomological attention, and since the appearance of the first brief species account by Schwarz in 1896, no fewer than six lists of the longhorned wood-boring beetles have been published.

Wickham (1898) recorded the collection of 26 species of cerambycids from the Lower Valley, and Townsend (1902) presented an annotated record of over 40 species from Texas and adjacent Tamaulipas, Mexico. Results of the 1904 and 1905 Kansas entomological expeditions to the Texas Gulf Coast were catalogued by Snow (1906), and included 22 species from the vicinity of Brownsville. Schaeffer (1908), in his extensive list of Cerambycidae from Brownsville, recorded 78 species and commented upon the validity of some of the previous accounts (not including Snow's list). Discrepancies in data citations, and identifications based upon outdated or synonymized names preclude a precise collation of data from these earliest accounts. We have, wherever possible, updated and explained changes in status or nomenclature.

Of greatest value to this study were the excellent species accounts of Linsley and Martin (1933) and Vogt (1949a). The former gave an annotated record of the results of two highly successful collecting trips to the Lower Valley region in 1930 and 1932, while the Vogt paper provided accurate host and habitat information for 83 cerambycid species. Linsley and Martin estimated that their list of 65 species brought the southern Texas total to 88, and their figure, combined with Vogt's account, boosted the total to approximately 100 species. Given the relatively small geographical area covered, the collection methods available to these workers, and the fact that only Vogt collected in the fall, this is a most remarkable figure.

For the present study, seven cerambycid collecting trips were made to southern Texas be-

tween 1972 and 1980, concentrating upon the spring and fall activity periods. Dates and collectors include the following: 12–18 May 1972, F. T. Hovore (FTH), E. F. Giesbert (EFG); 5–15 October 1975, FTH, EFG, R. L. Penrose (RLP); 2–6 May 1976, FTH, RLP; 9–19 May 1977, FTH, EFG, RLP; 10–13 May 1978, FTH and family; 21–28 October 1978, FTH, RLP; 10–16 May 1980, FTH, RLP, D. C. Carlson. The results of the individual surveys varied considerably due to the vagaries of weather, methodologies, localities visited, and the length of each stay. In total, 136 species of Cerambycidae were collected.

GEOGRAPHIC BOUNDARIES OF THE STUDY AREA

In order to reflect the ecological limits of the semitropical elements of the Texas cerambycid fauna, our list encompasses a slightly greater geographical area than did prior accounts. Specimen data indicate that the northernmost limits of the true semitropical fauna in Texas extend into the Nueces River drainage near Corpus Christi along the southeastern coastal strand, and northwest up the Rio Grande valley to the vicinity of Eagle Pass. These distributional limits correspond closely with the general parameters of the semitropical flora and fauna as expressed by Schwarz (1888, citing C. S. Sargent, Report of Forest Trees of North America). The Nueces River also marks the southernmost region of general distribution of the floral and faunal elements of the eastern woodlands, with the ranges of a number of widespread North American tree species extending south to the Corpus Christi–Kingsville area. Blair (1950), in discussing and redefining the concepts of biotic provinces in Texas, considered the region south of the Balcones Escarpment (below the Edwards Plateau) on the west, and the line between pedocal and pedalfers soils on the east (roughly corresponding to the drainage basin of the Nueces River), to comprise the Texan portion of the Tamaulipan Biotic Province. Within this province he later united the extreme southern counties (Starr, Hidalgo, Willacy, and Cameron), plus portions of adjacent Tamaulipas, into the Matamorán Biotic District, with the remainder regarded as the Nuecian District (Blair 1952). Our study region (Fig. 1) more or less corresponds to Blair's limits for the Texan portions of the Tamaulipan Biotic Province, although available records do not extend as far north along

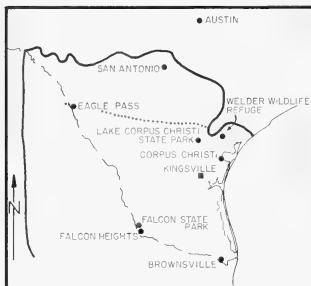


FIGURE 1. Southern Texas: Dotted line indicates the approximate boundaries of the study area; solid line indicates the northern limits of the Tamaulipan Biotic Province.

the Rio Grande. Our data citations include specimens from that portion of Texas south of Eagle Pass on the western border, and Copano Bay (just north of Corpus Christi) on the Gulf Coast. Most data, however, come from material gathered in the drainage basin of the Rio Grande from Falcon Lake (Zapata County) to Boca Chica (Cameron County); the Southmost sector of Brownsville; and from Lake Corpus Christi State Park and Welder Wildlife Refuge (both in San Patricio County). Much of the habitat within the remainder of the study area is dry upland Tamaulipan thorn-scrub (Texas Chaparral), mixed overstory brush savanna (overgrazed potential grassland), or cultivated land. Cerambycid species diversity is relatively low in these areas, and little collecting has been conducted beyond cursory beating and sweeping.

CLIMATE AND TOPOGRAPHY OF STUDY AREA

The lower Rio Grande valley is comprised largely of a deltaic plain, often quite narrow, extending from extreme southern Starr County through southern Hidalgo County and expanding to encompass all of Cameron County, southern Willacy County, and portions of adjacent Tamaulipas. The inland portions of southern Texas are of diverse geologic origins, with a patchwork of soil types and subsurface formations of varying depths and ages, many of which exert direct

controlling influences upon surface vegetational types. Most of the older sandstone formations of the upland portions of the Lower Valley are covered with brushlands or mesquite/huisache savannas, while the terrace deposits along the river valley proper support most of the substantial gallery forests. The deltaic plain is also covered with brushy plant formations, but they are denser and more luxuriant than those found in the drier uplands. Near the Gulf Coast, the plain gives way to open salt marshes and low, *Yucca*-dominated ridges, while to the north along the coast and inland there are deep, wind-blown sand deposits covered with prairie grass and scattered oak communities. For more complete discussions of the geology, soils, and vegetational characteristics of southern Texas, see: Coffey (1909); Hawker et al. (1925); Sellards et al. (1932); Trowbridge (1932); Clover (1937); Wynd (1944a, b); LeBlanc (1958); Box (1961); Thompson et al. (1972); and Williams et al. (1977).

The climate of southern Texas is generally rather mild, with warm dry summers and moderately cool winters. Winter frosts are not uncommon, but rarely last more than a few days; temperatures usually remain above -4°C . According to Clover (1937:42), "Killing frosts are rare, but frequent enough to make commercial growing of bananas and other tropical fruits impossible." These periodic hard frosts might also be a primary constraint upon the northward advance of the semitropical flora and fauna, and more severe winters undoubtedly result in temporary dieback of more cold-sensitive organisms, along with high rates of mortality among winter-active species. The record low temperature for Brownsville is -11°C , while temperatures at Welder Wildlife Refuge have gone as low as -12.7°C (Box and Chamrad 1966). Precipitation may occur during any month, with maxima in April–May and September. According to Porter (1977:30), "... there is actually great variation from month to month and from year to year. Protracted droughts are common but some years may have more than 1,000 mm of rain." March is the driest month (precipitation averages 26 mm at Brownsville), and September the wettest (precipitation averages 124.8 mm), with annual precipitation averages of 669 mm at Brownsville and about 800 mm at Welder Wildlife Refuge. Sudden, violent thunderstorms, common during spring and fall, drop several

hundred millimeters of rain in a few hours. The entire southern portion of the state is subject to occasional hurricane activity in late summer and early fall, with accompanying high winds, torrential rain, and coastal lowland inundation. Selected climatological studies of the Lower Valley include: Gunter and Hildebrand (1951); Had-dock (1963); Carr (1967); Orton et al. (1967).

HABITAT INFORMATION—HISTORICAL PERSPECTIVES

Agriculture and other forms of land development have more or less confined modern collecting in the lower Rio Grande valley to parks and sanctuaries. The remnants of the native floral communities are largely restricted to preserves, many of which are small and totally surrounded by developed land. Isolated stands of trees and brush do persist along resacas (old river channels) and roadsides, and these often contain surprisingly dense populations of insects. We cannot determine accurately how many, or what percentage, of the original floral and faunal components of the Lower Valley have been lost to land conversion, as much of the region (the river delta in particular) was cleared for agriculture by the late 1800s. Most of the original native vegetation was removed between 1880 and 1930, with little regard (and sometimes open contempt) for the unique ecosystems destroyed in the process. The typically narrow perspective of Lower Valley pioneers was typified by Kerbey (1939:52) in *National Geographic Magazine*

Westward-faring pioneers in the early days of the United States had to chop down forests of sizeable trees to earn their land. . . . Here on the semitropical frontier there was work again, and lots of it, before the land could be put to use. . . . I was amazed when I saw for the first time the dense tangle of virgin growth that still covers parts of the region. The sight of it gave me a healthy respect for the early comers who had imagination and energy enough to peel off this ugly and tenacious "rind" to get to the rich, productive earth beneath. . . . Clearing land in the Rio Grande Delta, and thereby transmitting virtually worthless wilderness areas into valuable farms . . . has been a slow and expensive process. Since a little after the turn of the century, about 450,000 acres have been cleared . . . and between 50,000 and 100,000 acres of good irrigable land still remain to be cleared.

The earliest accounts of the coleopterous fauna of the Lower Valley referred to the native tropical forests as occurring in small, isolated "islands" or "little jungles" (Wickham 1897:97). E. A.

Schwarz (1896:3) remarked that, "the Texan semi-tropical flora and fauna are doomed to almost complete extinction by the progress of agriculture, and already at the time of my visit, flourishing sugar-cane fields and corn-fields covered the major part of the area once occupied by the semi-tropical forest." Thirty-three years later, H. F. Schwarz (1929:426) sounded a similar, if less ominous, note, "The region will still continue verdant and attractive, but it will be with the blossom of citrus growth and other market products, and less and less with the bloom of the cactus, the huisache, and the Mexican mahogany. Let us hope that amid all the changes . . . representative groups of wild life may succeed in surviving, even if in diminished numbers." Linsley and Martin (1933:178) noted that by the early 1930s the spread of land conversion had reduced the original habitat to "half a dozen such thickets . . . and few of these are more than an acre or two in size," and that the Sabal Palm grove was being used as a public picnic ground, "where one may collect upon payment of the twenty-five cent admission price." In describing his 1946 and 1947 collecting localities, Vogt (1949b) noted that portions of several floral associations were then being cleared for agriculture and stated that practically all of the land north of the alluvial plain and delta region of the Lower Valley was under cultivation. In 1977, Vogt (pers. comm. to F. T. Hovore) further remarked that, "aside from Santa Ana Refuge and Bentsen (Rio Grande Valley State Park), almost no natural areas remain. Also weed cover has changed, apparently due to invasion of more exotic species. Even in the hills of Starr County farming and pasture improvement with exotic (South African) grasses has changed the ecology extensively." He concluded that, "Since many of the vegetation formations I studied have vanished, I would expect a complete faunal change in the Cerambycidae." Neck (1980), discussing the invertebrate fauna of the Lower Valley, stated, "There can be no doubt that the invertebrate fauna has been devastated by massive land clearing. However, a healthy fauna can be found in remnant tracts of brush. . . . There is no room for complacency, however; all remaining native brush tracts on the left bank should be preserved. As bleak as the situation is on the left (American) bank of the Rio Grande, native brush tracts are almost non-existent on the right (Mexican) bank."

ECOLOGICAL CONSIDERATIONS: THE LOWER VALLEY REGION

At present, agriculture has overwhelmed all but a few stands of native forest and scrub brush. In the delta of the Lower Valley, most of the remaining native flora lies along the deltaic plain and on the periodically inundated low coastal strand between Brownsville and Boca Chica beach. The National Audubon Society's Palm Grove Sanctuary at Southmost sector (near Brownsville), Resaca de la Palma State Park near Brownsville, Santa Ana National Wildlife Refuge near Alamo, and Anzalduas Park and Bentsen-Rio Grande Valley State Park, both near Mission, contain the major portions of the remaining Lower Valley hardwood forests. Although theoretically protected from further environmental destruction, these preserves are nevertheless subject to considerable unnatural stress from such factors as drift and seepage from application of agricultural chemicals on adjoining fields, irregularly fluctuating water tables (affected by irrigation and controlled river flow), and even the format of the environmental protection itself.

Anzalduas and Bentsen parks are managed to varying extents for recreational uses (picnicking, camping, sports, etc.), in some cases with regular chemical and mechanical vegetation control. Cerambycid collecting in the parks has frequently been well below our expectations (based upon observable floral elements and subjective assessment of potential), and in recent years, despite excellent collecting at other nearby localities, our results from park areas have been relatively poor. It may be that the ecological integrity of these communities has been diminished by continuously manicuring the vegetation in the natural areas. Efforts have recently been made by the Texas Parks and Wildlife Department to guard against ecosystem decline, and remedial measures (e.g., the prohibition of burning or removing dead wood, and restrictions on the use of topical pesticides) have been instituted in state parks and preserves.

Another factor that may contribute to the slow decline of faunas in relictual habitats, and one that would be most difficult to mitigate at this late date, is ecological isolation. Parks and preserves are separated from one another by broad zones of radically altered habitat, so there is little or no genetic exchange between populations of

organisms with limited mobility. Sanctuaries (where there is less vegetation removal and alteration) appear to be ecologically healthier than parks but are also geographically isolated and are gradually declining. Recent studies of avifaunal regimes in ecological "islands" among the remnant woodland tracts of the eastern United States (MacClintock et al. 1977; Whitcomb 1977; Simberloff 1978) concluded that regional extinctions of Neotropical migrants would occur in habitats which were either too small (minimum size based upon an aggregate of territorial, trophic, and other needs) or lacking the necessary biotic diversity. Similar studies involving birds and mammals in tropical ecosystems and "habitat islands" (Terborgh and Winter 1980; Wilcox 1980) predicted variable rates of population decline and extinctions based upon general and species-specific criteria, but overall these studies concluded that rates and percentages of species extinctions increase exponentially as habitat size decreases. Because they are relatively small, reproduce rapidly, and utilize minimal amounts of host material, insects are less vulnerable to some population pressures, particularly stochastic population death resulting from diminished territory size and insufficient gene pool size. We know of no detailed studies on habitat requirements for maintenance of population viability in Cerambycidae; but overall population vigor probably relates, in part, to the general biotic condition of the ecosystem and, more specifically, to the diversity, abundance and seral status of the woody plants. Overstoried and senescent communities with decreasing floristic diversity, or with heavy invasion of exotic species, would be expected to lose some more narrowly specialized phytophagous insect species.

Most sanctuary areas in the Lower Valley are old-growth Tamaulipan interior swamp and riparian hardwood forest, Tamaulipan semideciduous forest, or overstoried Tamaulipan thornscrub (plant formation terminology adapted from Brown et al. 1980), dominated by a mature climax sere; all appear to be losing floristic diversity to senescence. Few of the requisite cyclical and successional processes of growth and decomposition occur at natural rates. Periodic flooding no longer occurs because of artificial levee systems. Fire, essential to vegetational succession in many plant communities, particularly in arid or semi-arid regions, is suppressed within parks and preserves; their small size and lack of adjacent re-

fugia for wildlife practically precludes the use of fire to stimulate new growth and increase species diversity. The preserves are, in fact, extremely vulnerable to some of the very factors which once served to keep them vigorous and dynamic. Fire, flood, drought, and severe frosts, which together historically combined to influence the composition and distribution of much of the Texas semitropical habitat, could alone or in combination eliminate large numbers of species, with virtually no hope of any natural recolonization. Simberloff (1978:10) discussed the probabilities of species extinction in preserves, and noted that an interconnecting system of refuges would be a "bet-hedging strategy against catastrophes such as fire or epidemic diseases." Such a refuge network would no doubt also provide broader avenues of genetic exchange.

Natural habitats in southern Texas have been so drastically reduced, separated, and altered by human activity that many unique ecosystems have already been lost or radically reduced. And, despite the fact that most remnant forests of the Lower Valley are now in some type of preserve, urban and agricultural pressures on undeveloped land continue to mount. At this writing, the Lower Valley region has the most rapid rate of population growth in Texas. It seems then, that despite noble (if belated) attempts to preserve intact representatives of the original biota of the lower Rio Grande valley, the sad predictions of E. A. and H. F. Schwarz will at last be realized.

THE UPLAND REGION

Vast tracts of Tamaulipan thorn-scrub (chaparral) and a variety of savanna-woodland plant formations remain in the upper Rio Grande valley and northern portions of the study area, where it is still possible to find limited areas of more or less undisturbed habitat. Botanists (Clover 1937; Johnston 1963; Inglis 1964) have indicated that present upland chaparral regions are much more extensive now than they were prior to the introduction of livestock. Recent grazing has visibly altered formations and spatial relationships of many brushland plants, and in many areas exotic grasses and disturbed land-favoring genera of Compositae (=Asteraceae) grow in dense formations surrounding native trees and shrubs.

Although not as species-productive as the Lower Valley habitats, xeric upland communities nevertheless have strong representations of

certain cerambycid tribes (e.g., Purpuricenini, Acanthocinini), particularly genera associated with either herbaceous rangeland shrubs or the dominant leguminous tree species, mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*). Interestingly, beetles in the purpuricene genera *Tylosis*, *Lophalia*, *Parevander*, and *Crossidius*, adults of which are found on fall-blooming herbaceous or woody subshrubs (*Abutilon*, *Haplopappus*, *Viguiera*, *Verbesina*, and *Helianthus*), are apparently increasing in distribution and relative abundance. Of these cerambycids, only *Tylosis* had been previously recorded from the study area; Vogt (1949a) reported the presence of *Tylosis*, in the only other paper with records from the fall season. He encountered *Tylosis* in only two localities, despite the fact that he spent considerable time collecting from flowers in areas where these beetles are now very abundant. Vogt is a most capable and observant entomologist/collector, and it is improbable that he would have overlooked these large, brightly colored cerambycids. Their absence from previous accounts is more likely either a reflection of their recent advance (along with their hosts) into now-suitable disturbed land habitats, or an artifact of some sort of environmental phenomenon. Cyclical population fluctuations of more "tropical" species may occur as a result of unusual pluvial cycles, and temporary population retreat or dieback may follow repeated freezes. The plants with which these cerambycid genera are associated, either as adult food sources or as larval hosts (only *Tylosis* and *Crossidius* have actually been reared), are primarily "weedy" forms that are sensitive to environmental changes, quick to invade disturbed substrates, and coincidentally nurtured by agriculture.

A converse effect of accelerating land conversion and the attendant increase in herbaceous vegetation is the reduction or elimination of tree species, and this is nowhere more evident than in southern Texas. Habitat and host plant reduction may lead to decline and extinction in associated insects, with oligophagous species most vulnerable. Recent rearings of southern Texas Cerambycidae (Hovore and Giesbert 1976; Hovore et al. 1978; Turnbow and Wappes 1978, 1981; Hovore and Penrose 1982) have, fortunately, indicated considerable polyphagy in a number of deadwood-boring species (see Selected Rearings from Deadwood).

Dean (1953) and Manley and French (1976)

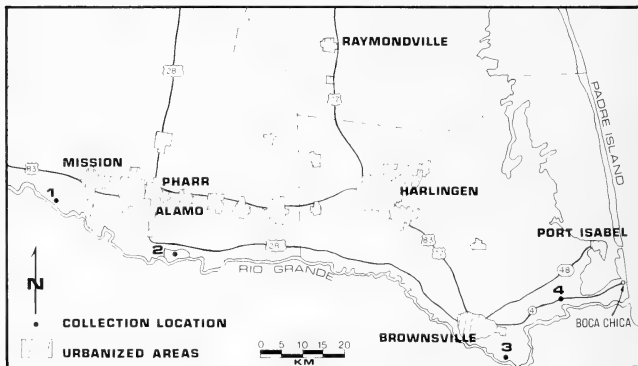


FIGURE 2. Lower Rio Grande valley collecting localities: 1) Bentsen-Rio Grande Valley State Park, 2) Santa Ana National Wildlife Refuge, 3) Audubon Society Palm Grove Sanctuary, 4) 16 km west of Boca Chica.

recorded rearing 18 species of Cerambycidae (and one species each of Bostrichidae and Buprestidae) from *Citrus* grown in the Lower Valley. Dillon and Dillon (1946) additionally list *Oncideres pustulatus* as having been taken on (but not necessarily infesting) *Citrus*. The breadth of host plant preferences shown by these rearings suggests that the net effect of tree species elimination may be mitigated by the abilities of entomofaunas to utilize alternative or introduced hosts, including ornamental and agricultural plants. Fox and Morrow (1981:889) stated that host plant selection "may have a strong genetic basis, controlled by only one locus or polygenic region, so that shifts in preferences for particular host plants can be very rapid." The potential genetic significance of colonization of new or introduced hosts by insect populations was hypothesized by Mayr (1954); populations on new hosts may quickly begin to function as sibling species, morphologically, reproductively (and therefore genetically) isolated from the parent populations (Fox and Morrow 1981). Based upon experiments with *Drosophila*, Templeton (1979) concluded that colonizing a new genetic environment can quickly lead to unique and possibly isolating changes in the morphology, ontogeny, physiology, and behavior of a species. Shifts in host plants might in turn lead

to discernible phenotypic differences between original, naturally occurring cerambycid populations and new-host pioneering populations. Should such changes occur in Cerambycidae in southern Texas, we will be better able to detect and quantify them if we take care to preserve adequate voucher samples of all species from all native hosts.

DESCRIPTIONS OF COLLECTING LOCALITIES

(Figures 1 and 2)

Audubon Society Palm Grove Sanctuary, Southmost sector, Brownsville, Cameron County

Clover (1937) catalogued the floral components of this unique remnant of the original tropical palmetto forests, listing the plant species encountered in a transect line from the margin of the Rio Grande River into the densest stand of palms. A later survey of the grove was conducted by Davis (1942).

The 425-ha sanctuary contains a subriparian gallery forest of mixed hardwood trees (*Ulmus*, *Celtis*, *Leucaena*, *Pithecellobium*, etc.) and mature *Sabal texana*, with elements of semideciduous forest, festooned along the margins with vines of *Clematis*, *Serjania*, *Melothria*, and *Cissus*. Beneath the tree canopy, understory vege-

tation is limited by shading, excessive dampness, and a rank layer of rotting fronds. Openings in the forest (most recently created by limited brush clearing and a small fire) exhibit luxuriant and varied herbaceous growth, interspersed with *Baccharis* and seedling *Leucaena*. For the few years that these clearings remain (before the *Leucaena* and other tree species shade out the herbaceous vegetation) they will provide excellent insect collecting. Unfortunately, a bamboolike grass (*Arundo donax*) has invaded the sanctuary along the southern and northern margins and appears to be spreading along paths and service roads.

A large stand of *Salix* grows along the margins of the sanctuary's crescent-shaped resaca, and as one moves away from the lower portion of the intermittent pond, there is a narrow row of large *Celtis* and *Sapindus* between the *Salix* and the adjoining cultivated lands. Another row of *Celtis*, *Ulmus*, *Fraxinus*, and herbaceous plants grows along the levee of the Rio Grande, extending about 2 km out from the main portion of the grove. Along the north margin of the resaca, and well above the water table, there is an extensive stand of *Prosopis*, *Condalia*, *Zizyphus*, and *Celtis*.

According to a recent publicity note from the Audubon Society (Line 1978), long range plans call for expansion of the palm grove to its former size, and restoring the native shrubs that were cleared for agriculture. In 1980 the Nature Conservancy conveyed about 900 ha of palm jungle habitat to the U.S. Fish and Wildlife Service for inclusion in a future refuge, the "Boscaje de la Palma" (The Nature Conservancy 1981).

Collecting in the sanctuary has been remarkably productive, yielding over 75 species of Cerambycidae, including several as yet unknown outside the grove area.

16 km west of Boca Chica on Rt. 4, Cameron County

This locality consists of a few acres of open brushland atop a loma, or clay dune, along the highway leading from Brownsville to Boca Chica beach. Dominant plants include *Zizyphus*, *Baccharis*, *Karwinskia*, *Yucca*, *Opuntia*, and *Haplopappus*, with a few scattered *Prosopis* and *Acacia*. A detailed study of the salt-flat-clay-dune coastal lowland area was presented by Johnston (1952). Collecting at this site was particularly

fruitful in the fall, yielding over 20 species of longhorned beetles.

Santa Ana National Wildlife Refuge, 9.7 km south of Alamo, Hidalgo County

Santa Ana National Wildlife Refuge consists of approximately 12,000 noncontiguous hectares of Tamaulipan semideciduous brush and mature forests along the Rio Grande. Significant areas of vegetation were altered during the construction of several artificial intermittent ponds as waterfowl enhancement projects. Fleetwood (1973) presented detailed information regarding plant formations on the refuge. We collected near the refuge headquarters in the 5,200-ha Santa Ana tract, in an overmature *Pithecellobium/Celtis/Ulmus* forest. Most material was attracted to lights placed along the wildlife drive or beaten from slash and downhanging branches along the west margin of Willow Lake.

Bentsen-Rio Grande Valley State Park, 4.8 km west of Mission, Hidalgo County

This 1,440-ha state park contains dense formations of most of the major native plant communities of the Lower Valley, including Tamaulipan semideciduous forest, Tamaulipan interior swamp, riparian hardwood forest, and mature thorn scrub. Portions of the present protected area were substantially altered by human use prior to 1953, and a major section of the resaca bank is maintained as a grass-lawn picnic and camping area.

Collecting techniques included ultraviolet and mercury vapor lights in the camping and picnic areas, beating and sweeping along roads and trails, and searching slash piles at night. Species totals were excellent in 1972 but decreased in successive visits, most notably in light-collected material. Nevertheless, a number of species taken during our survey are known only from the park.

Rob and Bessie Welder Wildlife Foundation Refuge, 11.3 km north of Sinton, San Patricio County

Welder Wildlife Refuge is managed in part as a working cattle ranch and experimental range. According to Box and Chamrad (1966), the property has been grazed for more than a century but has never undergone formal cultivation. There are 16 recognized plant formations on the prop-



FIGURE 3. Male *Oncideres pustulatus* on girdled branch of tepehuaje (*Leucaena pulverulenta*).



FIGURE 4. Male *Lochmaeocles cornuticeps cornuticeps* on tepehuaje. Larval frass may be seen protruding from ruptures in the bark.

erty, most of which are open-range habitats. Communities on arid sites are generally characterized by mixed grasses, cactus, and rangeland shrubs, while on more mesic sites riparian, semi-aquatic, or aquatic plants predominate. Some grassland communities are interspersed with thickets of leguminous trees, and most are bordered by large tracts of almost impenetrable brush.

We conducted most of our collecting in four habitats: the dense hackberry/anaqua and woodland/spiny aster communities at the extreme eastern edge of the refuge; the chaparral/bristlegrass community along the railroad right-of-way south of the main refuge entrance; and the live oak/chaparral community adjacent to the headquarters buildings (community terminology after Box and Chamrad 1966).

Lake Corpus Christi State Park, 8 km southwest of Mathis, San Patricio County

Dominant vegetation formations around Lake Corpus Christi are upland Tamaulipan semideciduous forest and thorn scrub, with minor influences from the more northern Balconian Biotic Province. Scrub communities are characterized by a mixture of *Condalia*, *Zanthoxylum*, *Diospyros*, *Leucophyllum*, and *Yucca*, with scattered invasions of *Prosopis*. Drainages are wooded mainly with *Ulmus*, *Celtus*, and *Ehretia*. Original bottomland communities were inundated when the Nueces River was impounded in the 1930s to form the lake.

Collecting techniques consisted primarily of beating and sweeping roadside vegetation, searching slash piles at night, and light collecting near the park maintenance area.

PHENOLOGY

Adult cerambycid activity in southern Texas is distinctly bimodal, the spring and fall peaks coinciding with seasonal patterns of moderate temperatures and increased precipitation. These activity peaks generally agree with those documented by Fuchs and Harding (1976) for arthropod predators in the Lower Valley. Although a number of species have been collected through the hot summer months, there is a general hiatus in cerambycid activity during July and August. Most summer records are for nocturnal Sonoran species that are apparently better able to tolerate high temperatures and low humidity. We have not seen enough material from the winter months to draw any meaningful conclusions regarding general activity, but it appears that a few species (such as *Placosternus difficilis*, *Eudermes reichei exilis*, and *Anelaphus spurcus*) may be encountered during any month of the year.

Adult activity within peak seasons fluctuates, with both species-abundance and rates of movement generally increasing in response to rises in temperature and humidity. Periods of extended drought may delay adult emergence. Unseasonably cool temperatures tend to suppress activity, especially of nocturnal species. Once emergence has occurred, rainfall has no more than a tran-

sitory effect upon beetle activity, except at night. Light collecting is rarely profitable during or immediately after heavy rainfall, although sudden rises in air temperature (and consequently in ambient humidity and numbers of mosquitoes) can initiate surges of dispersal activity.

During the severe drought in 1980, cerambycids breeding in living host plants (e.g., *Callona* in mesquite, *Mecas* spp. in Compositae) emerged somewhat earlier in spring than normal, while deadwood-feeding species were weeks or months behind normal activity patterns. Examination of a variety of infested wood revealed high rates of larval and pupal mortality of all woodboring insects, and numerous dead adult longhorns were found within their pupal chambers.

The protracted drought of the summer and fall of 1982 had even more severe effects upon collecting, and a half-day's beating in the palm grove yielded only two beetles. Extended dry periods must exert considerable selective pressure upon the insect fauna of the region, affecting the "tropical" species most dramatically.

INTRODUCTION TO SPECIES ACCOUNTS

Distributional ranges in the following accounts were drawn from recent literature and from specimen data. Activity periods for species with widespread distributions outside the study area include dates from other localities only where insufficient data were available from southern Texas.

Cited larval hosts represent rearing records or reliable immature associations from original literature sources. Some host listings cited from Linsley (1962a, b, 1963a, 1964) refer to records of adult collection, and do not represent larval hosts. Host citations that refer to specimen data follow the format of collector and institution abbreviations in the acknowledgments. Uncredited host citations are from our rearings, recorded for the first time herein. We have attempted to update and emend pertinent data citations from older literature, by including discussions of questionable records in the species accounts.

Common collecting localities are abbreviated in text as follows: Audubon Society Palm Grove Sanctuary (PG), 16 km west of Boca Chica (BC), Bentsen-Rio Grande Valley State Park (BRG), Lake Corpus Christi State Park (LCC), Rob and Bessie Welder Wildlife Foundation Refuge

(WWR), Santa Ana National Wildlife Refuge (SAR), Falcon State Park and Falcon Heights (these two localities are contiguous) (FSP). Locality data taken from specimens are cited as given on labels with metric equivalents in brackets following mileages.

The arrangement of species corresponds to Linsley (1962a, b, 1963a, 1964) and Linsley and Chemsak (1976, 1985), except that portion of the subfamily Lamiinae not yet treated in the Linsley monograph series, genera and species of which are ordered according to the *Checklist of Cerambycidae: the Longhorned Beetles* (Chemsak and Linsley 1982). Literature Cited includes all original species descriptions. See the Linsley monograph series for more complete taxonomic references, generic and species keys, species descriptions, and general bionomic information.

SPECIES ACCOUNTS

Parandrinae

Parandra (Archandra) *polita* Say, 1835:192

RANGE.—Central America to Indiana, Ohio, and northern Florida.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Fagus*, *Carya*, *Liriodendron* (Linsley 1962a), *Pinus* (Chemsak et al. 1980).

DISCUSSION.—Snow (1906) recorded collecting this species at Galveston, Galveston County, and Brownsville, Cameron County, and Linsley (1962a, fig. 2) shows a locality near Houston, Harris County. Adults were collected from beneath bark of decaying trunks of the larval hosts and at lights.

Prioninae

Archodontes melanopus serrulatus LeConte, 1854a:82

RANGE.—Southwestern U.S. from Texas to Arizona.

ADULT ACTIVITY.—June to September.

LARVAL HOSTS.—*Populus* spp., *Prosopis* (Linsley 1962a), *Citrus* (Dean 1953).

DISCUSSION.—The nominate subspecies bores within root crowns of living or dying *Quercus* in the southeastern U.S., and oak may also serve as a larval host for *serrulatus* in the oak-savanna habitats of southcoastal Texas. Adults are attracted to lights.

NEW LOCALITIES.—Flour Bluff, Nueces County, 26 September (TAI); Padre Island.

Stenodontes (Orthomallodon) *dasytomus dasytomus* (Say, 1824:326)
(Figure 5)



FIGURE 5. Male (left) and female (right) *Stenodontes* (*Orthomalodon*) *dasytomus dasytomus*.

RANGE.—Southeastern U.S. to eastern Mexico.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Platanus*, *Celtis*, *Quercus*, *Salix*, *Liquidambar*, *Bursera*, *Acer* (Linsley 1962a), *Carya* (Riley 1880), *Citrus* (Dean 1953), *Ulmus*.

DISCUSSION.—Larvae feed in decaying stumps and logs; adult beetles congregate under loose bark, often retreating into their emergence holes during the day. Pupae and teneral adults were taken from heartwood portions of a rotting *Celtis* stump in the Palm Grove Sanctuary, Cameron County, in May. Adults are commonly attracted to lights.

NEW LOCALITIES.—Anzalduas Park, Hidalgo County; SAR; BRG; WWR; LCC.

***Derobrachus geminatus* LeConte, 1853:233**

RANGE.—Southern California to Arizona, Texas, and northern Mexico.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Populus*, *Quercus*, *Prosopis* (Linsley 1962a), *Ulmus*, *Cercidium*, *Morus*, *Citrus* (Moore and Little 1967), *Vitis* (Thomas 1951).

DISCUSSION.—This is an upland species, associated with mesquite and paloverde; the larvae feed upon roots of living trees. Vogt (1949a) collected six males at lights in Rio Grande City, Starr County, in May, and we took specimens at street lights at Falcon State Park in September.

***Prionus* (*Neopolyarthron*) *imbricornis* Linnaeus, 1767a:622**

RANGE.—Atlantic states south to Florida and west to Nebraska and south-central Texas.

ADULT ACTIVITY.—March to September.

LARVAL HOSTS.—*Quercus*, *Castanea*, *Pyrus*, *Vitis*, maize, and

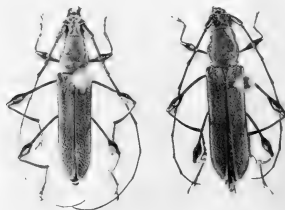


FIGURE 6. Male (left) and female (right) *Rhopalophora laevicollis*.

a wide variety of hardwoods and herbaceous shrubs (Linsley 1962a).

DISCUSSION.—One specimen in the TAI collection is labeled as this species (identification not verified) from Kingsville, Kleberg County. Adults are common at lights throughout the species range.

***Prionus* (*Antennalia*) *fissicornis* Haldeman, 1845:125**

RANGE.—Great Plains east of the Rocky Mountains, from Montana and Minnesota south to Texas.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—Grasses (Linsley 1962a).

DISCUSSION.—Linsley (1962a, fig. 16) showed this species from near Corpus Christi, Nueces County, and we have seen specimens from near Austin, Travis County, collected in early May (RWN).

Cerambycinae

***Smodicum cucujiforme* (Say, 1826:277)**

RANGE.—Eastern North America to Florida and Texas.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Robinia*, *Carya*, *Fagus*, *Celtis*, *Salix*, *Populus* (Linsley 1962b).

DISCUSSION.—Linsley's (1962b) account of this species included material later described as *Smodicum texanum* Knull (1966), and the record of *Salix* as a larval host was probably based upon observations of the latter taxon in the Lower Valley (Linsley and Martin 1933). Characters cited by Knull for separating the two species are difficult to interpret in material from southern

Texas, and it appears that *texanum* differs from *cucujiforme* only by its slightly paler coloration, more lightly pubescent dorsum, and minor differences in antennal proportions. Martins (1975), who examined only two male specimens of *texanum*, suggested that it may be a subspecies of *cucujiforme* but made no formal status change. Because of the difficulty in defining the taxonomic parameters and status of *texanum*, we are considering as *cucujiforme* only a single specimen from WWR (RHT), determined by R. H. Turnbow. All other south Texas specimens of *Smodicum* are referred to *texanum* pending resolution of the status of the two names.

Smodicum texanum Knull, 1966:137

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to June.

LARVAL HOSTS.—*Salix*?

DISCUSSION.—The taxonomic status of this form is uncertain (see *S. cucujiforme*, above), and material from southern Texas cannot be placed with certainty. Adults referred herein to *texanum* were collected at lights in several localities, and other south Texas specimens (presumably *texanum*) were collected from beneath bark of *Salix* (Linsley and Martin 1933) and *Celtis* (Vogt 1949a).

NEW LOCALITIES.—LCC; PG; SAR.

Malacopterus tenellus (Fabricius, 1801:335)

RANGE.—Southern California and the southern Great Basin to Texas, Mexico, and Central and South America.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Salix*, *Populus*, *Celtis* (Linsley 1962b).

DISCUSSION.—In southern Arizona, this species was cut from pupal cells in moist, punky trunks of dead willow (FTH, EFG), and J. E. Wappes beat an adult from *Celtis* foliage in the palm grove. The host record cited from Linsley (1962b) for *Celtis* referred to adults taken beneath bark. We collected specimens at lights in May and again in October.

NEW LOCALITIES.—BRG; Brownsville, Cameron County.

Methia constricticollis Schaeffer, 1908:351

RANGE.—Southeastern Texas to Mexico.

ADULT ACTIVITY.—April, May, and September.

LARVAL HOSTS.—*Celtis* (Turnbow and Wappes 1978), *Zanthoxylum* (Turnbow and Wappes 1981).

DISCUSSION.—Adults were reared from twigs of dead hackberry and colima and have been taken at lights.

NEW LOCALITIES.—BRG; SAR; WWR; FSP.

Styloxus fulleri fulleri (Horn, 1880:138)

RANGE.—South-central Texas.

ADULT ACTIVITY.—July to October.

DISCUSSION.—The larval habits of this subspecies are not recorded, but they are probably similar to those of the subspecies *f. californicus* (Fall) which girdles oak twigs. Vogt (1949a:140) recorded collecting "*Styloxus* sp." from Pharr, Hidalgo County, and stated that it was neither *fulleri* nor *texanus* (now considered a synonym of *fulleri*). Linsley (1962b), perhaps based upon a reassessment of Vogt's material, recorded *fulleri* from Hidalgo County. This beetle is evidently most active during the summer and is uncommon in collections. Adults are attracted to lights.

NEW LOCALITIES.—LCC; SAR; FSP.

Achryson surinamum (Linnaeus, 1767a:632)

RANGE.—Southern California, Baja California to Arizona and Texas, Mexico, Central and South America, and the West Indies.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Aspidosperma*, *Cercidium*, *Ficus*, *Prosopis*, *Acacia*, *Schnopsis*, *Pithecellobium*, *Ulmus*, *Celtis*, *Inga*, *Nectandra*, *Robinia*, *Tamarindus*, *Chlorophora*, *Brya* (Linsley 1962b), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—This species is very abundant on almost any sort of deadwood at night, and adults are readily attracted to lights. The larvae mine extensively within the dry sapwood and heartwood of branches and trunks of dead host plants.

NEW LOCALITIES.—BRG; Anzalduas Park, Hidalgo County; LCC; WWR; SAR.

Geropa concolor (LeConte, 1873:176)

RANGE.—Southern Texas to southern Mexico.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Ulmus*, *Acacia*, *Mimosa* (Linsley 1962b), *Pithecellobium* (Linsley and Martin 1933), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—This nondescript species was abundant on two-year dead *Acacia* trees at Welder refuge in May and October. The larval habits are similar to those of *Achryson surinamum*.

NEW LOCALITIES.—SAR; BRG; BC; LCC; Sinton, San Patricio County; 10 mi (ca. 16 km) E. jct. of Hwy. 4 and 1419, Cameron County (RHT).

Gracilia minuta (Fabricius, 1781:235)

RANGE.—Europe, Africa, introduced into North America.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Salix*, *Quercus*, *Rhamnus*, *Corylus*, *Aesculus*, *Betula*, *Ceratonia*, *Rubus*, *Rosa* (Linsley 1962b), *Citrus* (Manley and French 1976).

DISCUSSION.—This cosmopolitan species is often injurious to wood products. Specimens were reared from *Citrus* in the Lower Valley (Manley and French 1976).

Hypexilis pallida Horn, 1885:173

RANGE.—Southeastern Arizona to western and southern Texas, northern Mexico.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Salix* (Turnbow and Wappes 1981), *Ulmus*? (Hovore et al. 1978).

DISCUSSION.—Specimens were beaten and reared from willow, and beaten from elm. Adults are most commonly collected at lights.

NEW LOCALITIES.—SAR.

Eburia stigmatica Chevrolat, 1834:fasc. 3, no. 60

RANGE.—Southern Texas to central Mexico.

ADULT ACTIVITY.—March to May, October.

LARVAL HOSTS.—*Celtis* (Hovore et al. 1978).

DISCUSSION.—Adults have been collected from beneath loose bark of *Celtis* (Vogt 1949a), *Salix*, and *Acacia* (Linsley and Martin 1933) and reared from dry limbs of sugar hackberry. At night we collected numerous adults from recently felled hackberry and attracted several specimens to lights.

NEW LOCALITIES.—PG; BRG; Anzalduas Park, Hidalgo County; FSP; SAR.

Eburia ovicollis LeConte, 1873:180

RANGE.—Northern Mexico to southern Texas.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Prosopis* (Hovore and Giesbert 1976).

DISCUSSION.—Townsend (1902) collected adults from dead guava and by beating foliage. Linsley and Martin (1933) took a few specimens on ebony, and the senior author (in Hovore and Giesbert 1976) collected an adult male as it emerged from a branch of dead mesquite. Adults are attracted to lights and are most numerous in early summer.

NEW LOCALITIES.—PG; BRG; SAR; Kingsville, Kleberg County; WWR.

Eburia mutica LeConte, 1853:233

RANGE.—Central Texas to northern Mexico.

ADULT ACTIVITY.—April to June, October.

LARVAL HOSTS.—*Celtis* (Hovore et al. 1978), *Citrus* (Dean 1953), *Prosopis*, *Pithecellobium* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982), *Ulmus*.

DISCUSSION.—Previous lists variously recorded this species as *Eburia mutica*, *E. mutica* var. *manca* LeConte, or *E. tumida* LeConte. Adults are abundant on dead limbs of the larval hosts

at night and come to lights. Numerous specimens were taken from the trunk of a wind-thrown hackberry in Bentsen State Park, and pupae and teneral adults were cut from dead branches of that host.

NEW LOCALITIES.—WWR; Sinton, San Patricio County; LCC; PG; SAR; FSP.

Eburia haldemani LeConte, 1850:102

RANGE.—Arizona to the southeastern U.S. and Florida, south to northern Mexico.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Celtis* (Rice et al. 1985).

DISCUSSION.—Numerous adults were attracted to fermenting molasses bait in western and central Texas. The host record of *Celtis* is based upon collections from decayed hackberry in western Texas. Linsley and Martin (1933) took an adult beneath bark of *Salix* near Brownsville, Cameron County, and Vogt (1949a) collected a specimen under bark of *Ulmus*. It is occasionally attracted to lights.

NEW LOCALITIES.—BRG.

Tylonotus bimaculatus Haldeman, 1847:38

RANGE.—Eastern North America, south to Florida, southwest to southern Texas, and west to Arizona.

ADULT ACTIVITY.—May to August.

LARVAL HOSTS.—*Fraxinus*, *Betula*, *Juglans*, *Carya*, *Liriodendron*, *Ulmus*, *Ligustrum* (Linsley 1962b).

DISCUSSION.—A single specimen of this common eastern species was attracted to light in May at Bentsen-Rio Grande Valley State Park, Hidalgo County (FTH). In other parts of the range this species is often abundant on living trees, particularly ash.

Mannophorus laetus LeConte, 1854b:442

RANGE.—Western and southern Texas, northern Mexico.

ADULT ACTIVITY.—May, September to November.

DISCUSSION.—Adults frequent blossoms of Compositae, especially *Helianthus*, *Viguiera*, and *Verbesina*, but the larval host is unknown. It is an upland species, most commonly encountered along roadsides in thornscrub communities.

NEW LOCALITIES.—1.5–2 mi [ca. 2.4–3.2 km] E Sullivan City, Starr County; 6–8.5 [ca. 9.7–13.7 km] and 13–14 mi [ca. 21–22.6 km] E El Sauz, Starr County; Hwy. 755, 2.5 mi [ca. 4 km] NE Jct. 490, Starr County; Sam Fordyce Road, 0.5 mi [ca. 0.8 km] S Hwy. 83, Starr County; 16 mi [ca. 26 km] N, 1 mi [ca. 1.6 km] W Rio Grande City, Starr County.

Taranomis bivittata bivittata (Dupont, 1838:58)

RANGE.—New Mexico and Texas to central Mexico.

ADULT ACTIVITY.—May, July to November.

LARVAL HOSTS.—*Ficus* (Townsend 1902), *Acacia* (Linsley 1940), *Prosopis* (Rogers 1977a), "cosabe" (Duffy 1960), *Ulmus* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—Adults, which are common on new growth of mesquite and on freshly cut *Acacia*, may also be collected from a variety of blossoms, including *Jatropha*, *Eysenhardtia*, *Sphaeralcea*, and *Prosopis*. On some early lists, this species appeared in the genus *Ischnocnemis*.

NEW LOCALITIES.—PG; 1 mi [ca. 1.6 km] SE Los Indios, Cameron County; BRG; SAR; 3 mi [ca. 4.8 km] S Pharr, Hidalgo County; 5.3 mi [ca. 8.5 km] E Rio Grande City, Starr County; Hwy. 281, 1.6 mi [ca. 2.6 km] S 83 BR, Hidalgo County; Hwy. 649, 1–6 mi [ca. 1.6–9.7 km] N Jct. Rt. 83, Starr County; 7 mi [ca. 11.3 km] SW El Sauz, Starr County; WWR; 3–7 mi [ca. 4.8–11.3 km] N Sinton, San Patricio County.

Lophalia cyanicollis (Dupont, 1838:59)

RANGE.—Arizona to Texas and southern Mexico.

ADULT ACTIVITY.—October and November.

DISCUSSION.—This species was abundant in October on foliage and blossoms of a variety of herbaceous and woody plants, including *Verbesina*, *Karwinskia*, and *Baccharis*. Specimens from Mexico (Sinaloa) are more elongate and may represent a different subspecies.

NEW LOCALITIES.—PG; SAR; Pharr, Hidalgo County; Hwy. 4, 6.8–7.2 mi [ca. 11–11.6 km] E Jct. 1419, Cameron County; BC.

Gnaphalodes trachyderoides Thomson, 1860:236

RANGE.—Central America to southern Texas.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Acacia*, *Pithecellobium*, *Prosopis*, *Parkinsonia* (Linsley 1962b), *Celtis* (Hovore and Giesbert 1976), *Citrus* (Manley and French 1976), *Ulmus* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—Adults are very common at night on freshly cut wood, and are readily attracted to lights. Thus far, this species has not been encountered outside the Lower Valley region.

NEW LOCALITIES.—PG; SAR; Hwy. 4, 10 mi [ca. 16 km] E Jct. 1419, Cameron County; Anzalduas Park, Hidalgo County; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; Brownsville, Cameron County.

Stenaspis verticalis insignis Casey, 1924:262

RANGE.—Southcentral Texas to northern Mexico.

ADULT ACTIVITY.—June to November.

DISCUSSION.—Adults of this species, like those of its congener, *S. solitaria* (Say), are strongly attracted to certain plant exudates. Aggregations of beetles, including many mating pairs, were encountered on stems of *Baccharis* in San Patricio County in October. Many of the *Stenaspis*, along with other insects, appeared to be feeding

at oozing lesions created by scarab beetles (*Cotinis mutabilis* Gory and Percheron). Adults were also found on *Baccharis* foliage, and on blossoms and foliage of *Acacia*, *Serjania*, *Clematis*, *Cissus*, *Jatropha*, *Condalia*, and *Haplopappus*. Despite the abundance of adults of this large, red and blue species, the larval habits are unknown.

Specimens from central Texas (Comal County) have very little black coloration on the underside and pronotum and represent the typical subspecies phenotype, while material from further south shows varying degrees of character intermediacy with the nominate form or the western subspecies, *arizonicus* Casey.

NEW LOCALITIES.—6 mi [ca. 9.7 km] E Eagle Pass, Maverick County; PG; BC; 16 mi [ca. 26 km] N, 9 mi [ca. 14.5 km] W Rio Grande City, Starr County; 3–7 mi [ca. 4.8–11.3 km] N Sinton, San Patricio County; WWR.

Stenaspis solitaria (Say, 1824:410)

RANGE.—Southwestern U.S. to south Texas and northern Mexico, Baja California.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Prosopis*, *Acacia* (Linsley 1962b).

DISCUSSION.—Vogt (1949a) encountered this species in the uplands in May and June, and the host record for *Prosopis* (cited above from Linsley) was based upon observations of larvae he tentatively assigned to this genus. Pupae and adults of *S. solitaria* were taken from pupal cells in root crowns of dying *Acacia* in Arizona and western Texas (FTH). Adults frequent foliage and stems of *Acacia*, *Condalia*, and *Baccharis* in the southwestern U.S. and are very abundant on foliage of *Melochia* in the Cape Region of Baja California. Linsley and Cazier (1962) reported this species feeding upon, and apparently becoming intoxicated by, fermenting exudates of *Senecio* in Arizona.

NEW LOCALITIES.—3 mi [ca. 4.8 km] W, 5 mi [ca. 8 km] N Roma, Starr County.

Callona rimosa Buquet, 1840:142

RANGE.—Central Texas to northern Mexico.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Prosopis*, *Acacia* (Vogt 1949a).

DISCUSSION.—Vogt (1949a) discussed the larval habits of this bright metallic green species, commenting that adults were rarely collected except from their pupal chambers in bases of living mesquite and huisache. We took adults from foliage of infested mesquite and from foliage of *Baccharis* and other nonhost shrubs growing amongst the host trees, 2 mi [ca. 3.2 km] S Pharr,

Hidalgo County. We took several specimens in the Palm Grove Sanctuary, including an adventurous specimen beaten from hackberry foliage (RLP).

NEW LOCALITIES.—La Gloria, Starr County; Kingsville, Kleberg County; WWR.

Knulliana cincta cincta (Drury, 1773:85)

RANGE.—Eastern North America to western Texas, south to northern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Juglans*, *Carya*, *Castanea*, *Quercus*, *Celtis*, *Pyrus*, *Sapindus*, *Salix* (Linsley 1962b), *Prosopis* (Hovore and Giesbert 1976), *Citrus* (Dean 1953), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—This widespread species was abundant at night on limbs and trunks of newly felled hackberry, huisache, and tepehuaje in May and October. Adults are occasionally attracted to lights.

NEW LOCALITIES.—PG; SAR; BRG; Rio Grande City, Starr County; FSP; LCC; WWR.

Tragidion coquus (Linnaeus, 1758:393)

RANGE.—Eastern North America to Arizona, western and southern Texas.

ADULT ACTIVITY.—August to November.

LARVAL HOSTS.—*Quercus* (Linsley 1962b), *Prosopis* (Swenson, 1969).

DISCUSSION.—A single male of this variably colored species was collected on blossoms of *Haplophragma* 6 mi [ca. 9.7 km] E Eagle Pass, Maverick County, in October (FTH).

Batyle suturalis cylindrella Casey, 1893:587

RANGE.—Western and southern Texas.

ADULT ACTIVITY.—May to July.

DISCUSSION.—Adults of this entirely red subspecies were taken on *Opuntia* and *Helianthus* blossoms 2 mi [ca. 3.2 km] S Pharr, Hidalgo County in May, and it is common on roadside flowers throughout the upland portions of southern Texas.

NEW LOCALITIES.—PG; BRG; 1–5 mi [ca. 1.6–8.1 km] N of the Jct. of Hwy. 35 on Hwy. 83, Webb County; 3 mi [ca. 4.8 km] N Sarita, Kenedy County.

Plionoma suturalis (LeConte, 1858a:25)

RANGE.—Southern California and northern Baja California to Texas and northern Mexico.

ADULT ACTIVITY.—May to July, September to November.

LARVAL HOSTS.—*Prosopis* (Linsley 1962b).

DISCUSSION.—This species was encountered in the fall on fresh-cut mesquite and huisache, and in early summer on blossoms of leguminous trees.

Some earlier lists recorded this species in the genus *Sphaenothecus*.

NEW LOCALITIES.—Brownsville and Los Indios, Cameron County; LCC.

Tylosis oculatus LeConte, 1850:9

RANGE.—Western and southern Texas to southern Mexico.

ADULT ACTIVITY.—September to November.

LARVAL HOSTS.—*Abutilon*?

DISCUSSION.—As is typical of the genus *Tylosis*, adults frequent blossoms and foliage of malvaceous plants. Vogt (1949a) collected a small series of adults from roadside and canalbank stands of *Abutilon*, and we found these insects to be very abundant on a tall, red-flowered mallow in the Lower Valley. In the uplands, near Eagle Pass, we found large numbers of adults on a yellow-flowered, prostrate species of mallow. Larvae of *Tylosis jiminezii* Casey bore within roots of dead mallow (*Sphaeralcea* sp.) in western Texas (FTH, RLP), and the habits of *T. oculatus* are probably similar.

NEW LOCALITIES.—PG; SAR; BRG; Mission, Hidalgo County; 10 mi [ca. 16 km] SE Los Indios, Cameron County; BC; Sarita, Kenedy County (TAI); Kingsville, Kleberg County; 6 mi [ca. 9.7 km] E Eagle Pass, Maverick County.

Crossidius humeralis quadrivittatus Penrose, 1974:251

RANGE.—Southern Texas.

ADULT ACTIVITY.—September to November.

LARVAL HOSTS.—*Haplophragma* (sometimes listed as *Isocoma*) (Hovore and Giesbert 1976).

DISCUSSION.—This subspecies is widespread and abundant on blossoms of its larval host in October. Collections were made at a number of localities along the coastal strand from San Patricio County south into Cameron County. A series from 6 mi [ca. 9.7 km] E Eagle Pass, Maverick County suggests that vitate populations of *humeralis* may be distributed with the larval host in suitable habitats throughout southern Texas.

NEW LOCALITIES.—10–14 mi [ca. 16–22.6 km] W Boca Chica, Cameron County; Arroyo City, Willacy County; Riviera Beach, Kleberg County; Kingsville, Kleberg County; WWR; Laguna Salada, Brooks County.

Crossidius suturalis melanipennis Penrose in Giesbert and Penrose, 1984:62

RANGE.—Coastal portions of southern Texas to extreme northern Mexico.

ADULT ACTIVITY.—October to December.

LARVAL HOSTS.—*Haplophragma drummondii*.

DISCUSSION.—This highly melanic *suturalis* phenotype occurs with *C. humeralis quadrivittatus* in coastal habitats, where both may use the same species of host plant (*Haplophragma drum-*

mondi [T & G Greene]). Although the two species are microsympatric, they appear to be largely allochronic, peak numbers of *C. suturalis melanipennis* occur in November, when *C. humeralis quadrivittatus* activity wanes. Similar temporal stratification between the nominate forms of both species was observed in southeastern New Mexico (RLP).

NEW LOCALITIES.—Riviera Beach and Kingsville, Kleberg County; Laguna Salada, Brooks County.

Crossidius pulchellus LeConte, 1861:356

RANGE.—Alberta, Canada southward through the Great Plains to western Kansas, southern California, southern Texas, and northern Mexico.

ADULT ACTIVITY.—August to November.

LARVAL HOSTS.—*Gutierrezia* spp. (Linsley and Chemsak 1961), *Gymnosperma* (also listed as *Xanthocephalum*).

DISCUSSION.—A small series of a highly melanic population was collected in October from blossoms of *Gymnosperma glutinosa* (Spreng.) Less., 8 mi [ca. 13 km] SE Beeville, Bee County (RLP, FTH).

Elytroleptus divinus (LeConte, 1884:23)

RANGE.—North-central to southern Texas.

ADULT ACTIVITY.—April to July.

DISCUSSION.—Vogt (1949a) collected adults from blossoms and foliage of *Karwinskia* and *Condalia* in the upland regions of Hidalgo and Starr counties in April and May, and we have likewise found it to be relatively common on those plants. Larval habits of the genus *Elytroleptus* are unrecorded.

NEW LOCALITIES.—1 mi [ca. 1.6 km] and 3 mi [ca. 4.8 km] W Roma, Starr County; 3 mi [ca. 4.8 km] N Laredo, Webb County (AEL); 45–55 mi [ca. 73–89 km] E Carrizo Springs, Hwy. 83, in Webb County (AEL).

Parevander hovorei Giesbert in Giesbert and Penrose, 1984:59

RANGE.—Southern Texas to central Mexico.

ADULT ACTIVITY.—September to December.

DISCUSSION.—This orange and black species was previously recorded from southern Texas as *P. xanthomelas* (Guerin) (Hovore and Giesbert 1976). Earlier faunal accounts did not include this species, and it may be that it has only recently colonized, or recolonized, southern Texas.

Austin (1880:60) in his North American checklist stated, "... add *Evander* Thoms. 9730 *xanthomelas* (Guer.)," but Leng (1886) later stated that "*Evander*" had not been found within our faunal limits, and he dropped it from his checklist. (The name *Evander* was incorrectly ap-

plied to New World species and was later replaced by *Parevander aurivillius*).

Parevander is a Neotropical genus, with closely related species distributed into Central America; the adults are associated with disturbed-land plants (larval hosts are unknown). It therefore may be sensitive to long- or short-term environmental phenomena, experiencing population fluctuations or extinctions during droughts or frosts.

Parevander hovorei was taken in abundance in several previously well collected localities, often with *Mannophorus laetus*, from several members of the Compositae, including *Viguiera*, *Helianthus*, and *Verbesina*.

Trachyderes (Dendrobias) mandibularis (Audinet-Serville, 1834:42)

RANGE.—Southern Texas and northern Mexico.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Celtis* (Hovore and Giesbert 1976), *Leucaena* (Hovore and Penrose 1982), *Pithecellobium*, *Ulmus*, *Acacia*

DISCUSSION.—This species is extremely abundant throughout southern Texas, frequenting a variety of blossoms, utilizing numerous types of freshly cut wood for mating and ovipositing activities, and often aggregating in large numbers on stems of *Baccharis*.

Specimens from the study area are assignable to the subspecies *virens* Casey, although not all material at hand matches the phenotype characterization given by Linsley (1962b). As he noted, south Texas specimens vary considerably in coloration; some individuals exhibit an expanded elytral pattern similar to that of the nominate subspecies. In our field-collected and reared specimens about 70% of the males show the typical reduced elytral pattern, while the remainder of the males and all the females have a greatly expanded elytral pattern, with the basal and median dark fasciae broadly united along the lateral margins. Thus there are two distinct patterns, each different from that of any other population seen, with a few individuals resembling the lightly marked males of the nominate taxon. Further, all of our specimens have the third antennal segment wholly black (it is yellow-annulated in typical *mandibularis* Audinet-Serville from western Texas and southeastern Arizona, and in *m. reductus* Casey, from the lower Colorado River Valley of Arizona and California), and there is distinctive allometric reduction of the develop-

ment of the male mandibles. The largest male *virens* (26 mm long) have mandibles approximately 30% smaller than those of comparably sized *mandibularis* from southeastern Arizona and Mexico and nearly 40% smaller than those of similarly sized *reductus*.

Both *virens* and *reductus* appear to represent distinctive local phenotypes, but a study of overall species variability, including analysis of Mexican and Baja Californian material, is needed to resolve their taxonomic status. Chemsak and Linsley (1975a, 1982) list *reductus* and *virens* as synonyms of *mandibularis*, but J. A. Chemsak (pers. comm.) informed us that these were typographical errors, not synonymies. Hüdelpohl (1985) placed *Dendrobias* as a subgenus of *Trachyderes* Dalman, and eliminated all subspecies of *mandibularis*.

NEW LOCALITIES.—PG; BC; BRG; Pharr and Mission, Hidalgo County; LCC; WWR; 3–7 mi [ca. 4.8–11.3 km] N Sinton, San Patricio County.

***Lissonotus flavocinctus puncticollis* Bates, 1885:333**

RANGE.—Northern Mexico and Baja California to southern Texas.

ADULT ACTIVITY.—April to November.

LARVAL HOSTS.—*Acacia* (Vogt 1949a), *Leucaena* (JEW).

DISCUSSION.—Vogt (1949a) collected this species from goldenrod blossoms and on freshly cut *Acacia*, and J. E. Wappes reared these insects from tepehuaje collected in the Palm Grove Sanctuary. Adults have also been taken at light (AEL) and in pitfall traps in a cotton field (Huffman and Harding 1980). As with *Dendrobias* (discussed above), the described subspecies of *Lissonotus flavocinctus* are difficult to define geographically, and further study of Mexican populations is needed to clarify the relationships of the various phenotypes.

NEW LOCALITIES.—Pharr, Mercedes, and Mission, Hidalgo County.

***Psyrassa texana* Schaeffer, 1905b:160**

RANGE.—Southern Texas.

ADULT ACTIVITY.—May to August.

DISCUSSION.—Linsley and Martin (1933) beat adults from *Acacia* and attracted them to lights. Several specimens were beaten from *Celtis* (FTH) and *Fraxinus* (JEW) in the palm grove. *Psyrassa texana* is very close to, if not synonymous with, the Mexican species *P. castanea* Bates.

NEW LOCALITIES.—LCC.

***Psyrassa pertenuis* (Casey, 1924:248)**

RANGE.—Eastern North America from New York to Florida, west to southern Texas.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Magnolia*, *Prunus*, *Carya* (Linsley 1963a).

DISCUSSION.—Numerous specimens of this common Austroriparian species were collected at lights at Welder Wildlife Refuge in May.

***Psyrassa brevicornis* Linsley, 1934:164**

RANGE.—Lower Rio Grande valley and lower Gulf Coast to Kleberg County.

ADULT ACTIVITY.—May to September.

DISCUSSION.—Linsley (1963a) stated that adults were captured on dead branches of *Acacia* and *Pithecellobium*, and numerous specimens were taken at lights.

NEW LOCALITIES.—BRG; PG; SAR; FSP; Kingsville, Kleberg County (TAI).

***Psyrassa sallaei* Bates, 1885:255**

RANGE.—Southern Texas to north-central Mexico.

ADULT ACTIVITY.—September to October.

DISCUSSION.—The original description of this species is rather general, and may be applied to a number of Mexican species of *Psyrassa*, some of which are as yet undescribed. We therefore refer south Texan material to *sallaei* by comparison with determinations by Linsley (1963a) and Vogt (1949a, determined by Linsley). Texas specimens were taken at light (JEW) and by beating *Sapindus* (Vogt 1949a) and *Cordia* (Turnbow and Wappes 1978).

NEW LOCALITIES.—PG.

***Stenosphenus notatus* (Olivier, 1795:61)**

RANGE.—Eastern North America to southern Texas.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Carya*, *Celtis* (Linsley 1963a).

DISCUSSION.—J. E. Wappes reared a single specimen of this Alleghenian species from wood of an unidentified legume from Santa Ana Refuge.

***Stenosphenus lugens* LeConte, 1862:41**

RANGE.—Southern Texas to Mexico.

ADULT ACTIVITY.—August to November.

LARVAL HOSTS.—*Acacia* (Linsley 1963a), *Celtis* (Turnbow and Wappes 1978), *Leucaena* (Vogt 1949a; Hovore and Penrose 1982), *Zanthoxylum*.

DISCUSSION.—Although rare in collections, adults of this species were extremely abundant on dead branches of their hosts and on blossoms

and foliage of *Baccharis*, *Serjania*, *Cissus*, and *Clematis*.

NEW LOCALITIES.—PG; BC; BRG; SAR.

***Stenosphenus dolosus* Horn, 1885:179**

RANGE.—Central and southern Texas.

ADULT ACTIVITY.—April to June, September to November.

LARVAL HOSTS.—*Prosopis*, *Acacia* (Linsley 1963a), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—This beetle is relatively abundant in both spring and fall on blossoms and stems of *Helianthus* (Linsley and Martin 1933), *Solidago* and *Baccharis* (Vogt 1949a), *Aster*, and *Cissus*. Snow's record (1906) for *S. novatus* Horn (a Baja Californian species) may almost certainly be referred to this species.

NEW LOCALITIES: PG; BRG; Rio Grande City, Starr County; 1.4 mi [ca. 2.3 km] SE Carrizo Springs, Dimmit County; 1.8 mi [ca. 3 km] ESE Eagle Pass, Maverick County; Pharr, Hidalgo County; 25 mi [ca. 40 km] S Sarita, Kenedy County; Kingsville, Kleberg County; WWR.

***Aneflus sonoranus* Casey, 1924:241**

RANGE.—Southern California to Sonora, Mexico, and southern Texas.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Acacia* (WHT).

DISCUSSION.—Vogt (1949a) collected a single adult in June from decadent *Condalia* in Starr County, and R. H. Turnbow took specimens at lights in Bentsen State Park, Hidalgo County, and in Zapata County. W. H. Tyson (pers. comm.) stated that larvae bore within living branches and trunks of catclaw acacia.

NEW LOCALITIES.—FSP.

***Aneflus prolixus insoletus* Chemsak and Linsley, 1963:88**

RANGE.—Southern Texas to east-central Mexico.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Acacia* (Rice et al. 1985).

DISCUSSION.—Turnbow and Wappes (1978) recorded collecting adults at lights and from slash piles in September. The larvae breed in living roots and stem bases of *Acacia berlandieri* (Rice et al. 1985).

***Aneflus protensus protensus* (LeConte, 1858b:82)**

RANGE.—Southeastern Arizona to Baja California, northern Mexico and southern Texas.

ADULT ACTIVITY.—June to September.

LARVAL HOSTS.—*Prosopis* (Linsley 1963a).

DISCUSSION.—Vogt (1949a) collected adults from dead mesquite branches in Starr County in

June and July. In Arizona this species is commonly attracted to lights.

NEW LOCALITIES.—FSP.

***Aneflomorpha tenuis* (LeConte, 1854a:81)**

RANGES.—Southwestern Texas to northern Mexico.

ADULT ACTIVITY.—May to September.

DISCUSSION.—Adults have been taken on *Acacia* (Linsley and Martin 1933), on blossoms of *Karwinskia* (Turnbow and Wappes 1981), and at lights.

NEW LOCALITIES.—FSP; BRG; LCC; WWR; SAR.

***Aneflomorpha seminuda* Casey, 1912:294**

RANGE.—Western to southern Texas.

ADULT ACTIVITY.—April to July.

DISCUSSION.—This nocturnal longhorn, which is not uncommon at lights in western Texas, was recently recorded from the Lower Valley region (Turnbow and Wappes 1978).

NEW LOCALITIES.—BRG (AEL).

***Aneflomorpha opacicornis* Linsley, 1957b:285**

RANGE.—Western to southern Texas.

ADULT ACTIVITY.—July to September.

DISCUSSION.—Specimens tentatively assigned to this species were collected at lights in Falcon Heights, Zapata County, in September (RHT, JEW).

***Axestinus obscurus* LeConte, 1873:177**

RANGE.—Southeastern Arizona to western and southern Texas and northern Mexico.

ADULT ACTIVITY.—May to July.

DISCUSSION.—Although we have not seen any south Texas specimens of this Sonoran elaphidiine, we include it herein by the type locality: "Rio Grande Valley?" (fide Linsley 1963a). Adults are common at lights in western Texas, southern New Mexico, and southeastern Arizona, but larval habits are unknown. Specimens in the University of California, Berkeley, collection are from "La Gloria, south of Monclova," Coahuila, Mexico, approximately 200 km southwest of Laredo, Webb County.

***Sphaerion exutum* (Newman, 1841:93)**

RANGE.—Argentina and Brazil to southern Mexico and southern Texas (based upon records from Blackwelder [1946] and Linsley [1961a]).

ADULT ACTIVITY.—May.

DISCUSSION.—This tropical species was first recorded from the U.S. on the basis of eight specimens collected on dead ebony at Bentsen-Rio

Grande Valley State Park in May, 1972 and May, 1973 (Giesbert and Hovore 1976). An additional male specimen was taken at that locality on dead *Acacia* in May, 1980 (FTH).

***Enaphalodes hispicornis* (Linnaeus, 1767a:634)**

RANGE.—North America from California to Idaho, Minnesota, New Jersey, Florida, Texas, and extreme northern Mexico.

ADULT ACTIVITY.—June to October.

LARVAL HOSTS.—*Quercus* (Linsley 1963a).

DISCUSSION.—Linsley (1963a, fig. 23) showed a locality for this widely distributed species near Corpus Christi, Nueces County. The larval host, oak, occurs in dense formations on the sand-sheets of Kleberg County and sporadically over much of the northern portion of the study area.

***Enaphalodes taeniatus* (LeConte, 1854a:81)**

RANGE.—Central to southern Texas and extreme northern Mexico.

ADULT ACTIVITY.—April to September.

LARVAL HOSTS.—*Citrus* (Dean 1953).

DISCUSSION.—This attractive beetle is never particularly common; a few specimens have been taken under loose bark of willow (Linsley and Martin 1933) and at lights.

NEW LOCALITIES.—PG; BRG; SAR.

***Enaphalodes rufulus* (Haldeman, 1847:32)**

RANGE.—Eastern North America from Canada to Florida, western and southern Texas.

ADULT ACTIVITY.—June to August.

LARVAL HOSTS.—*Quercus*, *Acer* (Linsley 1963a).

DISCUSSION.—Several specimens of *E. rufulus*, the red oak borer, were taken at lights at Welder Wildlife Refuge, and we observed evidence of heavy infestation in oak near the refuge headquarters. The southern limits of *E. rufulus* in Texas probably correspond to those of the primary host, oak.

***Enaphalodes atomarius* (Drury, 1773:93)**

RANGE.—Eastern North America from Canada to Florida, west to Texas, Arizona, and Central America.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Quercus*, *Castanea*, *Celtis*, *Juglans*, *Carya*, *Chamaerops* (Linsley 1963a).

DISCUSSION.—We have not seen any specimens from the study area, but Linsley (1963a, fig. 26) showed the species as occurring in the Lower Valley, and Townsend (1902) reported taking a specimen in a mail sack from Alice, Jim Wells County. Chemsak et al. (1980) recently recorded specimens from Honduras, and there

is a specimen in the TAI collection (determination not verified) of either this species or its cryptic sibling, *E. cortiphagus* (Craighead), from Welder Wildlife Refuge.

***Eustromula validum* (LeConte, 1858b:82)**

RANGE.—Southern California to southern Texas, northern Mexico and Baja California.

ADULT ACTIVITY.—May to August.

LARVAL HOSTS.—*Prosopis*, *Cercidium*, *Parkinsonia* (Linsley 1963a), *Salix* (Hovore and Giesbert 1976).

DISCUSSION.—This nondescript species is commonly attracted to lights in the desert regions of the American southwest. Vogt (1949a) took a single specimen at a light in Starr County in May.

***Elaphidion linsleyi* Knull, 1960:7**

RANGE.—Western to southern Texas.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Salix* (Turnbow and Wappes 1981), *Baccharis*, *Ungnadia* (Rice et al. 1985).

DISCUSSION.—The presence of a somewhat intermediate condition in the development of the femoral spines in southern Texas material, particularly female specimens, suggests that this taxon may only be a western subspecies of the widespread *E. mucronatum* (Say). In the south Texas hypodigm, femoral spines range from short and rounded to prolonged and acute, but they are never as pronounced as in typical *mucronatum*. It has also been suggested (Turnbow and Wappes 1981, based upon analysis of two separate reared series of specimens displaying intergrading characters) that *linsleyi* may be hybridizing with *E. mimeticum* on *Salix* in the Brownsville (Cameron County) area.

Vogt's (1949a) record of *Elaphidionoides incertus* from willow may be based in part upon specimens of this species, or "*linsleyi* × *mimeticum*" hybrids. Larvae, pupae, and adults of *E. linsleyi* were cut from injured *Baccharis* near Del Rio, Val Verde County (FTH, RLP).

***Elaphidion mimeticum* Schaeffer, 1905a:132**

RANGE.—Southern Texas and extreme northeastern Mexico.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Salix*.

DISCUSSION.—Adults of this species hide during the day beneath loose bark of willow, acacia, hackberry, and ash (Linsley and Martin 1933) and may be found at night on dead host trees. They have also been taken in molasses bait and have been attracted to lights. *Elaphidion mimeticum* was recorded on some earlier lists as

the very similar-appearing *E. irroratum* Linnaeus, an Antillean species.

NEW LOCALITIES.—PG; BRG; FSP; WWR; SAR.

***Elaphidionoides villosus* (Fabricius, 1792:302)**

RANGE.—Eastern North America to Texas and Arizona.

ADULT ACTIVITY.—March to July.

LARVAL HOSTS.—*Quercus*, *Carya*, *Castanea*, *Prunus*, *Vitis*, *Abies*, *Malus*, *Tilia*, *Wisteria*, *Cladrastis*, *Gleditsia*, *Celtis*, *Acer*, *Juglans*, among others (Linsley 1963a), *Citrus* (Dean 1953).

DISCUSSION.—This is a common eastern species, utilizing a broad variety of larval hosts. Recent rearings from Rio Grande valley *Citrus* provide the only known southern Texas records, and we have not been able to verify the determination.

***Elaphidionoides incertus* (Newman, 1840:28)**

RANGE.—Eastern North America to southern Texas.

ADULT ACTIVITY.—May to September.

LARVAL HOSTS.—*Morus*, *Quercus*, *Carya* (Linsley 1963a).

DISCUSSION.—Vogt (1949a) recorded the capture of two specimens from beneath bark of willow (see discussion of *E. linsleyi*, above), and we took a few adults, including a mating pair, from dead *Celtis* at night in Bentsen State Park and Santa Ana Refuge. Adults are attracted to lights and fermenting molasses baits.

NEW LOCALITIES.—PG; WWR.

***Elaphidionoides aspersus* (Haldeman, 1847:32)**

RANGE.—Atlantic states to Iowa and Texas.

ADULT ACTIVITY.—May to August.

LARVAL HOSTS.—*Carya*, *Quercus* (Linsley 1963a).

DISCUSSION.—There appear to be more than two species involved in the material examined in the *incertus-aspersus* species complex, and determinations of specimens listed herein follow the concepts of Linsley (1963a). Verified records include a specimen from Brownsville, Cameron County (RWN) and another from Kingsville, Kleberg County (TAI).

***Anelaphus niveivestitus* (Schaeffer, 1905a:132)**

RANGE.—Southern Texas.

ADULT ACTIVITY.—April to July.

DISCUSSION.—This diminutive species is commonly attracted to lights, and has been beaten from branches of ash (Linsley and Martin 1933), hackberry, and tepehuaje. R. H. Turnbow took specimens in fermenting molasses bait in the Palm Grove Sanctuary.

NEW LOCALITIES.—BRG; WWR.

***Anelaphus debilis* (LeConte, 1854b:442)**

RANGE.—Central Texas to northeastern Mexico.

ADULT ACTIVITY.—March to June, October.

LARVAL HOSTS.—*Prosopis* (Hovore and Giesbert 1976), *Baccharis*, *Pithecellobium*, *Celtis* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982), *Acacia*.

DISCUSSION.—Adults of this species were commonly collected at lights, at fermenting molasses bait (RHT), and by beating dead branches of larval hosts. Linsley and Martin's (1933) record of "*Anoplium truncatum* LeConte," and Vogt's (1949a) "*Anelaphus truncatus* (Hald)" probably referred to *A. debilis*, *A. spurcus*, or *A. inermis*. All three are similar in coloration and form and were consistently misidentified in material examined during this study.

NEW LOCALITIES.—FSP; Rio Grande City, Starr County; 6–7 mi [ca. 9.7–11.3 km] NE Roma, Starr County; Zapata, Zapata County; PG; LCC; WWR.

***Anelaphus spurcus* (LeConte, 1854b:442)**

RANGE.—Central Texas to northeastern Mexico.

ADULT ACTIVITY.—April to June.

DISCUSSION.—Adults were attracted to lights in spring and early summer and were taken from beneath loose bark of dead ebony and tepehuaje.

NEW LOCALITIES.—PG; SAR; BRG; Zapata and Lopeño, Zapata County; LCC; WWR.

***Anelaphus inermis* (Newman, 1840:29)**

RANGE.—Southeastern U.S. to Texas, West Indies, and Mexico.

ADULT ACTIVITY.—April to June, September to November.

LARVAL HOSTS.—*Citrus*, *Quercus*, *Carya*, *Ichyomethia* (Linsley 1963a).

DISCUSSION.—This widespread species was collected at lights and by beating freshly fallen *Yucca* trunks in Starr County in May. Hubbard (1885) and Manley and French (1976) reported rearing adults from *Citrus*. Specimens from the Antillean faunal region differ slightly from Texan and Mexican specimens and may prove to be a separate subspecies.

NEW LOCALITIES.—3 mi [ca. 4.8 km] W, 5 mi [ca. 8 km] N Roma, Starr County; PG; BRG; LCC; WWR; FSP.

***Anelaphus moestus moestus* (LeConte, 1854b:442)**

RANGE.—Western Arizona to Texas and northern Mexico.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Juglans* (Linsley 1963a), *Quercus* (Hovore and Giesbert 1976), *Celtis* (Turnbow and Wappes 1978), *Rhus* (Rice et al. 1985).

DISCUSSION.—This beetle is abundant throughout its range, commonly coming to lights and fermenting molasses bait. Vogt (1949a) took

adults beneath *Celtis* bark and on fire-killed *Opuntia*.

NEW LOCALITIES.—PG: BRG; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; FSP.

***Elaphidionopsis fasciatipennis* Linsley, 1936:467**

RANGE.—Western and southern Texas to northern Mexico.

ADULT ACTIVITY.—May to September.

DISCUSSION.—This attractive species is very rare in collections; the few specimens we saw were collected at lights in western Texas. A single specimen was attracted to building lights at Falcon Heights, Zapata County, in September (RHT).

***Heterachthes ebenus* Newman, 1840:9**

RANGE.—Eastern portions of North and South America; Mexico; West Indies.

ADULT ACTIVITY.—January to August.

LARVAL HOSTS.—*Pinus* (Craighead 1923).

DISCUSSION.—If the larval association with *Pinus* is valid, then other plants must also serve as hosts, since pines are not found over most of the range of this species. Two specimens were taken at Welder Wildlife Refuge, one from dead huisache in May (FTH) and one in a UV light trap in August (RHT).

***Heterachthes nobilis* LeConte, 1862:41**

RANGE.—Southern Texas.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Prosopis* (Linsley 1963a; Hovore and Giesbert 1976).

DISCUSSION.—Adults are not common in collections, most specimens having been taken at lights or on decadent mesquite. A few adults were reared from fire-killed branches of this host.

NEW LOCALITIES.—BRG; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; Rio Grande City, Starr County; SAR; WWR.

***Neocompsa exclamationis* (Thomson, 1860:201)**

RANGE.—Southern Texas to Chiapas, Mexico.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Mimosa* (Craighead 1923), *Leucaena* (Hovore and Penrose 1982), *Zanthoxylum*.

DISCUSSION.—This large ibidionine has been taken during the day from rotten branch stubs of *Acacia*, *Mimosa*, and *Celtis* (Linsley and Martin 1933), from beneath loose bark, and on slash of colima and ebony. Adults were common at lights in the palm grove and were also found at night on tepehuaje blossoms.

NEW LOCALITIES.—BRG; Anzalduas Park, Hidalgo County.

***Neocompsa mexicana* (Thomson, 1865:573)**

RANGE.—Southern Texas to Guatemala and Costa Rica.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Acacia* (Craighead 1923), *Pithecellobium* (Linsley 1963a), *Celtis* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982), *Zanthoxylum*.

DISCUSSION.—This species appeared on previous lists as "*Ibidion townsendi* Linell," and was also once referred to as *Neocompsa hippopsioides* (Bates) (Martins and Chemsak 1966); both names are now considered synonyms of *N. mexicana*. Large numbers of adults were reared and taken from dead tepehuaje branches in the palm grove.

NEW LOCALITIES.—BRG; SAR.

***Neocompsa intricata* Martins, 1970:1088**

RANGE.—Eastern Mexico to southern Texas.

ADULT ACTIVITY.—May to October.

DISCUSSION.—This species was previously collected in Texas, but earlier material was recorded as either "*Compsa textilis* var. *alacris* Bates" (Linsley and Martin 1933), or "*Compsa alacris*" (Linsley 1963a). According to Martins (1970), *Neocompsa alacris* (Bates) is distributed primarily along the Pacific slope of Mexico and Central America, and the occurrence of this species in Texas is very doubtful. Linsley (1963a) recorded "*Compsa quadriplagiata* (LeConte)" (= *Neocompsa*) from southern Texas, based upon the type locality (Brownsville, Cameron County) of a junior synonym, *Ibidion pubescens* Casey. Martins considered the Casey holotype to be mislabelled, and extant distributional data for *Neocompsa quadriplagiata* restricts it to Baja California Sur and the Pacific slope of Mexico.

Single specimens of *N. intricata* were beaten from *Baccharis* (RLP) and taken from herbaceous foliage (JEW) in October.

NEW LOCALITIES.—BC; WWR.

***Neocompsa puncticollis orientalis* Martins and Chemsak, 1966:466**

RANGE.—Southern Texas to Oaxaca, Mexico.

ADULT ACTIVITY.—May to August.

DISCUSSION.—Vogt (1949a) collected a single specimen, tentatively referred to this subspecies by Martins (1970), at lights in Pharr, Hidalgo County, in August.

***Piezocera serraticollis* Linell, 1896:394**

RANGE.—Southern Texas, and perhaps also southern Mexico to Panama.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Celtis* (Turnbow and Wappes, 1978).

DISCUSSION.—Specimens of this peculiar beetle were beaten from dead branches of *Celtis*, *Pithecellobium*, and *Prosopis*. Martins (1976) suggested that *serraticollis* and *P. monochroa* Bates may be conspecific; due to insufficient material, Martins retained the two taxa as distinct, tentatively assigning several specimens from Mexico and Central America to *serraticollis*.

NEW LOCALITIES.—PG; BRG.

Obrium rufulum Gahan, 1908:142

RANGE.—Eastern North America to Texas.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Fraxinus* (Linsley, 1963a).

DISCUSSION.—This Alleghenian species is known from the study area by material from Kingsville, Kleberg County, collected in April (TAI).

Obrium maculatum (Olivier, 1795:32, 39)

RANGE.—North America from eastern Canada to Florida and southern California, south to Costa Rica.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Carya*, *Quercus*, *Castanea*, *Celtis*, *Morus*, *Machura*, *Cercis*, *Acacia* (Linsley 1963a), *Ficus* (Townsend 1902), *Citrus* (Manley and French 1976), *Leucaena* (Vogt 1949a; Hovore and Penrose 1982), *Sapindus* (Vogt 1949a).

DISCUSSION.—Adults are abundant on dead twigs and branches of the larval hosts, and are also readily attracted to lights.

NEW LOCALITIES.—PG; 8 mi [ca. 13 km] SE Zapata, Zapata County; BRG; FSP; LCC; WWR.

Obrium mozinnae Linell, 1896:395

RANGE.—Southern Texas to Tamaulipas, Mexico.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Leucaena* (Hovore et al. 1978), *Prosopis* (Turnbow and Wappes 1978).

DISCUSSION.—This tiny, bicolored species is often abundant on blossoms of leguminous trees and shrubs and is also attracted to lights.

NEW LOCALITIES.—PG; BRG; Anzalduas Park, Hidalgo County; SAR; La Lomita Park, Hidalgo County; Southmost sector, Brownsville, Cameron County.

Nathriobrium methioides Hovore, 1980:116

RANGE.—Southern Texas.

ADULT ACTIVITY.—November to January.

LARVAL HOSTS.—*Pithecellobium* (Hovore 1980), *Diospyros* (Turnbow and Wappes 1981), *Zanthoxylum* (Rice et al. 1985).

DISCUSSION.—This unusual, monotypic genus appears most closely related to genera from southern South America. The few known specimens, all reared, emerged from ebony, Texas persimmon, and colima. Turnbow and Wappes

(1981) described and figured the larval workings in persimmon.

NEW LOCALITIES.—PG.

Plinthocoelium suaveolens plicatum (LeConte, 1853:233)

RANGE.—Central Texas to Arizona and northern Mexico.

ADULT ACTIVITY.—May to August.

LARVAL HOSTS.—*Bumelia* (Linsley 1964).

DISCUSSION.—R. H. Turnbow (pers. comm.) reported the collection of a single specimen in a light trap at Welder Wildlife Refuge in August. This is the only light collection record we have seen for the species, but some tropical Calli-chromatini readily come to UV lights. Adults were collected from foliage of the larval host in fermenting baits.

Plinthocoelium schwarzi (Fisher, 1914:97)

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to May.

DISCUSSION.—This metallic green species fades postmortem to deep cobalt blue. Adults frequent blossoms of *Condalia* and *Cissus* in the upland regions of the Lower Valley, and are strong, swift flyers, making capture quite difficult. When disturbed they emit a milky substance described by Vogt (1949a) as having an odor like that of butyraldehyde. This substance may act as an alarm pheromone, as many individuals will take flight when one is captured.

NEW LOCALITIES.—PG; 3 mi [ca. 4.8 km] W, 5 mi [ca. 8 km] N Roma, Starr County.

Ornithia mexicana mexicana (Sturm, 1843:354)

RANGE.—Southern Texas to Panama.

ADULT ACTIVITY.—April to August.

DISCUSSION.—The only North American record for this striking species is Vogt's (1949a) collection of a single specimen from beneath bark of *Celtis*. We have not seen Vogt's specimen and so have listed it as the nominate subspecies. Linsley's figure (1964:10, fig. 3) is of the form designated as *zapotensis* Tippmann, from Guatemala and Sinaloa, Mexico. Adults of both subspecies are common on a variety of deadwood and on blossoms in Mexico and Central America.

Hylotrupes bajulus (Linnaeus, 1758:396)

RANGE.—Europe, Asia, North and South America, Asia Minor, eastern Mexico, and Texas.

ADULT ACTIVITY.—July to September.

LARVAL HOSTS.—*Pinus*, *Picea*, *Abies*, *Populus*, *Alnus*, *Cor-*

ylus, *Quercus*, *Genista*, *Conium*, *Acacia*, *Tamarix*, among others (Duffy 1960).

DISCUSSION.—This is the "Old House Borer" of economic literature—a species capable of causing considerable structural damage to a wide variety of wood products, including framing timbers, roofing, and flooring. It has been spread into many areas in North America in imported wood; a single record from Brownsville, Cameron County (RWN) has been seen from southern Texas.

Megacyllene caryae (Gahan, 1908:141)

RANGE.—Eastern North America to Texas and northern Mexico.

ADULT ACTIVITY.—September to November (Texas and northern Mexico only).

LARVAL HOSTS.—*Carya*, *Juglans*, *Morus*, *Celtis*, *Maclura*, *Vitis*, *Ulmus*, *Fraxinus*, *Gleditsia*, *Prosopis* (Linsley, 1964).

DISCUSSION.—Adults of this large clytine are common in the fall on freshly cut mesquite, being most active during the late afternoon. This species was reared from burned mesquite logs gathered near Rio Grande City, Starr County, and specimens were collected in San Patricio County from stems and foliage of *Baccharis*, in company with *Stenaspis*, *Placosternus*, and *Dendrobias*. Interestingly, *M. caryae* is active only during the spring months over most of its range, but is a fall-active species in southern Texas.

NEW LOCALITIES.—BRG; LCC; WWR; Corpus Christi, Nueces County; 3–7 mi [ca. 4.8–11.3 km] N Sinton, San Patricio County.

Placosternus difficilis (Chevrolat, 1862:263)

RANGE.—Florida and the West Indies, northern Mexico, Texas, and southern California.

ADULT ACTIVITY.—February to November.

LARVAL HOSTS.—*Prosopis*, *Acacia*, *Pithecellobium*, *Platanus* (Linsley 1964), *Citrus* (Manley and French 1976), *Leucaena* (Hovore and Penrose 1982).

DISCUSSION.—Adults are active day and night, running rapidly along freshly cut branches of their host plants and feeding on the blossoms of *Koeberlinia*, *Acacia* (Vogt 1949a), *Baccharis*, *Bumelia*, *Clematis*, and *Solidago*. They are readily attracted to lights, and are common in both the spring and fall activity periods. This is the *Cyl-lene crinicornis* of older lists.

NEW LOCALITIES.—PG; BRG; Anzalduas Park, Hidalgo County; SAR; 27 mi [ca. 44 km] S Sarita, Kenedy County; Kingsville, Kleberg County; Sinton, San Patricio County; WWR; LCC.

Placosternus erythropus (Chevrolat, 1835:fasc. 4, no. 95)

RANGE.—Texas to Guatemala.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Acacia*, *Prosopis* (Duffy 1960).

DISCUSSION.—In the fall, adults were abundant on *Baccharis* stems and on a variety of blossoming vines in the palm grove and at Welder Wildlife Refuge, and on *Condalia* and *Bumelia* flowers in the uplands near El Sauz, Starr County. Duffy cited host records for this species (listed as "*Megacyllene* [*Cyllene*] *erythropha*") by quoting older references, and we have seen no reared material.

NEW LOCALITIES.—Hwy. 649, 1.6 mi [ca. 2.6 km] N Jct. Rt. 83, Starr County; 3–7 mi [ca. 4.8–11.3 km] N Sinton, San Patricio County.

Ochraethes citrinus Chevrolat, 1860:474

RANGE.—Western Texas to southern Mexico.

ADULT ACTIVITY.—September to November.

DISCUSSION.—This species is included on the basis of several old specimens labelled only as having come from Hidalgo or Cameron County. We have not verified the determination and therefore list these specimens as *citrinus*, following Linsley (1964). Valid *citrinus* localities seen include 17 km S Saltillo, Coahuila, Mexico (FTH), and Big Bend National Park, Brewster County, Texas (MER). Most specimens were taken from blossoms of *Compositae*.

Tanyochraethes tildeni Chemsak and Linsley, 1965:148

RANGE.—Southern Texas to extreme northern Mexico.

ADULT ACTIVITY.—October to November.

DISCUSSION.—Adults of this species were taken from inflorescences of *Eriogonum* and *Solidago* growing on the sandsheets of Kenedy County in October (Hovore and Giesbert 1976). The yellow elytral vestiture is typically arranged into humeral, antemedian, median, and postmedian bands that have internally coalesced with the sutural vitta. In our material, however, many individuals have portions of the pattern, or even the entire elytral surface, suffused with yellow pubescence. In some specimens the patterns were altered or obliterated by abrasion.

Neoclytus mucronatus vogti Linsley, 1957a:35

RANGE.—Southern Arizona to southern Texas and northern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Celtis*, *Ulmus*, *Parkinsonia* (Vogt 1949a), *Prosopis* (Turnbow and Wappes 1978).

DISCUSSION.—A series of this colorful subspecies was taken from fresh-cut *Celtis* in May and again in October, in Bentsen State Park, Hidalgo County. Adults were also collected on *Baccharis*, and several beetles were found at night on dead elm trees. Larvae heavily infest dead trunks and

branches of the hosts, reducing most of the heartwood to frass and fecula. Typically, *N. m. vogti* is lighter in coloration and more strikingly marked than the widely distributed nominate subspecies; however, as Linsley (1957a) noted, there is considerable intermediacy in coloration in material from central and eastern Texas. Specimens from near San Antonio, Bexar County, cannot be placed with certainty in either subspecies; most of these specimens closely resemble material from the eastern U.S.

NEW LOCALITIES.—2 mi [ca. 3.2 km] S Pharr, Hidalgo County; WWR; LCC.

***Neoclytus acuminatus hesperus* Linsley, 1935b:163**

RANGE.—Colorado, New Mexico, southern Texas.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Quercus* (Linsley 1964), *Acacia* (Linsley and Martin 1933), *Citrus* (Manley and French 1976), *Baccharis*, *Prosopis* (Turnbow and Wappes 1978), *Zanthoxylum* (Turnbow and Wappes 1981), *Celtis*.

DISCUSSION.—Adults are wary and quick to fly at the slightest disturbance, making capture difficult. The nominate subspecies, often called the “red-headed ash borer,” is a well-known pest that breeds on a variety of hardwood trees in the eastern U.S. Lighter integumental coloration, the primary separating character for the subspecies *hesperus*, is variable and difficult to quantify in material examined from the total species range. The subspecies was originally defined from a single specimen from Colorado, and uniformly reddish coloration is found in a number of populations peripheral to the range of *N. a. acuminatus*, including those from southern Texas material.

NEW LOCALITIES.—PG; BRG; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; LCC; WWR.

***Neoclytus augusti* Chevrolat, 1835:fasc. 4, no. 73**

RANGE.—Southern Texas to northern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Sapindus* (Vogt 1949a), *Citrus* (Manley and French 1976, 1977), *Prosopis*, *Ulmus*, *Celtis* (Turnbow and Wappes 1978).

DISCUSSION.—Vogt (1949a) collected a series of adults from weakened *Baccharis*, and Hovore (1983) discussed *augusti*-like material from *Baccharis* in western Texas. On earlier lists (except Manley and French 1976, 1977) this species appeared as *N. abbreviatus* Schaeffer, a junior synonym.

***Eudercus reichei exilis* Casey, 1893:591**

RANGE.—Southern Texas to Tamaulipas, Mexico

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Sapindus* (Vogt 1949a), *Celtis*, *Prosopis* (RHT), *Acacia*, *Zanthoxylum*.

DISCUSSION.—Although this tiny ant-mimicking beetle was recorded as having been beaten (Vogt 1949a) or reared (Linsley 1940) from a variety of shrubs and trees, specific host data were rather scant. Our *Acacia* specimens emerged from a branch, 3 cm in diameter, girdled by *Oncidereus pustulatus* LeConte at Kingsville, Kleberg County. Adults are very common on deadwood and at blossoms of a variety of woody and herbaceous plants. Linsley (1964) cited the distribution of this subspecies as Hidalgo and Cameron counties, but specimens from Zapata County on the west side of the state, and San Patricio County on the Gulf Coast, based upon the relative development of the antennal spines, are also referable to *exilis*. The nominate taxon is distributed throughout the southcentral U.S.

NEW LOCALITIES.—BRG; PG; SAR; LCC; 8 mi [ca. 13 km] SE Zapata, Zapata County; 5.3 mi [ca. 8.5 km] E Rio Grande City, Starr County; WWR; La Lomita Park, Hidalgo County; 3 mi [ca. 4.8 km] S Mission, Hidalgo County.

***Tetranodus niveicollis* Linell, 1896:396**

RANGE.—Southern Texas south to Oaxaca, Mexico.

ADULT ACTIVITY.—May to June.

LARVAL HOSTS.—*Pithecellobium* (Turnbow and Wappes 1981).

DISCUSSION.—Adults were beaten from *Mimosa*, *Acacia* (Linsley and Martin 1933), and *Prosopis* (FTH), and two specimens were reared from dead ebony gathered near Boca Chica, Cameron County.

NEW LOCALITIES.—PG; LCC; Brownsville, Cameron County.

***Pentanodes dietzii* Schaeffer, 1904:222**

RANGE.—Southern Texas.

ADULT ACTIVITY.—Unknown.

DISCUSSION.—The unique holotype and allotype were reportedly collected at Brownsville, Cameron County, with no further data supplied by their describer. No other specimens are known.

***Dihammophora dispar* Chevrolat, 1859:52**

RANGE.—Southern Texas to Mexico.

ADULT ACTIVITY.—Unknown for Texas; one specimen seen from Oaxaca, Mexico in August.

DISCUSSION.—This species is occasionally collected from blossoms and on deadwood in Mexico. Aside from Schaeffer's (1908) record from Brownsville, Cameron County, based upon material in the Dietz collection (which contains a number of unduplicated records), we know of no other Texas specimens.

***Rhopalophora angustata* Schaeffer, 1905b:162**

RANGE.—Southern Texas and northern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Citrus* (Manley and French 1976), *Pithecellobium*, *Eysenhardtia* (Turnbow and Wappes 1978), *Zanthoxylum*, *Diospyros* (Turnbow and Wappes 1981).

DISCUSSION.—This graceful species was abundant on flowering *Baccharis* at Welder Wildlife Refuge in October, and adults were also beaten from dead twigs of granjeno and ebony (Hovore and Giesbert 1976). Specimens have been collected from blossoms of *Monarda* (Vogt 1949a) and *Clematis*.

NEW LOCALITIES.—PG; LCC; 5.3 mi [ca. 8.5 km] SE Rio Grande City, Starr County; 3 mi [ca. 4.8 km] N Roma.

***Rhopalophora laevicollis* (LeConte, 1873:193) (Figure 6)**

RANGE.—Southern Texas to southern Mexico.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Citrus* (Manley and French 1976), *Pithecellobium*, *Diospyros*, *Zanthoxylum* (Turnbow and Wappes 1981).

DISCUSSION.—Adults often are common on fresh-cut limbs of larval hosts, on *Celtis*, and at blossoms of *Clematis*, *Cissus*, *Serjania*, *Samolus*, *Helianthus*, *Mimosa*, *Baccharis*, and *Haplopappus*.

NEW LOCALITIES.—PG; Rio Grande City, Starr County; LCC; WWR.

***Rhopalophora rugicollis* (LeConte, 1858b:83)**

RANGE.—Texas and northern Mexico to northern Arizona and the Cape Region of Baja California.

ADULT ACTIVITY.—March to June.

LARVAL HOSTS.—*Celtis* (Tyson 1970), *Pithecellobium* (Turnbow and Wappes 1978).

DISCUSSION.—Linsley and Martin (1933) took this species on willow (Linsley and Martin 1933) in the Lower Valley, and in other portions of the species range, adults have been collected from blossoms of *Mimosa*, *Acacia*, *Lupinus*, and *Ceanothus*.

NEW LOCALITIES.—LCC.

***Rhopalophora longipes longipes* (Say, 1823:426)**

RANGE.—Eastern North America to Kansas and Texas.

ADULT ACTIVITY.—May to June.

LARVAL HOSTS.—*Cercis*, *Cornus* (Linsley 1964).

DISCUSSION.—Two specimens, which are tentatively referred to this common eastern species, were collected from white Compositae growing along the roadside 11 mi [ca. 18 km] S Three Points, Webb County, in May (FTH). Although *R. l. meeskei* Casey is known from as near as montane western Texas, the relative pronotal

proportions of the two specimens preclude their placement with that subspecies. *Rhopalophora longipes* rather closely resembles *R. bicolor*ella Knoll, from southern Arizona, but it differs by having slightly coarser pronotal punctures, very slightly sparser elytral punctation, and a less-pubescent dorsal surface. Other *longipes*-like specimens have been seen from central Mexico and the Cape Region of Baja California, and the Neotropical species of *Rhopalophora* need a comprehensive taxonomic review before a definitive determination can be made on our material.

***Agallius lepturoides* (Chevrolat, 1849:12)**

RANGE.—Southern Texas(?) to Honduras.

ADULT ACTIVITY.—Unknown for Texas.

DISCUSSION.—This exotic species has been listed from Texas several times, but we have been unable to locate or collect any U.S. material. The genus is structurally similar to other Agallini (*Zagymnus* and *Osmopleura*), species of which breed in dead fronds and floral scapes of Palmetaceae. A similar host association for *Agallius* would restrict its range in Texas to remnant sabal palmetto groves in the Lower Valley.

***Ancylocera bicolor* (Olivier, 1795:32)**

RANGE.—Southeastern North America to western Texas.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Carya*, *Quercus* (Fattig 1947), *Celtis* (Turnbow and Wappes 1978), *Acacia* (Turnbow and Wappes 1981).

DISCUSSION.—Vogt (1949a) collected this peculiar-looking beetle on *Acacia*, *Baccharis*, and fresh-cut *Leucaena*. We took numerous specimens in southern Texas from cedar elm slash and from blossoms of *Verbesina*. We collected an adult female from roadside Compositae near Uvalde, Uvalde County, in western Texas (FTH). In Florida, Turnbow and Hovore (1979) encountered numerous adults feeding on fungus growing on old stumps and logs of oak.

NEW LOCALITIES.—BRG; LCC; WWR; Resaca de la Palma State Park, Cameron County; Anzalduas Park, Hidalgo County; 11 mi [ca. 18 km] S Three Points, Webb County.

Lepturinae***Strangalia virilis* LeConte, 1873:212**

RANGE.—Texas and Oklahoma.

ADULT ACTIVITY.—May to June.

LARVAL HOSTS.—*Quercus* (Linsley and Chemsak 1976).

DISCUSSION.—Adults of this striking species have been recorded as visiting blossoms of a va-

riety of plants (Linsley and Chemsak 1976), and it is particularly abundant on horsemint (*Monarda punctata*) in central and eastern Texas. A single specimen was seen from Lake Corpus Christi State Park, San Patricio County, in June (H. Flaschka).

***Pseudostrangalia cruentata* (Haldeman, 1847:64)**

RANGE.—Eastern North America from Canada to Texas.

ADULT ACTIVITY.—April to June.

DISCUSSION.—One specimen has been seen from southern Texas, labelled "Brownsville, VII-2-65" (JC).

***Leptura (Stenura) gigas* LeConte, 1873:223**

RANGE.—Texas and northern Chihuahua, Mexico.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Salix* (Vogt 1949a).

DISCUSSION.—Adults of this large red-and-black species are difficult to capture, being strong and agile flyers and spending much of their time high in the foliage of their host trees. By their color, form, and swift, buzzing flight these insects closely resemble pompilid wasps of the genus *Pepsis*, which they may mimic. Adults are attracted to fermenting molasses bait, and occasionally come to lights. Larvae bore in decaying logs or rotting portions of living willow trees, particularly wind-broken branch butts and heaved-over scars (Hovore 1983).

NEW LOCALITIES.—PG; Anzalduas Park, Hidalgo County.

***Cyphonotida laevicollis laevicollis* (Bates, 1880:39)**

RANGE.—Southern Texas to El Salvador.

ADULT ACTIVITY.—October.

DISCUSSION.—Vogt (1949a) collected five specimens on flowers of *Bumelia*, and we took numerous specimens on blossoms of *Clematis*, *Serjania*, and *Cissus* in the Palm Grove Sanctuary in the fall.

NEW LOCALITIES.—SAR; Brownsville, Cameron County; BRG; Mission, Hidalgo County.

Lamiinae

***Parmenosoma griseum* Schaeffer, 1908:344**

(Figure 7)

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Opuntia* (Mann 1969), *Yucca* (Rice et al. 1985).

DISCUSSION.—Most specimens of this flightless species were collected by beating basal rosettes of fallen *Yucca* and *Agave*, both of which probably serve as larval hosts.



FIGURE 7. *Parmenosoma griseum* (left) and *Ataxia tibialis* (right).

NEW LOCALITIES.—3 mi [ca. 4.8 km] W, 5 mi [ca. 8 km] N Roma, Starr County; Lopeño, Zapata County.

***Moneilema armatum* LeConte, 1853:234**

RANGE.—Southern portions of the Great Plains from Colorado and Kansas south to Mexico (distribution given for all forms of *armatum*).

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Opuntia*.

DISCUSSION.—Raske (1971) considered southern Texas *armatum* to belong to the subspecies *punctatum* Psota, 1930:133, distinguished from more northern populations by the more coarsely punctate dorsal surface. This feature varies clinally from north to south in populations of *armatum*, reaching its highest degree of development in the form *rugosipenne* Fisher from central Mexico (also considered by Raske to be a subspecies of *armatum*). Linsley and Chemsak (1985) did not recognize subspecies in *Moneilema armatum*.

Moneilema larvae bore in stems and root collars of living cactus; *M. armatum* larvae show a preference for the prickly pear cactus *Opuntia* (Raske 1971).

NEW LOCALITIES.—3 mi [ca. 4.8 km] N Roma, Starr County; Lopeño, Zapata County; 10 mi [ca. 16 km] N Laredo, Webb County; 14 mi [ca. 22.5 km] SE Three Points, Webb County.

***Moneilema blapsides ulkei* Horn, 1885:188**

(Figure 8)

RANGE.—Central Texas to northern Mexico.

ADULT ACTIVITY.—April to December.

LARVAL HOSTS.—*Opuntia* (Mann 1969).

DISCUSSION.—This species is both dimorphic



FIGURE 8. Male (left) *Moneilema blapsides ulkei*, female (middle) *Moneilema mundelli*, female (right) *Moneilema blapsides ulkei*. See species accounts for a discussion of the relationships of these taxa.

and dichromatic. Males have a black, densely punctate dorsum, usually with a finely reticulated pattern of whitish pubescence intermixed with indistinct brownish hairs. Females are usually wholly black, glabrous, and at most very sparsely punctate. *Moneilema mundelli* Fisher, 1931:200 (Fig. 8) may only be a morph of this species, differing primarily by the white-reticulated dorsal pubescence of the females and the more clearly defined pubescent pattern of the males. Linsley and Chemsak (1985) synonymized *mundelli* under *M. b. ulkei*.

Adults of all forms of *M. b. ulkei* were abundant on *Opuntia* atop the so-called Yucca Ridges northeast of Brownsville, Cameron County, while the typical form was found at a number of upland localities.

NEW LOCALITIES.—11 mi [ca. 18 km] S Three Points, Webb County; 10 mi [ca. 16 km] N Laredo, Webb County.

Neoptychodes trilineatus (Linnaeus, 1767b:532)

RANGE.—Southern U.S. to northern South America. West Indies, Tahiti, Baja California.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Ficus*, *Alnus*, *Morus* (Dillon and Dillon 1941), *Chlorophora*, *Spondias*, *Inocarpus* (Duffy 1960), *Salix* (Linsley et al. 1961), *Celtis* (JC), *Juglans*.

DISCUSSION.—Horton (1917) recorded the species' life history on fig trees in Louisiana, and Linsley et al. (1961) stated that *N. trilineatus* is a primary borer in willow and mulberry in southeastern Arizona. Dillon and Dillon (1941) listed *N. trilineatus* from Brownsville, Cameron County; and its occurrence in the Lower Valley would be expected, but we have not encountered it during the course of this study.

Plectrodera scalator (Fabricius, 1792:278)

RANGE.—Eastern North America, from Great Lakes states west to New Mexico and south to Texas.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Populus*, *Salix* (Milliken 1916).

DISCUSSION.—Adults of this boldly patterned species were collected from yard and tree lawn plantings of *Populus* in Kingsville, Kleberg County, in May. This is the southernmost record that we are aware of for the species; this species may have been introduced in ornamental plantings of the host tree. Adults frequent foliage and trunks of larval hosts. The larvae mine the living root crown, often seriously damaging the plant. Milliken (1916), Craighead (1950), and Solomon (1980) described the immature stages and discussed the life history in other portions of the species range.

Goes fisheri Dillon and Dillon, 1941:122

RANGE.—Western to southern Texas.

ADULT ACTIVITY.—June to August.

DISCUSSION.—Originally described from Uvalde in western Texas, the few specimens we saw were from the Balcones Escarpment region of the state. A single south Texas specimen is known, labeled "Raymondville, Willacy County, VIII-1969," J. E. Wappes (pers. comm.) stated that this specimen "was in alcohol UVL material along with some *Oncideres pustulata*." Although the pubescence of the specimen is rubbed and matted, it compares well with the original characterization of *G. fisheri*.

Goes tessellatus (Haldeman, 1847:51)

RANGE.—Eastern North America south to Florida, west to Texas.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Quercus*, *Castanea*, *Amelanchier* (Dillon and Dillon 1941), *Ulmus* (Linsley and Chemsak, 1985).

DISCUSSION.—A single specimen was from Lake Corpus Christi State Park, San Patricio County, collected in mid-June by R. Heitzman (TCM).

Goes pulverulentus (Haldeman, 1847:51)

RANGE.—Eastern North America south to northern Florida, west to Texas.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Betula*, *Carpinus*, *Ostrya*, *Quercus*, *Ulmus*, *Platanus*, *Fagus* (Craighead 1923), *Prunus* (Knull 1946).

DISCUSSION.—Dillon and Dillon (1941) recorded this eastern monochamine from Corpus Christi, Nueces County. Solomon (1972) gave

details of its bionomics on oak in Mississippi, and based upon his observations, it is probable that the species occurs on oak in the sandsheet regions south of Corpus Christi and Kingsville, Kleberg County.

***Dorcaschema wildii* Uhler, 1855:417**

RANGE.—Eastern North America to southern Texas.

ADULT ACTIVITY.—May to August.

LARVAL HOSTS.—*Morus*, *Toxylon* (= *Maclura*) (Craighead 1923).

DISCUSSION.—A single specimen of this Alleghenian species was taken at Welder Wildlife Refuge in July (RHT). Adults are often common on foliage and infested branches of mulberry and come to lights. Solomon (1968) detailed the life history of *D. wildii* on *Morus* in Mississippi.

***Dorcaschema alternatum* Say, 1823:405**

RANGE.—Eastern North America to Florida and Texas.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Morus* (Craighead 1923), *Toxylon* (= *Maclura*) (Knull 1946).

DISCUSSION.—Dillon and Dillon (1948) assigned specimens from southern Texas (Kingsville, Kleberg County) to the subspecies *D. a. octovittata* Knull (described in 1937 from the Davis Mountains, Jeff Davis County, Texas). Material at hand from the type locality of *octovittata* differs markedly in coloration and pubescent pattern from all other *alternatum* populations examined, and material from southern Texas definitely does not belong with the west Texan form. Linsley and Chemsak (1985) did not recognize subspecies in *D. alternatum*.

NEW LOCALITIES.—Pharr, Hidalgo County; Brownsville, Cameron County; WWR; Nueces and Lavaca counties (TAI).

***Parmenonta wickhami* Schaeffer, 1908:350 (Figure 9)**

RANGE.—Southern Texas.

ADULT ACTIVITY.—May to December.

DISCUSSION.—Two specimens of this flightless longhorn were swept from herbaceous vegetation at Welder Wildlife Refuge in May, and numerous adults were beaten from *Celtis*, *Condalia*, and *Clematis* in the palm grove.

***Adetus brousi* (Horn, 1880:137) (Figure 9)**

RANGE.—Kansas to northern Mexico.

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Cucumis* (= *Cucurbita*) (Horn 1880).

DISCUSSION.—This species breeds in dried



FIGURE 9. *Parmenonta wickhami* (left), *Adetus brousi* (middle), and *Desmiphora aegrota* (right).

stems of wild gourd and possibly other Cucurbitaceae; adults have been taken from foliage of the larval host. In southern Texas, specimens were beaten from tangles of vines in the palm grove and were attracted to lights.

***Dorcasta cinerea* (Horn, 1860:571)**

RANGE.—Texas.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Datura*, *Nicotiana*, *Solanum*, *Gossypium*, *Verbesina* (Linsley and Chemsak 1985), *Matelea* (Rice et al. 1985).

DISCUSSION.—Adults were collected by sweeping or beating the larval hosts; a few specimens were attracted to lights. We took numerous specimens from stems of sunflower (*Helianthus*) near Kingsville, Kleberg County, and we found the species infesting *Nicotiana trigonophylla* at Falcon Heights, Zapata County, in May. Turnbow and Wappes (1978) took a female beetle on an *Oncideres*-girdled *Acacia* twig at Bentsen-Rio Grande Valley State Park, Hidalgo County. Huffman and Harding (1980) took a single specimen in a pitfall trap in a *Citrus* grove.

NEW LOCALITIES.—PG; SAR; Lopeño, Zapata County; Arroyo Salado at Hwy. 83, Starr County; Jct. Hwys. 649 and 2686, Starr County; San Ygnacio, Zapata County; LCC; 4 mi [ca. 6.5 km] S Agua Dulce, Nueces County.

***Ataxia hubbardi* Fisher, 1924:253 (Figure 10)**

RANGE.—Southern U.S. from Arizona to Louisiana.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Xanthium*, *Helianthus*, *Ambrosia*, *Silphium*, *Vernonia*, *Cirsium*, *Erigeron*, *Gossypium*, *Smilax*,



FIGURE 10. *Ataxia hubbardi*.

Thurberia, *Verbesina* (Linsley and Chemsak 1985), *Apocynum* (Williams 1941).

DISCUSSION.—Adults are collected at lights and by beating or sweeping dead stems of the larval hosts. Rogers (1977b) presented life history data for *A. hubbardi* on sunflowers in Texas.

NEW LOCALITIES.—BRG; Pharr and Mission, Hidalgo County; San Ygnacio, Zapata County; FSP; WWR; 4 mi [ca. 6.5 km] S Agua Dulce, Nueces County.

***Ataxia crypta* (Say, 1831:5)**

RANGE.—Eastern North America south into northern Mexico.

ADULT ACTIVITY.—March to November.

LARVAL HOSTS.—*Quercus*, *Castanea*, *Pyrus*, *Xanthium*, *Verbesina*, *Ambrosia*, *Thurberia*, *Smilax*, *Gossypium* (Craighead 1923), *Salix* (Hovore et al. 1978), *Acer*, *Celtis* (Leng and Hamilton 1896), *Acacia* (Turnbow and Wappes 1981), *Prunus* (Linsley and Chemsak 1985).

DISCUSSION.—This species breeds in a wide variety of host plants, and adults are abundant on dead branches of hardwood trees. A few specimens were beaten from dead *Yucca* near El Sauz, Starr County (FTH). Earlier host records for this species in herbaceous plants are considered erroneous, referring to the more recently described *Ataxia hubbardi*. In material examined during this study, the two species were consistently mixed and misidentified. Adults are readily attracted to lights.

NEW LOCALITIES.—PG; BRG; Anzalduas Park, Hidalgo County; Lopeño, Zapata County; FSP; 8 mi [ca. 13 km] SE Zapata, Zapata County; BC; Kingsville, Kleberg County; LCC; WWR.

***Ataxia tibialis* Schaeffer, 1908:348**

(Figure 7)

RANGE.—Brownsville, Cameron County, and vicinity.

ADULT ACTIVITY.—May and June.

DISCUSSION.—We know of only seven specimens, all from the palm grove; some specimens were collected from dead *Zanthoxylum*, some by miscellaneous beating and some at lights.

***Desmiphora hirticollis* (Olivier, 1795:11)**

(Figure 11)

RANGE.—Southern Texas to Mexico and South America (Argentina), West Indies.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Sapium* (Duffy 1960).

DISCUSSION.—Vogt (1949a) found this species feeding upon terminal shoots of *Cordia* in June and September, and a few adults have been beaten from this shrub. Specimens have also been taken at lights. In Central America this species is common at night on dead trunks and branches of a variety of hardwood trees. In southern Mexico it is abundant on healthy green leaves of an undetermined species of nettle (FTH, EFG).

NEW LOCALITIES.—PG; Anzalduas Park, Hidalgo County; SAR; BRG; 4 mi [ca. 6.5 km] W Sullivan City, Starr County; 10 mi [ca. 16 km] E Rio Grande City, Starr County; Pharr, Hidalgo County; LCC.

***Desmiphora aegrota* Bates, 1880:116**

(Figure 9)

RANGE.—Southern Texas to Panama.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Malvaviscus* (Rice et al. 1985).

DISCUSSION.—This tropical species was only recently recorded from North America (Turnbow and Wappes 1981), and the oldest record seen is a specimen labeled "Southmost, Cameron County, 20-X-74" (UCB). We collected adults from the vinelike stems of turk's cap (*Malvaviscus arboreus* var. *drummondii*) in the palm grove both day and night, and M. Rice subsequently reared it from dead stems of this plant. In Central America *D. aegrota* has been beaten from dead branches of hardwood trees.

***Eupogonius pauper* LeConte, 1852:159**

RANGE.—Eastern North America south to Florida and Mexico.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Morus*, *Cornus*, *Juglans*, *Cercis*, *Celastrus*, *Acer*, *Fraxinus*, *Asimina*, *Zanthoxylum*, *Carpinus*, *Carya*, *Castanea*, *Gleditsia*, *Hamamelis*, *Prunus*, *Quercus*, *Rhus*, *Tilia*, *Ulmus* (Linsley and Chemsak 1985).

FIGURE 11. *Desmiphora hirticollis*.

DISCUSSION.—On previous lists, this eastern species was erroneously identified as *E. fulvovestitus* Schaeffer, or recorded as *E. vestitus* (Say), an unavailable name due to homonymy (Dillon and Dillon 1953; Breuning 1974). Specimens from southern Texas differ from typical material from the eastern U.S. by having yellowish pubescence (whitish, gray, or cinereous in eastern populations) and a reddish-brown integument (typically dark brown to piceous). Adults were beaten from *Fraxinus* (Linsley and Martin 1933) and *Ulmus* (FTH, RLP) at several localities in southern Texas.

NEW LOCALITIES.—PG; BRG; SAR; LCC; WWR.

***Eupogonius fulvovestitus* Schaeffer, 1905a:134**

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to May.

DISCUSSION.—In addition to Schaeffer's original record, the only specimens we saw were collected by D. J. and J. N. Knull, labeled simply "Hidalgo County" (Knull published this record in 1954 but added no further data).

***Pygmaeopsis viticola* Schaeffer, 1908:348**

RANGE.—Southern Texas.

ADULT ACTIVITY.—May to September.

DISCUSSION.—Schaeffer (1908:348) stated that this species was taken from "heavy dead stems of vines inside the palmetto grove. . . ." Linsley

FIGURE 12. *Ecyrus arcuatus* (left) and *Ecyrus penicillatus* (right).

and Martin (1933) beat specimens from jungle vines at the same site, and Vogt (1949a) took single specimens by sweeping weeds and at lights. We have seen no recently collected material.

***Callipogonius cornutus* (Linsley, 1930:86)**

RANGE.—Southern Texas to Veracruz and Jalisco, Mexico.

ADULT ACTIVITY.—April to June, October to November.

LARVAL HOSTS.—*Salix* (Hovore et al. 1978).

DISCUSSION.—This cryptically colored pogo-notherine was abundant on fresh broken willow during spring and early summer in the palm grove, and adults were later reared from this host. Hovore et al. (1978) discussed the larval habits of this species and listed ecologically associated Coleoptera. *Callipogonius cornutus* is very closely related to *C. hircinus* (Bates) from Veracruz, Mexico, and the two may prove to be conspecific.

***Ecyrus penicillatus* Bates, 1880:137**

(Figure 12)

RANGE.—Southern Texas to Veracruz and Sinaloa, Mexico.

ADULT ACTIVITY.—April to August, October.

LARVAL HOSTS.—*Pithecellobium* (Rice et al. 1985).

DISCUSSION.—This beetle resembles a bird dropping when resting on dead twigs or in a death-feigning posture (legs and antennae drawn tight to the body) on the beating sheet. This species is uncommon; most material has been beaten from dead branches of *Celtis* or *Salix* or has been attracted to UV lights. The species appeared as *E. fasciatus* Hamilton on some previous lists.

NEW LOCALITIES.—PG; Sam Fordyce Road, 0.5 mi [ca. 0.8 km] S Hwy. 83 (N. M. Downie).



FIGURE 13. Male (left) and female (right) *Lochmaecolus cornuticeps cornuticeps*.

***Ecyrus arcuatus* Gahan, 1892:259**
(Figure 12)

RANGE.—Central Texas to Guatemala.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Acacia* (Linsley 1935a), *Prosopis*.

DISCUSSION.—This species is abundant on dead branches of its hosts, particularly in the fall. Numerous adults were taken at night from trunks and limbs of uprooted second-growth mesquite and huisache at Welder Wildlife Refuge in October, and from fresh-cut mesquite at Bentsen-Rio Grande Valley State Park in May. Linsley (1940) recorded rearing it from leguminous plants which had been girdled by *Oncideres pustulatus*, and we bred it from dead mesquite. Adults occasionally come to lights.

Some earlier authors regarded *arcuatus* as a subspecies (*texasus* Schaeffer, 1908:347) of the eastern *Ecyrus dasycerus* (Say). Chemsak and Linsley (1975b) cited specimens of *arcuatus* from X-Can, Quintana Roo, Mexico, and Petén, Tikal, Guatemala.

NEW LOCALITIES.—PG; BC; Mission, Hidalgo County; 8 mi [ca. 13 km] SE Zapata, Zapata County; LCC; SAR.

***Lochmaecolus cornuticeps cornuticeps* (Schaeffer, 1906:20)**
(Figures 4, 13)

RANGE.—Southern Texas and northern Mexico.

ADULT ACTIVITY.—April to October

LARVAL HOSTS.—*Salix* (Hovore et al. 1978), *Leucaena* (Vogt 1949a; Hovore and Penrose 1982), *Celtis*, *Acacia* (Knull 1937).

DISCUSSION.—This large oncidierine, abundant on dead tepahuaje and hackberry in the palm grove, was not encountered in any other Lower

Valley habitat. Vogt (1949a) took adults at Pharr, Hidalgo County, and we saw two specimens labeled "Raymondville" (UCB), so it does occur in other areas, but apparently less commonly than in the grove. Adults come to lights, and a single female came to molasses bait in October. Hovore and Penrose (1982) discussed the larval habits in *Leucaena* and gave comparative characters for separating larvae of *L. c. cornuticeps* from larvae of *Oncideres pustulatus*.

***Oncideres pustulatus* LeConte, 1854a:82**
(Figure 3)

RANGE.—Texas and northeastern Mexico to southern Arizona(?).

ADULT ACTIVITY.—August to December.

LARVAL HOSTS.—*Acacia*, *Pithecellobium*, *Prosopis*, *Parkinsonia*, *Mimosa* (Linsley 1940), *Leucaena* (Vogt 1949a; Hovore and Penrose 1982), *Citrus* (Dillon and Dillon 1946), *Albizia* (Thomas in Ferris 1980).

DISCUSSION.—The life history of this species, commonly called the huisache girdler, has been recorded by High (1915, as *O. putator* Thomson), Linsley and Martin (1933), Vogt (1949a), Duffy (1960, as *O. putator*), Thomas in Ferris (1980), and Hovore and Penrose (1982). The girdling habits of adult beetles can be very destructive to smaller trees, and severe growth deformities can result from pruning distal portions of the trunk and lateral branches. Thomas in Ferris (1980), however, stated that at least one host (*Albizia julibrissin*, introduced) gains increased longevity by regular prunings, suggesting a mutualistic relationship between *O. pustulatus* and its host. *Leucaena* saplings girdled near the base may grow into shorter, more compact trees than ungirdled saplings; a compact shape could be advantageous to a soft-wood species during severe storms.

Dillon and Dillon (1946) and Linsley and Chemsak (1985) stated that *O. pustulatus* is confined to Texas and adjacent Mexico, but Papp (1959) recorded it from New Mexico and Arizona, based upon material from the LACM collection (Ramsey Canyon and Huachuca Mountains, Arizona; Santa Fe, New Mexico; "Rio Grande Canyon, south of Taos, New Mexico" data fide R. R. Snelling). We have seen no other Arizona or New Mexico collections.

NEW LOCALITIES.—PG; Brownsville, Cameron County; SAR; BC; Kingsville, Kleberg County; WWR.

***Oncideres cingulata texana* Horn, 1885:195**
(Figure 15)

RANGE.—Texas.

ADULT ACTIVITY.—May to November.

LARVAL HOSTS.—*Prosopis*, *Acacia*, *Pithecellobium* (Linsley 1940), *Citrus* (Manley and French 1976), *Gliditala* [sic] (*Gleditsia*) (Dillon and Dillon 1946), *Parkinsonia*, *Celtis*.

DISCUSSION.—Rogers (1977a) reported on the bionomics of *O. cingulata* ssp. in north-central Texas, and stated that a small percentage of mature larvae pass a second winter in the host, pupating and emerging the following spring. If this pattern applies to *texana* in the study area, it might account for what appear to be two distinct broods each year. Specimens taken in May are, on average, slightly smaller in size and are less densely pubescent dorsally than those found in the fall; the pubescence difference is not attributable to abrasion.

Habits of *O. c. texana* were recorded in older literature under "*O. cingulata*," "*O. cingulator*," and "*O. texana*." Determining which subspecies of *cingulata* was being discussed in older papers on biology is difficult, as most works did not differentiate records geographically. It appears that few of the early bionomic reports attributed to *texana* actually refer to the taxon as currently recognized.

Adults are extremely abundant on mesquite and huisache throughout the southern portion of the state. We have observed girdling and ovipositing in species of trees not known to actually serve as larval hosts (retama, hackberry), but we have not reared any specimens from these plants. Adult beetles are commonly attracted to lights.

NEW LOCALITIES.—PG; BC; BRG; LCC; WWR.

Cacostola salicicola (Linsley, 1934:184)
(Figure 14)

RANGE.—Southern Texas, western Mexico.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Leucaena*, *Salix* (Turnbow and Wappes 1981).

DISCUSSION.—Adults were beaten from dead willow twigs in the palm grove in May and October, and the species was subsequently reared from this host. Turnbow and Wappes (1981) reported rearing a single specimen from *Oncideres*-girdled tepehuaje, also from the palm grove. Linsley (1934) noted that adults pose with the mesothoracic legs and antennae oriented at an angle to the linear axis of the body and the abdomen raised, perhaps mimicking the appearance of a spider or a broken twig. Similar posturing was observed in the ataxiine *Epectasis hiekei* Breuning in Mexico (FTH).

Specimens of either this or a very closely related species were taken from dead shrubs (but



FIGURE 14. *Cacostola lineata* (left) and *Cacostola salicicola* (right).

not *Salix* or *Leucaena*) near Mazatlán, Sinaloa, Mexico (FTH, EFG), and the species may be widely distributed in Mexico.

On older lists this species was placed in the genus *Cylindrataxia* Linsley.

NEW LOCALITIES.—"Hidalgo" (American Museum of Natural History); Southmost sector, Brownsville, Cameron County, LCC.

Cacostola lineata (Hamilton, in Leng and Hamilton, 1896:142)
(Figure 14)

RANGE.—Southern Texas.

ADULT ACTIVITY.—April to October.

DISCUSSION.—A rare species in collections, *C. lineata* appears to be confined to the extreme Lower Valley region. We collected numerous adults from dead *Baccharis* growing on the low hills west of Boca Chica beach, and we beat additional specimens from *Salix*, *Celtis*, *Condalia*, and tangles of vines and shrubs in the palm grove. Linsley and Martin (1933) recorded *C. lineata* as a new species of *Aporataxia*, listing the then undescribed *C. salicicola* as *lineata*.

NEW LOCALITIES.—10 mi [ca. 16 km] W Boca Chica, Cameron County.

Hippopsis lemniscata (Fabricius, 1801:330)

RANGE.—Eastern North America to Central and South America.

ADULT ACTIVITY.—April to September.

LARVAL HOSTS.—*Melothria*, *Coreopsis*, *Bidens*, *Ambrosia* (Leng and Hamilton 1896), *Vernonia*, *Xanthium* (Schwitzgebel and Wilbur 1942), *Erigeron* (Harris and Piper 1970), *Erechtites*, *Ageratum*, *Sesamum* (Duffy 1960), *Helianthus* (Rogers 1977b), *Amaranthus*, *Desmodium*, *Glycine*, *Rudbeckia* (Linsley and Chemsak 1985).



FIGURE 15. *Oncideres cingulata texana*.

DISCUSSION.—Larvae bore in stems of herbaceous plants, principally Compositae. Craighead (1923) described the larva, and Piper (1977) gave a fully referenced account of the life history and habits of this species. Adults are readily attracted to lights and may be swept from their hosts during the day. A single specimen was beaten from *Aster spinosus* at Anzalduas Park, Hidalgo County, in company with *Mecas linsleyi* Knull.

NEW LOCALITIES.—PG; SAR; BRG; LCC; WWR.

***Spalacopsis texana* Casey, 1891:146**

RANGE.—Southern Texas.

ADULT ACTIVITY.—May to October.

DISCUSSION.—Tyson (1973) collected this species from "*Hostelezky*" [sic] and lantana. R. L. Penrose swept numerous specimens from grasses and understory vegetation at Welder Wildlife Refuge in May and beat a mating pair from *Baccharis* at that site in October. The larval host is not known, but *S. texana* probably breeds in dead stems of grasses, annual Compositae, or other pithy plants.

NEW LOCALITIES.—BC; South Padre Island, Cameron County (PAU); Sarita, Kenedy County (TAI).

***Thryallis undatus* (Chevrolat, 1834:fasc. 3, no. 61)**

(Figure 16)

RANGE.—Southern Texas to Mexico and Guatemala.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Leucaena* (Vogt 1949a; Hovore and Penrose 1982), *Celtis* (Tumbow and Wappes 1981), *Pithecellobium*, *Acacia* (Rice et al. 1985).

DISCUSSION.—This rotund beetle is common in the palm grove on dead branches of its larval hosts, and adults also were beaten from dead branches of willow and ebony. Vogt's (1949a) collection of a single specimen near Mission, Hidalgo County, is the only Texas record for *T. undatus* outside the Palm Grove Sanctuary.

***Aegomorphus quadrigibbus* (Say, 1835:195)**

RANGE.—Southern Texas and Mexico.

ADULT ACTIVITY.—April to July.

LARVAL HOSTS.—*Castanea*, *Ficus*, *Fagus*, *Tilia*, *Acer*, *Carya*, *Cercis*, *Ulmus*, *Quercus*, *Betula*, *Celtis* (Linsley and Chemsak 1985).

DISCUSSION.—We did not encounter this species in the study area, but we collected several specimens matching Knull's (1958) description of the form *lucidus* from dead *Celtis* and *Acer* in Goliad and Bastrop counties in south-central Texas. The genera *Acanthoderes* and *Aegomorphus* contain over 30 species north of Panama and many more in South America, and these species are difficult to separate or define by older descriptions. *Aegomorphus quadrigibbus* occurs in Mexico and may have been recorded there under other specific names. Knull (1944) collected adults from *Prosopis* near Brownsville, Cameron County (recorded as *Psapharochrus*).

***Graphisurus triangulifer* (Haldeman, 1847:45)**

(Figure 17)

RANGE.—Ohio to Alabama and Texas.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Celtis* (Leng and Hamilton 1896).

DISCUSSION.—Specimens were collected from hackberry and at lights at Welder Wildlife Refuge. Schwarz (*in* Leng and Hamilton 1896) reported larvae boring under the bark of *Celtis*, and Riley (1890) and Craighead (1923) also listed the same host. We found numerous adults on dead and dying hackberry in Goliad and Bastrop counties, and several beetles subsequently emerged from dead *Celtis* gathered at those sites (ETH). Adults occasionally come to lights. *An-tecruris apicalis* (Bates) from Mexico may be conspecific with *G. triangulifer*, differing only slightly in the extent of the elytral maculations.

FIGURE 16. *Thryallis undatus*.

Lagocheirus texensis Dillon, 1956:139
(Figure 17)

RANGE.—Western to southern Texas.

ADULT ACTIVITY.—May to October.

DISCUSSION.—This species was originally described from material labeled "Dimmit County." Vogt (1949a, as *L. procerus* Casey) recorded two specimens, presumably of *texensis*, beaten from cut *Yucca* in Starr County; we also beat this species from dead *Yucca*, 7 mi [ca. 11 km] SW El Sauz, Starr County (FTH). Specimens were taken at lights at Falcon Heights, and A. E. Lewis (pers. comm.) collected it at light near Uvalde, Uvalde County, in western Texas.

Dillon did not include *texensis* in his generic revision (1957), so the taxonomic position of this species is somewhat uncertain. *Lagocheirus texensis* is very closely related to, if not synonymous with, *L. undatus* Voet from Mexico and Central America.

NEW LOCALITIES.—Rio Grande City, Starr County.

Astyliidius parvus (LeConte, 1873:234)

RANGE.—Mississippi to southern Texas.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Ficus* (Townsend 1902), *Pithecellobium* (Turnbow and Wappes 1978), *Zanthoxylum* (Turnbow and Wappes 1981).

FIGURE 17. *Lagocheirus texensis* (left) and *Graphisurus triangulifer* (right).

DISCUSSION.—Most specimens of this greenish longhorn were beaten from dead branches of ebony, persimmon, and hackberry. Vogt (1949a, as *A. leiopinus* Casey) took three specimens at lights in Pharr, Hidalgo County.

NEW LOCALITIES.—PG; LCC; WWR.

Leptostylus transversus ssp.

DISCUSSION.—A single specimen of this widespread, polytypic species was taken from a light trap at Welder Wildlife Refuge in June (RHT), and several similar appearing specimens from dead *Acer* and *Celtis* at Goliad, Goliad County, in May (RLP, FTH). They exhibit the general facies of the subspecies *dietrichi* Dillon (from the southeastern U.S.), but their coloration is more like that of the subspecies *asperatus* (Haldeman) from central and western Texas.

Leptostylus gibbulosus vogti Dillon, 1956:141

RANGE.—Southern Texas, Mexico(?).

ADULT ACTIVITY.—December to May.

LARVAL HOSTS.—Fruit of *Sapindus* (Vogt 1949a).

DISCUSSION.—The unusual larval habits of this species were reported in detail by Vogt (1949a), who discovered the host to be mature fruits of soapberry. Although he reared large numbers of adults from the fruits, he did not collect them by any other method, and the few additional specimens seen by us bear no collecting data. The nominate subspecies occurs from northern Mexico to Colombia (Dillon 1962) where it is commonly beaten from deadwood.



FIGURE 18. *Sternidius texanus* (left), *Sternidius mimeticus* (middle), and *Sternidius wiltii* (right).

Leptostylopsis luteus Dillon, 1956:147

RANGE.—Southern Texas.

ADULT ACTIVITY.—October.

DISCUSSION.—This species is very rare in collections, and we have seen only two specimens: one from dead *Acacia* at Welder Wildlife Refuge (EFG), the other beaten from dead *Baccharis* near Boca Chica, Cameron County (RLP), both in October. The type specimen reportedly came from “Esper Ranch” (Esperanza Ranch), near Brownsville, Cameron County.

Sternidius wiltii (Horn, 1880:124)

(Figure 18)

RANGE.—Southern Texas and northern Mexico.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Acacia* (Linsley 1940).

DISCUSSION.—Adults of this relatively large *Sternidius* were beaten from *Oncideres*-girdled twigs and branches, and Linsley (1940) reported rearing them from unspecified legumes girdled by *O. pustulatus* and from *Acacia* pruned by *O. cingulata texana*. We collected numerous specimens from girdled huisache at Welder Wildlife Refuge and from drought-stressed mesquite near Boca Chica, Cameron County. Adults have been attracted to lights.

NEW LOCALITIES.—PG: Southmost sector, Brownsville, Cameron County; FSP; LCC.

Sternidius mimeticus (Casey, 1891:49)

(Figure 18)

RANGE.—Texas.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Leucaena* (Hovore and Penrose 1982), *Acacia*, *Celtis*.

DISCUSSION.—Although *S. mimeticus* and *S. texanus* are both abundant throughout the study

area on a variety of hosts, published accounts are difficult to correlate with current nomenclature. Examination of type specimens has shown that “*Liopus houstoni*” Casey was correctly placed by Dillon (1956) as a synonym of *mimeticus*, but *L. texanus* Casey, also synonymized under *mimeticus*, is distinctly different. Texas records for *S. crassulus* LeConte (a Baja California species) no doubt refer to *mimeticus*. This species may also be the *Leptostylus biustus* of Townsend (1902), recorded as infesting fig twigs and dead cotton. Adults were commonly beaten from known larval hosts and numerous other woody plants and were attracted to lights.

NEW LOCALITIES.—PG; BC; SAR; Mission, Hidalgo County; Resaca de las Palmas State Park, Cameron County; LCC; WWR: 4 mi [ca. 6.5 km] S Pharr, Hidalgo County; 1 mi [ca. 1.6 km] E Los Indios, Cameron County.

Sternidius texanus (Casey, 1913:315)

(Figure 18)

RANGE.—Southern Texas and northeastern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Leucaena* (Hovore and Penrose 1982), *Acacia*

DISCUSSION.—This species is very closely related to described taxa in the *Sternidius alpha* complex and may ultimately prove to be synonymous with *S. naevicornis* Bates from Mexico or *S. alpha misellus* (LeConte) from the eastern U.S. The genus *Sternidius* needs taxonomic review before names can be applied with certainty to the various phenotypes, particularly from the southeastern U.S. and Mexico. Variation in body coloration and elytral vestiture is extreme in our long series from southern Texas; this series encompasses most of the phenotypic diversity recorded for both of the aforementioned species and intergrades broadly with material from western and southern Mexico.

Previous listings of *Leiopus alpha* (Say) probably refer to this species.

NEW LOCALITIES.—PG; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; Brownsville, Cameron County; WWR.

Astyleiopus variegatus (Haldeman, 1847:47)

RANGE.—Eastern North America to southern Texas, Utah, and southern Arizona.

ADULT ACTIVITY.—May (in the study area).

LARVAL HOSTS.—*Castanea*, *Juglans*, *Morus*, *Ulmus*, *Robinia*, *Celastrus* (Craighead, 1923), *Celtis*.

DISCUSSION.—A single female was beaten from *Celtis* at Welder Wildlife Refuge in May (FTH), and numerous adults were taken from fresh-cut logs of this host at Goliad (RLP, FTH). A spec-

imen was subsequently reared from a larva taken from beneath dead *Celtis* bark at this locality.

Valenus inornata Casey, 1891:50

RANGE.—Northwestern Arizona to northern Mexico.

ADULT ACTIVITY.—May to October.

DISCUSSION.—No larval habits have been recorded for this species, but adults are generally associated with *Yucca*. Numerous specimens were beaten from dead, persistent foliage of *Yucca* in Zapata and Starr counties, and a series of beetles was collected in western Texas from freshly trimmed leaves of ornamental *Agave* (FTH). Adults are attracted to lights.

NEW LOCALITIES.—3 mi [ca. 4.8 km] W Roma and 5–7 mi [ca. 8–11 km] SW El Sauz, Starr County; FSP; 8 mi [ca. 13 km] SE Zapata, Zapata County.

Dectes texanus aridus Casey, 1913:343

RANGE.—Southern Texas to central Mexico.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Helianthus*.

DISCUSSION.—The five subspecies of *D. texanus* are poorly defined and of dubious taxonomic value; southern Texas material is phenotypically intermediate between *aridus* and the nominotypical taxon. Our placement follows that of Dillon (1956). Larvae of *D. texanus* sensu lato girdle stems of Compositae, and we beat adults from sunflowers near Mission, Hidalgo County, and from various herbaceous plants along the margins of the palm grove. Vogt (1949a) took specimens from *Solidago* south of Pharr, Hidalgo County; R. H. Turnbow swept a series from *Parthenium* at Santa Ana National Wildlife Refuge, Hidalgo County; and Townsend (1902) beat a specimen from *Abutilon* near Brownsville, Cameron County.

Lepturges angulatus canus Casey, 1913:317 (Figure 19)

RANGE.—Eastern to southern Texas, northern Mexico.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Ficus* (Townsend 1902), *Pithecellobium*, *Celtis* (Turnbow and Wappes 1978), *Leucaena* (Hovore and Penrose 1982), *Acacia*.

DISCUSSION.—Linsley and Martin (1933:182) stated that this longhorn was "abundant on every type of tree and shrub," and this beetle is indeed exceedingly common in certain habitats, most notably *Celtis*-dominated semideciduous woodlands. Adults are rapid runners and are difficult to collect from the beating sheet with appendages intact. This species, and possibly also the follow-



FIGURE 19. *Lepturges inflatus* (left) and *Lepturges angulatus canus* (right).

ing, appeared on earlier lists as *Lepturges symmetricus* (Haldeman).

NEW LOCALITIES.—PG; BC, BRG; 2 mi [ca. 3.2 km] S Pharr, Hidalgo County; SAR; LCC; WWR.

Lepturges inflatus Bates, 1872:216 (Figure 19)

RANGE.—Southern Arizona and southern Texas to southern Mexico and Panama.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Leucaena* (Hovore and Penrose 1982), *Morus*.

DISCUSSION.—This tropical species was only recently reported from the U.S. (Marqua 1976) from specimens collected at light in southeastern Arizona. South Texan material is lighter in color and more heavily maculate than specimens from Arizona, and it is possible that more than one taxon is being included under the name *inflatus*.

Larvae mine the cambium layer of dead branches of tepehuaje. We took adult specimens on dead mulberry at night (SAR). Adults come to lights.

Lepturges inflatus is very similar to the preceding species in general coloration and form, which may account for its having been omitted from previous lists.

NEW LOCALITIES.—PG.

Lepturges vogti Hovore and Tyson, 1983:349

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to October.

LARVAL HOSTS.—*Yucca* (Hovore and Tyson 1983).

DISCUSSION.—This is the species Vogt (1949a) recorded from *Yucca treculeana* in the uplands as "*Lepturges* sp. near *confluens*." It is more



FIGURE 20. *Mecas (Dylobolus) rotundicollis* (left) and *Mecas (Mecas) marginella* (right).

closely related to *L. yucca* Schaeffer (western Texas to Arizona) and *L. subglaber* Casey (Durango, Mexico), from which it differs conspicuously by the distinctly patterned elytra and more slender form. Larvae mine dead, persistent leaves of *Yucca*. Adults were reared and beaten from this host, and collected at lights.

NEW LOCALITIES.—BC; LCC; WWR; FSP.

***Urgleptes celtis* (Schaeffer, 1905b:168)**

RANGE.—Southern Texas.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Leucaena* (Hovore and Penrose 1982), *Celtis*.

DISCUSSION.—Schaeffer (1905b) and Linsley and Martin (1933) collected this species from hackberry, and we reared it in large numbers from this host and from tepehuaje.

NEW LOCALITIES.—PG; BRG.

***Urgleptes knulli* Dillon, 1956:337**

RANGE.—Southern Texas to central Mexico.

ADULT ACTIVITY.—May to August.

DISCUSSION.—Specimens were taken in the palm grove by beating dead *Celtis* and miscellaneous vegetation. This is probably "*Lepturges minutus*" of Linsley and Martin (1933).

***Cyrtinus pygmaeus* (Haldeman, 1847:42)**

RANGE.—Eastern North America to Texas.

ADULT ACTIVITY.—March to May.

LARVAL HOSTS.—*Quercus*, *Carya*, *Cornus*, *Liriodendron*, *Robinia*, *Acer* (Craighead 1923).

DISCUSSION.—Vogt (1949a) swept one specimen from succulent vegetation and took another on *Sapindus*, both in Hidalgo County. We have not seen those specimens and so have not been able to verify the determination.

***Mecas (Dylobolus) rotundicollis* (Thomson, 1868b:196) (Figure 20)**

RANGE.—Oklahoma to Arizona, Texas, and Mexico, south to Costa Rica.

ADULT ACTIVITY.—May to June in southern Texas.

DISCUSSION.—Adults of this lampyrid-mimic were common on foliage of capitana (*Verbesina microptera*) at Welder Wildlife Refuge in May (Hovore et al. 1978); frostweed, the common name cited by Hovore et al. for *V. microptera*, was incorrect. Chemsak and Linsley (1973) recorded a single specimen from Brownsville, Cameron County, and two specimens from Tamaulipas, Mexico.

***Mecas (Mecas) marginella* LeConte, 1873:239 (Figure 20)**

RANGE.—Southeastern U.S. to New Mexico.

ADULT ACTIVITY.—March to May.

DISCUSSION.—Several specimens were swept from roadside vegetation 27 mi [ca. 43.5 km] S Catarina, Webb County (AEL). We took numerous adults from Compositae in western Texas.

NEW LOCALITIES.—15 mi [ca. 24 km] SE Three Points, Webb County.

***Mecas (Mecas) confusa* Chemsak and Linsley, 1973:163**

RANGE.—Kansas to Texas.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Heterotheca*.

DISCUSSION.—We swept adults of this all-gray species from roadside vegetation at Lake Corpus Christi State Park, San Patricio County, and along Highway 77, 41 mi [ca. 66 km] N Raymondville, Kenedy County (RLP, FTH). We collected larvae and adults of *M. confusa* and *M. pergrata* from pupal chambers in dead root crowns of *Heterotheca* sp. (probably *subaxillaris*), 10 mi [ca. 16 km] S Sarita, Kenedy County, and we took both species from foliage of this plant at a number of localities in south-central Texas.

NEW LOCALITIES.—6 mi [ca. 9.7 km] E Riviera, Kleberg County (TAI); 40 mi [ca. 64.5 km] N Pharr, Hidalgo County (AEL).

***Mecas (Mecas) cineracea* Casey, 1913:360**

RANGE.—Southeastern and Great Plains states to southern Rockies, Texas, and northern Mexico.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Helenium*, *Baileya* (Chemsak and Linsley 1973).

DISCUSSION.—This species is common in roadside stands of Compositae throughout central Texas, but Vogt's (1949a) collection from *He-*

lenium near Mission, Hidalgo County, is the only south Texas record under the name *cineracea*. *Mecas inornata* of Townsend (1902) and Linsley and Martin (1933) may also be this species, but we have not examined their material. Older accounts, as well as more recent biological papers (Rogers 1977b), have broadly applied the nomina dubia, *Mecas inornata* (Say), to several different species and may therefore have variously referred to *M. confusa*, *M. cineracea*, or *M. cana saturnina* (see Chemsak and Linsley 1973, for a full discussion of this problem). *Mecas cineracea* probably utilizes a variety of plants as larval hosts.

NEW LOCALITIES.—3 mi [ca. 4.8 km] N Eagle Pass, Maverick County; 7 mi [ca. 11.3 km] N San Ygnacio, Zapata County; 1–5 mi [ca. 1.6–8 km] NW Jct. Hwy. 35 on RL 83; WWR; 24 mi [ca. 39 km] S Sarita, Kenedy County.

***Mecas (Mecas) pergrata* (Say, 1824:407)**

RANGE.—Great Plains to southeastern U.S., New Mexico, Texas, and northern Mexico.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Aster* (Craighead 1923), *Helianthus* (Chemsak and Linsley 1973), *Heterotheca*.

DISCUSSION.—Although it is one of the most widespread species of *Mecas*, *M. (M.) pergrata* is not particularly common in collections. Craighead (1923) described the larva and its feeding habits in stems and roots of *Aster*. Adults were swept from roadside vegetation near Refugio, Refugio County, at Lake Corpus Christi State Park, San Patricio County, and 11–14 mi [ca. 17.7–22.5 km] S Three Points, Webb County, and a few beetles were taken from pupal cells in roots of *Heterotheca* 10 mi [ca. 16 km] S Sarita, Kenedy County. Townsend (1902) and Linsley and Martin (1933) recorded collecting *pergrata* near Brownsville, Cameron County, but we have not seen their material, and they may in part refer to the then-undescribed *Mecas linsleyi*.

NEW LOCALITIES.—Kingsville, Kleberg County (TAI); 24 mi [ca. 39 km] S Sarita, Kenedy County; Freer, Duval County (TAI).

***Mecas (Mecas) linsleyi* Knull, 1975:130**

RANGE.—Southern Texas.

ADULT ACTIVITY.—March to May.

DISCUSSION.—Adults of *M. linsleyi* were taken at several localities, always in association with spiny aster (*Aster spinosus*), which is probably the larval host. It may be distinguished from the similar-appearing *M. pergrata* by its larger size, longer, all-black antennae, and more elongate prothorax. The type locality is Bentsen-Rio Grande Valley State Park, Hidalgo County.

NEW LOCALITIES.—Anzalduas Park, Hidalgo County; 3 mi [ca. 4.8 km] E Rio Grande City, Starr County.

***Mecas (Mecas) cana saturnina* (LeConte, 1859:21)**

RANGE.—Great Plains to Alabama, Texas, and northern Mexico.

ADULT ACTIVITY.—April to August.

LARVAL HOSTS.—*Ambrosia*, *Xanthium*, *Helianthus*, *Gailardia* (Chemsak and Linsley 1973).

DISCUSSION.—Specimens were taken from roadside stands of *Ambrosia* and mixed herbaceous plants at several localities in southern Texas, often in company with one or more other *Mecas* species.

NEW LOCALITIES.—3 mi [ca. 4.8 km] W, 5 mi [ca. 8 km] N Roma, Starr County; 11–14 mi [ca. 17.7–22.5 km] S Three Points, Webb County; 6 mi [ca. 9.7 km] E Riviera, Kleberg County; Padre Island, Kleberg County(?) (TAI).

***Tetraopes discoideus* LeConte, 1858a:26**

RANGE.—Rocky Mountain states to Kansas, south to Texas and El Salvador.

ADULT ACTIVITY.—May to October.

LARVAL HOSTS.—*Asclepias* spp. (Chemsak 1963).

DISCUSSION.—Knull (1948) recorded the collection of this widespread and common species on low milkweed in May at Brownsville, Cameron County, and Chemsak (1963) listed it from San Benito, Cameron County. We have seen no other south Texas material.

***Tetraopes texanus* Horn, 1878:49**

RANGE.—Eastern Oklahoma to western and southern Texas.

ADULT ACTIVITY.—April to June.

DISCUSSION.—In his review of the genus *Tetraopes*, Chemsak (1963) cited no larval hosts for this species, but all *Tetraopes* species are considered host specific on *Asclepias*. Adults of *T. texanus* have been taken from foliage and blossoms of several different species of milkweed in both lowland and montane habitats in western and central Texas, but we have not collected it in the study area. Chemsak (1963) listed *texanus* from Boca Chica, Cameron County and “mouth of Rio Grande.”

***Tetraopes thermophilus* Chevrolat, 1861:190, 254**

RANGE.—Southern Texas to El Salvador along the tropical belt (fide Chemsak 1963).

ADULT ACTIVITY.—August to October.

LARVAL HOSTS.—*Asclepias*.

DISCUSSION.—This species was encountered on stems and foliage of milkweed on disturbed substrates along roadsides and railroad rights-of-way in Mission, Hidalgo County, in October. Vogt's (1949a) record of *T. femoratus* from Pharr, Hi-

dalgo County, probably refers to *thermophilus*. Chemsak (1963) examined specimens from Beeville, Bee County; Victoria, Victoria County; and Brownsville, Cameron County.

***Tetraopes femoratus* LeConte, 1847:93**

RANGE.—Western and central states to Ohio, south to Mississippi, Texas, and Central America.

ADULT ACTIVITY.—June to September.

LARVAL HOSTS.—*Asclepias* (Chemsak 1963).

DISCUSSION.—Two specimens of this widespread, polytypic species were swept from roadside vegetation 5–8 mi [ca. 8–13 km] S Guerra, Jim Hogg County, in September (JEW, RHT). This is the southernmost record for *femoratus* in Texas by about 800 km. Phenotypically, this material best fits Chemsak's (1963:64) characterization of the "Great Plains series" of *T. femoratus*.

***Cathetopteron amoena* (Hamilton in Leng and Hamilton, 1896: 161)**

RANGE.—Southern Texas.

ADULT ACTIVITY.—April to October.

LARVAL HOSTS.—*Celtis* (Turnbow and Wappes 1978).

DISCUSSION.—Adults of this beautiful lamiine sun themselves on the upper surfaces of hackberry leaves. Numerous specimens have been beaten from *Celtis* foliage or swept from herbaceous plants growing nearby. Portions of the head and thorax described by Hamilton (*in* Leng and Hamilton 1896) as white are, in living specimens, delicate peach-pink (fading postmortem to white).

NEW LOCALITIES.—BRG; Anzalduas Park, Hidalgo County; PG.

***Hemierana marginata* (Fabricius, 1798:48)**

RANGE.—Eastern North America to southern Texas.

ADULT ACTIVITY.—April to June.

LARVAL HOSTS.—*Vernonia* (Schwitzgebel and Wilbur 1942).

DISCUSSION.—This species is frequently collected by sweeping herbaceous vegetation, and many so-called host records represent collections of adults from plants that may not actually serve as larval hosts. Adults were common in May on *Verbesina* at Welder Wildlife Refuge (Hovore et al. 1978) and Lake Corpus Christi State Park. Schwitzgebel and Wilbur (1942) recorded details of the larval biology in ironweed in Kansas.

***Hemierana suturalis* Linell, 1896:398**

RANGE.—Southern Texas, Florida(?).

ADULT ACTIVITY.—May to July.

LARVAL HOSTS.—*Bernardia*

DISCUSSION.—Most specimens seen were taken by beating or sweeping miscellaneous vegetation. Townsend (1902) collected several adults by beating tangles of *Clematis* and *Ehretia* in the palm grove in June. Specimens in the USNM collection bear data indicating that they were reared from larvae collected in roots and stems of myrtle croton (*Bernardia myricaefolia*) at Brownsville, Cameron County.

We saw specimens of this species that were labeled as coming from Central Florida, and Blatchley (1930) reported beating it from oak in the Everglades (as *Amphionycha*). If these records are accurate, the species either has a very unusual distribution or is distributed across the Gulf Arc and simply has not been collected in intermediate areas.

QUESTIONABLE RECORDS

The following species, which have either been previously recorded from southern Texas or have been encountered in curated material examined during this study, appear to represent either adventitious, misidentified, or mislabeled material.

***Ergates spiculatus neomexicanus* Casey, 1890:491**

Linsley (1962a, fig. 8) showed a locality in the Lower Valley, probably based upon specimens from structural timber. *Pinus* is the larval host.

***Megaderus bifasciatus* Dupont, 1836:5**

A single specimen in the Carnegie Museum, Pittsburgh, Pennsylvania labeled as coming from Brownsville, Cameron County, is the only record we saw for southern Texas. This locality may be erroneous, as the remaining six specimens in the Carnegie series are labeled "El Paso." According to Riley (1880) and Beutenmüller (1896), *Megaderus* was collected from cedar timber (*Juniperus*) in Comal County, Texas, in December and it was recently taken from beneath bark of rotting *Pinus* in Honduras (Chemsak et al. 1980). We have seen specimens from Comal (USNM) and Bastrop (UCB) counties in central Texas, and from Chihuahua, Mexico (UCB).

***Callidium texanum* Schaeffer, 1917:185**

Vogt (1949a) collected two specimens on "cedar" fence posts in Hidalgo County, noting that the wood had been imported from northern Texas. This beetle breeds in juniper, and the probability of its becoming established in southern

Texas is therefore very remote. The nearest natural occurrence of *C. texanum* that we saw was in Sutton County, 8 mi [ca. 13 km] SW Roosevelt (FTH, RLP).

Strangalepta abbreviata (Germar, 1824:523)

Papp (1955) listed this common eastern lepturine as *S. vittata* (Olivier) from Brownsville, Cameron County. Linsley and Chemsak (1976) recorded the distribution as reaching only as far south as Georgia.

Taricanus truquii Thomson, 1868a:74

Leng and Hamilton (1896), and Dillon and Dillon (1946) recorded this Mexican ocinicerine as occurring in Texas or the southern U.S., without further data. The nearest Mexican locality we have seen thus far is in Veracruz.

Ataxia spinicauda Schaeffer, 1904:224

Chemsak and Linsley (1982) listed this Antillean species from Florida and Texas. It has often been collected in Florida (Schaeffer 1908; Turnbow and Hovore 1979), but we have seen no material from Texas.

SELECTIVE REARINGS FROM DEADWOOD

During the course of this project, F. T. Hovore, R. L. Penrose, R. H. Turnbow, and J. E. Wappes conducted a series of selective rearings of Cerambycidae from host plant material gathered at Lake Corpus Christi State Park, Bentsen-Rio Grande Valley State Park, the Palm Grove Sanctuary, and in Southmost sector, Brownsville, Cameron County. The results of these rearings, along with a compilation from literature of species utilizing *Citrus*, are presented below. Species cited as having been taken "on *Citrus*" have not been included, as these may not be actual rearing records. Both English and Spanish common names, where known, are listed for the host plants.

LEGUMINOSEAE

Leucaena pulverulenta (Schlect.) Benth.—Lead Tree, Tepehuaje

Achryson surinamum, *Geropa concolor*, *Eburia mutica*, *Gnaphalodes trachyderoides*, *Taranomis b. bivittata*, *Dendrobias mandibularis virens*, *Stenosphenus lugens*, *Anelaphus debilis*, *Neocompsa exclamations*, *N. mexicana*, *Obrium maculatum*, *O. mozinnae*, *Lochmaeocles c. cornuticeps*, *Cacostola salicicola*, *Oncideres pustulatus*, *Sternidius mimeticus*, *S. texanus*, *Lepturges angulatus canus*, *L. inflatus*, *Urgleptes celtis*, *Thryallis undatus*.

Prosopis glandulosa Torr.—Mesquite

Eburia mutica, *E. ovicollis*, *Knulliana c. cincta*, *Stenosphenus dolosus*, *Anelaphus debilis*, *Heterachthes nobilis*, *Obrium mozinnae*, *Placosternus difficilis*, *Megacyllene caryae*, *Neoclytus acuminatus hesperus*, *N. augusti*, *N. mucronatus vogli*, *Oncideres cingulata texana*, *Sternidius wiltii*, *Ecyrus texanus*.

Acacia farnesiana (L.) Willd.—Sweet Acacia, Huisache

Achryson surinamum, *Geropa concolor*, *Gnaphalodes trachyderoides*, *Taranomis b. bivittata*, *Stenosphenus dolosus*, *Neocompsa mexicana*, *Obrium maculatum*, *Placosternus difficilis*, *Neoclytus acuminatus hesperus*, *Oncideres pustulatus*, *O. cingulata texana*, *Sternidius wiltii*, *S. mimeticus*, *S. texanus*, *Ecyrus texanus*.

RUTACEAE

Citrus paradisi Macf., and *C. sinensis* L. (Osbeck)—Grapefruit and Sweet Orange (compiled from Dean [1953] and Manley and French [1976])

Archodontes melanopus serrulatus, *Stenodontes d. dasytomus*, *Eburia mutica*, *Gracilia minuta*, *Gnaphalodes trachyderoides*, *Knulliana c. cincta*, *Dendrobias mandibularis* ssp., *Enaphalodes taeniatus*, *Elaphidionoides villosus*, *Anelaphus inermis*, *Obrium maculatum*, *Placosternus difficilis*, *Neoclytus acuminatus hesperus*, *N. augusti*, *Eudermes reichei exilis*, *Rhopalophora angustata*, *R. laevicollis*, *Oncideres cingulata texana*.

SALICACEAE

Salix nigra Marsh.—Black Willow

Hypexilis pallida, *Elaphidion linsleyi*, *E. mimeticum*, *Lepidura gigas*, *Lochmaeocles c. cornuticeps*, *Cacostola salicicola*, *Callipogonius cornutus*, *Ataxia crypta*.

ULMACEAE

Celtis pallida Torr.—Spiny Hackberry, Granjeno

Methia constricticollis, *Stenosphenus lugens*, *Piezocera serraticollis*, *Neoclytus augusti*, *Ancylocera bicolor*, *Lepturges angulatus canus*, *Cathetopteron amoena*, *Urgleptes celtis*.

Celtis laevigata Willd.—Sugar Hackberry, Palo Blanco

Stenodontes d. dasytomus, *Eburia stigmatica*, *E. mutica*, *Gnaphalodes trachyderoides*, *Knulliana c. cincta*, *Dendrobias mandibularis virens*, *Neocompsa mexicana*, *Obrium maculatum*, *Neoclytus acuminatus hesperus*, *Lochmaeocles c. cornuticeps*, *Oncideres cingulata texana*, *Sternidius mimeticus*, *Urgleptes celtis*, *Thryallis undatus*.

Ulmus crassifolia Nutt.—Cedar Elm, Olmo
Gnaphalodes trachyderoides, *Taranomis b. bivittata*, *Neoclytus augusti*.

ORIGINS AND AFFINITIES OF THE SOUTH TEXAS CERAMBYCIDAE: PALEOECOLOGICAL INFORMATION

Although south Texas Cerambycidae are predominantly neotropical in origin, the overall fauna is a composite of genera derived from numerous geographic regions. The complex array of probable routes and times of movement im-

plies that present faunal concepts may have to be further refined before we completely understand the mosaic pattern of species origins and distribution. Independent analyses of the origins of other faunal elements (i.e., reptiles, amphibians, and birds) have yielded somewhat differing theories regarding centers of generic differentiation and boundaries of present faunal regions. In the following analysis we utilized the faunal systems defined and discussed by Linsley (1939, 1958, 1961*b*, 1963*b*) and Halffter (1976), which we feel represent the most useful zoogeographic assessments thus far applied to neotropical Coleoptera. We have combined or modified their concepts only where necessitated by more recent taxonomic and distributional information. (For a more thorough discussion of faunal affinities, regional definitions, and global relationships for North American Cerambycidae, see Linsley [1961*b*].)

During the early Cenozoic, tropical flora and fauna from Middle and South America extended over much of what is now North America; southern Texas was within the extensive Neotropical Tertiary Geoflora. Insect populations spread along a number of environmental corridors, with many Neotropical forms reaching the southern and eastern portions of the continent via the lowlands of the Gulf Arc corridor.

Subsequent periods of glacial maxima, with mesic and xeric interglacial episodes, forced many Neotropical organisms to retreat southward into refugia in the hot, humid lower valleys and deltaic plains of the major river systems along the southern boundary of the North American continental land mass. Relatively mild climate during the present interglacial period has permitted many species to extend (or reextend) their ranges away from refugial areas, northward into the mesic eastern deciduous forests, eastward and westward across the lowlands of the Gulf Arc, or northward from southern Mexico through the subtropical Mexican forests into Texas. The arid climate now dominating much of eastern Mexico appears to have disrupted the southern portion of the Gulf Arc corridor, and may serve as an interposed ecological limit to the Austroriparian, Tamaulipan, and Mexican Tropical faunal regions. Thus, a number of Neotropical genera and species found in southern Texas also occur in the vicinity of Veracruz, Mexico, but do not seem to be present in the intervening portions of the Mexican coastal plain.

In addition to repeated terrestrial movements of Neotropical floras and faunas through Texas during shifting climatological regimes, Gulf Stream currents have undoubtedly introduced a number of Central American or Antillean Cerambycidae into the Texas fauna via infested driftwood. A number of species with limited distributions in South, Central, or North America and in the Antillean faunal region may have been dispersed into portions of their present ranges by this method (e.g., *Desmiphora hirticollis*, *Placosternus difficilis*, *Anelaphus inermis*, *Heterachthes ebenus*). Although the rate at which cerambycids are transported by floating wood is not known, the oceanic corridor may provide for constant introduction and reintroduction of Neotropical species to the south-coastal portions of North America.

The lower Rio Grande valley, with its rich deltaic soils and comparatively hot, humid subclimate surrounded by more xeric habitats, has repeatedly been a refugium for mesic-adapted neotropical organisms—a retreat from glacial advances as well as the northernmost extension of tropical forms. According to Porter (1977, discussing mesostenine Ichneumonidae), Pleistocene climatic alterations produced in southern Texas a multiple overlap of northern and southern Neotropical ichneumonid species, and this pattern appears to pertain to the cerambycid fauna as well.

TAXONOMIC AND ANALYTICAL PROBLEMS

Genera are often rather subjective taxonomic entities. In certain cerambycid tribes many genera appear transitional (e.g., *Aneflomorpha* and *Psyrrassa*) or polyphyletic (e.g., *Deltaspis* and *Anelaphus*). Others have not been treated taxonomically since their original description. Attempting to analyze composite or poorly defined genera can produce confused results, but it is beyond the scope of this project to redefine generic concepts for Neotropical Cerambycidae.

Further, genera regarded as arising in a particular faunal region may belong in generic complexes with origins or relatives in South America, Eurasia, Africa, or Micronesia.

In the following discussion we have, where possible, employed a species aggregate and related genera method of analysis. A concentration of modern species in a single faunal region may suggest that the region represents the ancestral

home of the genus, particularly in genera with taxonomically and bionomically well-defined species. The distribution of closely related genera may also provide clues to the origin and developmental direction of a genus. The genus *Ancylocera* Serville is an example: according to Viana (1971), there are six species of *Ancylocera* in Mexico (one of which, *A. macrotela* Bates, extends southward to Nicaragua), one species in Colombia, and two species in central and southern South America (Brazil, Argentina, and Uruguay). Viana included six other genera in the Ancylocerini, but Chemsak (1967) had removed one of them, *Championa*, to the Sphaerionini (Elaphidionini [=Elaphidini] of Chemsak and Linsley 1982). Of the remaining five genera, *Ceralocyna* Viana has two Mexican and six South American species, and *Lallancyna* Viana has three species, one each in Panama, Brazil, and Argentina. The other three genera (*Cercoptera* Spinola, *Callancyla* Aurivillius, *Corallancyla* Tippman) are entirely confined to South America, mainly in Brazil and Argentina. *Ancylocera bicolor* has in the past been considered as Austroriparian in origin, and as a species, it may well have evolved in one of the southeastern North American refugia. However, it is apparent from its congeneric and tribal affinities that the genus is present in the Austroriparian region as a relict of Neotropical Tertiary expansion from Central and South America.

As noted earlier, certain genera that appear to be well defined and taxonomically compact within a limited geographical region such as North America may, in other portions of their ranges, intergrade so evenly with one another that they form supergeneric phenoclines. Intermediate character states exhibited in some Neotropical generic complexes preclude absolute placement of certain species in any genus; in taxonomically homogeneous groups such as the Elaphidionini (sensu Linsley 1963a), there may exist a virtual continuum of character transition between even the most seemingly disparate genera. For example, several southwestern species of *Enaphalodes* are structurally similar to species in *Elaphidion*, which is, at one character extreme, close to certain species of *Elaphidionoides*, which in turn shows intermediacy with *Aneflus*, *Anelaphus*, and *Aneflomorpha*. These genera are in turn related to *Psyrrassa*, *Micropsyrrassa*, and *Stenosphenus* (via *Aneflomorpha*); *Meganeflus*, *Micraneflus*, and *Neaneflus* (via *Aneflus*); or

Gymnopsyra, *Peranoplium*, *Anopliomorpha*, and *Elaphidionopsis* (via *Anelaphus*). Because there is a transformation series between more derivative genera in a number of tribes, and because relatively little is known concerning the biologies and immature life stages of most Neotropical cerambycids, determinations regarding the rate and direction of phylogenetic progression must for now be viewed as speculative. We have, therefore, used the species aggregate analysis method rather conservatively.

Further, certain elements of the Neotropical Cerambycidae are as yet so poorly known taxonomically as to preclude any meaningful assessment without systematic revision. The value of taxonomic refinement in cerambycid faunal analysis was made obvious by the separation of *Leptostylopsis* from *Leptostylus* (Dillon 1956). A clear zoogeographic division appeared when the characters used to segregate North American species were applied to Middle American forms. Of the 64 species remaining in *Leptostylus* (fide Chemsak and Linsley 1982), all but 16 are from North or Central America, while all of the 24 species reassigned to *Leptostylopsis* are restricted to the West Indies, Florida, or the southern U.S.

GENERIC ORIGINS AND AFFINITIES

A number of genera from Texas and Mexico either have species distributions that display no distinct faunal affinities, or have their nearest relationships within Old World generic complexes. Centers of origin will only be determined by careful study of the beetles and their host plants. Even this approach may not fully resolve the question of generic origin, as Chemsak (1963) explained in his monographic study of *Tetraopes*.

Genera distributed widely over a number of faunal regions include *Crossidius*, *Dectes*, *Hemerana*, and *Mecas*; one common attribute of these genera is that they utilize as larval hosts such plant genera as *Gutierrezia*, *Gymnosperma*, *Haplopappus*, *Chrysothamnus*, *Helianthus*, *Aster*, *Ambrosia*, and *Heterotheca*, most species of which are primary invaders of disturbed substrates. The very broad distributions of some species may be an artifact of the recent spread of their host plants along road and railway grades and into agriculturally altered habitats.

None of the naturally occurring genera in southern Texas are of recent northern origin, but

one Nearctic genus, *Leptura*, is represented by a single species, *L. (Stenura) gigas*. The presence of a Nearctic lepturine may be explained by an early austral ancestry for the subgenus *Stenura*. This taxon contains three very closely related species, together displaying a tricentric pattern of Miocene-Pleistocene relictual distributions. *L. (S.) emarginata* Fabricius is widespread in eastern North America, apparently having spread from the Carolinian faunal region northward and westward to the Great Plains and New England states, and south to central Florida and east central Texas. *Leptura gigas* is confined to the southern two-thirds of Texas, and the rarely collected *L. (S.) splendens* Knull is apparently localized in southeastern Arizona. All three species are very similar in form and coloration, and the known larval habits are nearly identical. *Leptura emarginata* breeds in decaying portions of living hardwood trees or in old stumps and snags, while *L. gigas* infests rotting scars, branch butts, and stumps of the riparian tree genus *Salix*, and to a lesser extent *Populus* and perhaps *Quercus*. Thus, it appears that the present species of *Stenura* arose from a common progenitor that became dispersed into Pleistocene refugia in the southeastern U.S., Texas, and Arizona. Isolation led to species differentiation, with the derivative taxa redistributing themselves into suitable habitats during the recent postglacial (or interglacial) period. *Leptura gigas* and *L. splendens* appear to be constrained by the extreme aridity of the regions surrounding their present ranges, but *L. emarginata* has undergone considerable range expansion, spreading through the mesic forests of the eastern and central U.S. The time of arrival of the *Stenura* progenitor is somewhat problematical, but a Holarctic ancestor would probably have been an early entrant to the Neotropical fauna. The only known fossil species of *Leptura* are found in the Florissant shales of Colorado, indicating that the genus *sensu lato* was present along the southern boundary of the Arcto-Tertiary Geoflora by at least the mid-Oligocene.

The only other Nearctic genera recorded from southern Texas (*Ergates* and *Callidium*) have been taken only as adventitious emergences from imported coniferous fencing and wood products. Two species with very broad host preferences, *Gracilia minuta* and *Hylotrupes bajalus*, are more or less cosmopolitan in distribution, having been spread by commerce into numerous regions in both the Old and New Worlds.

The Alleghenian fauna (in the restricted sense defined by Linsley [1961b]) is rather poorly represented in southern Texas, with only a single species each in *Tylonotus*, *Pseudostrangalia*, and *Astyleiopus*, and two in *Dorcaschema*; however, a number of "Alleghenian" species (in otherwise Neotropically distributed genera) such as *Tragidion coquus*, *Enaphalodes rufulus*, *E. atomarius*, *Elaphidionoides* spp., *Obrium rufulum*, *Megacyllene caryae*, *Rhopalophora longipes*, *Cyrtinus pygmaeus*, and *Eupogonius pauper* reach the study area from the northeast.

The Sonoran fauna enters southern Texas from the west, through the arid portions of the northern Mexican plateau. Many genera of Sonoran origin are more or less restricted to the Chihuahuan Desert, ranging through northern Mexico into extreme southeastern Arizona, southern New Mexico, and east to western and southern Texas. Other genera are more broadly distributed, ranging over the Chihuahuan, Sonoran, and Colorado desert regions from Texas to California. Most species in Sonoran genera are associated with hardwoods and leguminous trees and shrubs, many of which are derivatives of several vegetation types found in the Madro-Tertiary Geoflora (Axelrod 1958). According to Halffter (1976: 8), "the Sonoran cenocron has a two-fold phyletic-biogeographic origin (ancient South American and Paleoamerican) resulting in adaptation to aridity and marked endemism, both of which indicate a strong degree of *in situ* evolution." Sonoran representatives in the south Texas fauna include *Aneflus* (*sensu stricto*), *Styloxus*, *Moneilema*, *Eustromula*, *Taranomis*, *Plionoma*, *Valemus*, and perhaps also *Methia* and *Aneflomorpha*. The latter two genera have species in the Californian, Mexican Montane, Mexican Tropical, Austroriparian, and (*Methia* only) Antillean faunal regions.

The remainder of the southern Texas Cerambycidae are clearly Neotropical, with regions and probable times of phyletic origin ranging from ancient South American to more recent Mexican Plateau faunas. Three monobasic genera—*Pygmaeopsis*, *Cathetopteron*, and *Nathriobrium*—are presently known only from southern Texas. *Nathriobrium* appears to be an isolated relative of the South American genera *Necydaliella*, *Paraleptidea*, and *Cambaia*. The other two genera, although considered to be Tamaulipan endemics, are closely related to Middle American (*Cathetopteron* to various Hemilophini) or Flor-

idan-Antillean (*Pygmaeopsis* to *Zaplopus*) genera. Both would be expected to occur in suitable habitat in adjacent portions of Mexico.

In all, 61 of the Neotropical species listed herein are currently known to occur in North America only in the Tamaulipan Biotic Province. Several wide-ranging monobasic genera (*Geropa*, *Gnaphalodes*, *Ornithia*) reach their northernmost distributional limits in southern Texas, and altogether over 70 of the 172 species now known to occur naturally in the study area have their general ranges extending only south into the American tropics.

A few genera, such as *Elaphidion*, *Spalacopsis*, *Cyrtinus*, and *Leptostylopsis*, have the largest number of their species in the Antillean faunal region, and *Pentanodes* presently contains but two species, *dietzii* from Texas, and *albofasciata* Fisher from Cuba.

Austroriparian faunal elements extending southwest into southern Texas include species in *Archodontes*, *Plectrodera*, *Graphisurus*, *Astyliidius*, and possibly also *Knulliana*.

The majority of the Neotropical cerambycid species in Texas belong to genera extending north from the Mexican Montane or tropical faunal regions of southern Mexico, and Central and South America. Genera reaching southern Texas from the Mexican Montane fauna often have one or more species in the Sonoran region. In some species, such as *Cyphonotida laevicollis*, allopatric subspecies of a single species are found in several different faunal regions. *Prionus*, *Hypexilis*, *Elytroleptus*, *Ochraethes*, *Tylosis*, *Lophalia*, *Mannophorus*, *Tetraopes*, and possibly *Cyphonotida* appear to have originated in the Mexican Montane faunal region.

Genera with primarily Mexican Tropical (Mesoamerican region of Halffter [1976]) distributions include *Psyrassa*, *Parevander*, *Ancylocera*, *Parmenonta*, *Thryallis*, *Strangalia*, and possibly also *Obrium*, *Eudermes*, and *Stenosphenus*. The latter three genera have species in the Vancouverian (*Obrium* only), Sonoran, Mexican Montane, Austroriparian, and Alleghenian faunal regions.

Central and South American genera extending northward through Mexico or across the Caribbean into southern Texas (and rarely into other faunal regions as well) include *Sphaerion*, *Piezocera*, *Neocompsa*, *Tetranodus*, *Dihammophora*, *Dendrobias*, *Lissonotus*, *Megaderus*, *Dorcasta*, *Desmiphora*, and *Cacostola*. The genera

Parandra, *Stenodontes*, *Smodicum*, *Achryson*, *Eburia*, *Heterachthes*, *Neoclytus*, *Rhopalophora*, *Neoptychodes*, *Adetus*, *Ataxia*, *Eupogonius*, *Oncideres*, *Lepturges*, *Urgleptes*, *Hippopsis*, and *Leptostylus* are Pan-American in distribution, occurring collectively from the Californian and Sonoran regions to the Floridan-Antillean region, through the West Indies and into portions of Central and South America.

SUMMARY

The longhorned wood-boring beetles (Coleoptera: Cerambycidae) of southern Texas have been the subjects of entomological investigations for nearly a century, beginning with a brief collecting account by E. A. Schwarz in 1896. Since then, no fewer than seven species lists have been compiled, providing records and distributional data for approximately 100 species. With the addition of the data contained in the present list, the total number of species naturally occurring in the southern portion of Texas stands at 178.

The study area considered herein encompasses a larger geographical area than did most prior accounts; it roughly corresponds to the Texan portions of the Matamorán and Nuecían districts of the Tamaulipan Biotic Province. Collections and field observations for the project were concentrated in the drainage of the Rio Grande River from Zapata County to Cameron County (with particular emphasis upon remnant forest habitats), and the southern Gulf Coast woodlands (most notably at Lake Corpus Christi State Park and Welder Wildlife Foundation Refuge, San Patricio County).

Remnant forest habitats in the lower Rio Grande valley are now almost entirely restricted to parks and preserves, the bulk of most original native floral communities having been eliminated by agriculture and urbanization. Although the sanctuaries are protected from further direct environmental degradation, most are continually subjected to unnatural stress, from outside elements such as agricultural chemical drift and fluctuating water tables, and from within by certain resource management practices. Older interior swamp and hardwood forests, as well as some semideciduous forests and brushland communities, are overmature and appear to be declining. Normal cyclical and successional processes no longer occur within the refugia, and many areas exhibit community senescence and

lowered species diversity and abundance. Geographical isolation in most of the refugia also contributes to the apparent loss of species diversity, by limiting genetic exchange and by making species vulnerable to ecological catastrophes arising from otherwise natural successional and cyclical events. Fire, flood, protracted drought, or severe frost could alone or in combination eliminate sensitive species from isolated habitats, with no natural pathways available for recolonization from other refugia.

Vast tracts of brushland and savanna-woodland habitat remain in the upland portions of southern Texas, but even these have been substantially altered by long-term cattle grazing. This, combined with the introduction of exotic grasses, has changed community compositions and spatial relationships, favoring the spread and increased density of disturbed-land plant genera such as *Abutilon*, *Haplopappus*, and *Viguiera*. Increases in relative abundance and overall distributions of longhorned beetles associated with these plants have also been observed.

Reduction in the number and diversity of host plant species has no doubt already led to the decline or extinction of certain oligophagous species of insects. Mitigating this situation, however, is the polyphagy exhibited by a number of Cerambycidae, which permits exploitation of alternative native hosts and introduced plant species. Twenty species of cerambycids have been reared from girdled limbs of tepehuaje (*Leucaena pulverulenta*), indicating that such natural polyphagy exists, and 15 genera of Cerambycidae have been recorded as breeding in wood of grapefruit and sweet orange (*Citrus* spp.).

Adult cerambycid periodicity is distinctly bimodal; peak spring and fall activity coincides with moderate temperatures and increased precipitation. Summer-active forms are typically nocturnal genera of Sonoran faunal origin. Drought may inhibit or delay emergence of adults of deadwood-boring species, but appears to have less effect upon species breeding within living hosts.

Distributional data indicate that 170 cerambycid species, in 103 genera, naturally occur in southern Texas. The subfamily Cerambycinae comprises over half the fauna with 95 species in 56 genera; Lamiinae are represented by 65 species in 38 genera; Prioninae by 5 species in 4 genera; Lepturinae by 4 species in 4 genera; and Parandrinae by a single species of *Parandra*. The

genus containing the greatest number of south Texan species (7) is *Mecas*, while 17 genera have 3 or more species in the study area.

Although primarily Neotropical in overall origin, southern Texas Cerambycidae also show elements of the Nearctic, Alleghenian, and Sonoran faunal regions. Endemism is fairly pronounced at the species level, with 61 taxa (about 35% of the total) known in the U.S. only from the Tamaulipan Biotic Province. There are 3 monobasic genera, which are at present known only from the lower Rio Grande valley: *Pygmaeopsis*, *Cathopterone*, and *Nathriobrium*.

The Sonoran fauna enters southern Texas from the west via arid portions of the northern Mexican Plateau and is represented by 11 species in 7 genera. Only 4 Alleghenian genera occur in the region, but a number of "Alleghenian" species in otherwise clearly Neotropical genera extend into southern Texas from the east. The Nearctic fauna is represented by a single species of *Lectura*, displaying a relictual Miocene-Pleistocene distributional pattern. *Gracilia minuta* and *Hylotrupes bajulus* are widely distributed by commerce and have essentially cosmopolitan distributions.

The Neotropical species have arisen from a number of apparent centers of evolutionary diversification, including the Mexican Montane, Mexican Tropical, and Central and South American faunal regions, and to a lesser extent, the Antillean region. Seventeen genera are thought to be Pan-American in overall distribution.

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- cenizo—*Leucophyllum frutescens* (Berl.) I. M. Johnston
colima—*Zanthoxylum fagara* (L.) Sarg.
coyotillo—*Karwinskia humboldtiana* (R. & S.) Zucc.
ebony—*Pithecellobium flexicaule* (Benth.) Coulter
granjeno—*Celtis pallida* Torr.
honey mesquite—*Prosopis glandulosa* Torr.
huisache—*Acacia farnesiana* (L.) Willd.
lotebush ("lote")—*Zizyphus obtusifolia* (Hook.) Weberb.
Mexican ash, fresno—*Fraxinus berlandieriana* A. D. C. (Lower Valley)
Mexican olive—*Cordia boissieri* D. C.
red ash—*Fraxinus pennsylvanica* v. *subintegerrima* (Vahl.) Fern. (Welder Wildlife Refuge)
red mulberry—*Morus rubra* L.
retama—*Parkinsonia aculeata* L.
Spanish dagger, yucca—*Yucca treculeana* Carr.
sugar hackberry—*Celtis laevigata* v. *texana* (Scheele) Sarg.
tepehuaje, lead tree—*Leucaena pulverulenta* (Schlect.) Benth.
Texas palmetto—*Sabal texana* (Cook) Becc.
Texas kidneywood—*Eysenhardtia texana* Scheele
Texas persimmon—*Diospyros texana* Scheele
western soapberry, jaborcillo—*Sapindus saponaria* v. *drummondii* (H. & A.) Benson

APPENDIX A

List of Common and Scientific Names of Plants Cited in Species Accounts

(Terminology according to Correll and Johnson 1970)

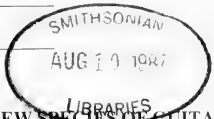
anaqua—*Ehretia anacua* (Berl.) Johnston
black willow—*Salix nigra* Marsh
brasil—*Condalia Hookeri* M. C. Johnston
cedar elm—*Ulmus crassifolia* Nutt.

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**RHINOBATOS PUNCTIFER, A NEW SPECIES OF GUITARFISH
(RHINOBATIFORMES: RHINOBATIDAE) FROM THE RED SEA,
WITH NOTES ON THE RED SEA BATOID FAUNA**

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ABSTRACT: A new species of guitarfish, *Rhinobatos punctifer*, is described from a single 705-mm specimen from the Gulf of Aqaba, Red Sea. Apparently the specimens reported as *R. schlegelii* by Gohar and Mazhar (1968) from Suez were the same species. *Rhinobatos punctifer* belongs in the subgenus *Rhinobatos*. It is characterized by a moderately long, angular, blunt-tipped snout (preoral snout 2.8 times mouth width); broad rostral ridges well separated along their length; large eyes (greatest eye diameter 1.3 times interorbital space); oblique broad nostrils, their width 1.3 in mouth width; mouth nearly straight, its width 6.7 in distance from snout to anus; origin of dorsal fin posterior to pelvic bases by a distance 1.5 in interdorsal space; regularly spaced, small white spots on head, disc, pelvic fins, and tail; no pale edge on snout.

INTRODUCTION

Norman (1926), in a revision of the guitarfish genus *Rhinobatos* Linck, 1790, reported two species from the Red Sea: *R. halavi* (Forsskål 1775), and doubtfully *R. thouni* (Anonymous 1798). In *Fishes of the Red Sea and Southern Arabia*, Fowler (1956) accepted these two species and listed also *R. schlegelii* Müller and Henle, 1841 and *R. granulosus* Cuvier, 1829. Fowler based his inclusion of *R. schlegelii* on a listing by Zugmayer (1913), who reported the species from Oman, not from the Red Sea. (Norman [1926] gave the distribution of *R. schlegelii* only as China and Japan.) Fowler (1956) specifically listed the Red Sea

among the localities for *R. granulosus*; but he examined no Red Sea material, and neither of the references he gave with the species included the Red Sea. Nor could Fowler have been citing the Red Sea record of *R. granulosus* by Bamber (1915) because Fowler followed Norman in considering this a misidentification of *R. halavi*. We, therefore, regard Fowler's (1956) record of *R. schlegelii* from the Red Sea as false and that of *R. granulosus* as very doubtful.

Gohar and Mazhar (1964) reported four white-spotted specimens of *Rhinobatos*, "ranging from 62 to 80.5 cm in length," from the Suez market as *R. schlegelii*. Apparently their specimens were not retained.

The junior author obtained a specimen from fishermen in the Gulf of Aqaba, Red Sea, which appears to be the same species as that reported as *R. schlegelii* by Gohar and Mazhar (1964). Com-

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parison of this specimen with published accounts and material of species of *Rhinobatos* convinced us that it is not *R. schlegelii* but a new species that we name *R. punctifer*. The holotype has been deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). Specimens of related species were examined at the British Museum (Natural History), London (BM [NH]). Photographs are provided herein of the holotype (Fig. 1) and of specimens of two other species of the genus that have been recorded from the Red Sea, *R. halavi* (Fig. 2) and *R. thouin* (Fig. 3). (The photo of *R. thouin* is of an Indonesian specimen; we have not seen Red Sea material of this species.)

The new species falls in Norman's (1926) subgenus *Leiobatus* Rafinesque, 1810 of the genus *Rhinobatos*. However, because of the inclusion of *R. rhinobatos* (Linnaeus, 1758) in *Leiobatus* and the assignment of *R. rhinobatos* as type species of *Rhinobatos* by absolute tautonymy, *Leiobatus* of Norman should be considered a junior synonym of the subgenus *Rhinobatos* Linck, 1790. Norman (1926) listed seven species in *Leiobatus* (*Rhinobatos*): *R. schlegelii*, *R. rhinobatos*, *R. holcorhynchus* Norman, 1922, *R. formosensis* Norman, 1926, *R. annandalei* Norman, 1926, *R. lionotus* Norman, 1926, and *R. hynnicephalus* Richardson,

1846. Additional species include *R. albomaculatus* Norman, 1930, *R. irvinei* Norman, 1931, and *R. punctifer*. All of the species in Norman's subgenus *Leiobatus* agree in having a moderately long, pointed, angular snout and anterior nasal flaps extending medially onto the internasal space but not nearly meeting on the midline of the snout.

Rhinobatos punctifer can be distinguished from all other species in this group by a combination of characters including its broad but elongated and angular snout, broad, well-separated rostral ridges, reduced spination, and white spots. Characters distinguishing *R. punctifer* are presented in the diagnosis below.

Rhinobatos punctifer, new species

Figure 1

HOLOTYPE.—BPBM 20843, 705 mm total length, adolescent male, Red Sea, Gulf of Aqaba, from fishermen through Coral World, Eilat, J. E. Randall, 8 August 1976

DIAGNOSIS.—A *Rhinobatos* with a moderately elongate, broad and bluntly round-tipped, angular snout, with a slightly concave margin towards tip; tip of snout not laterally expanded; preoral snout 2.8 times mouth width; preorbital snout 2.3 times distance between spiracles; distance from tip of snout to anterior edge of eye 1.5 in distance

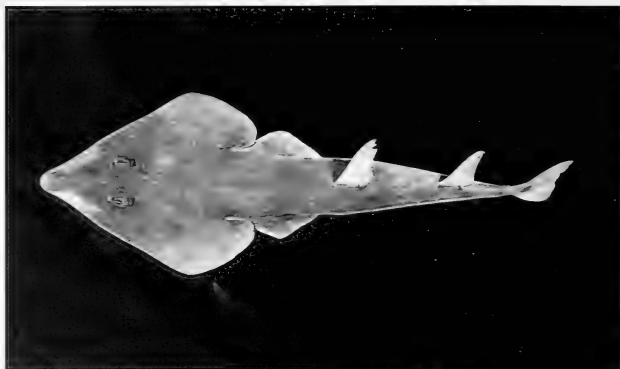


Figure 1. Holotype of *Rhinobatos punctifer*, BPBM 20843, 705 mm, Gulf of Aqaba

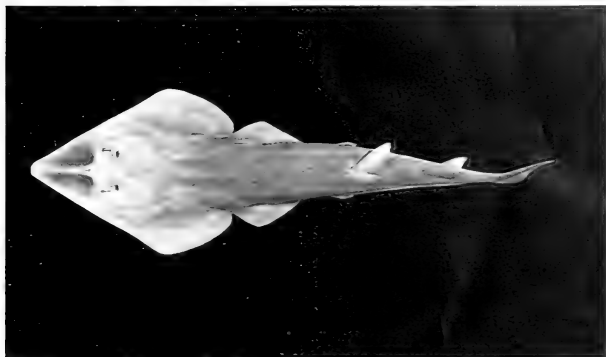


Figure 2. *Prionace glauca* BSBM 2094. 42 cm. 1969.



Figure 3. *Prionace glauca* BSBM 2095. 43 cm. 1969.

from posterior edge of eye to pectoral axil; rostral ridges of snout broad, thick, widely separated from each other along their lengths, slightly divergent basally but then somewhat convergent anteriorly, not fused together or touching each other over precerebral cavity of rostrum; eyes large, length of eyeball 1.3 times interorbital space, 3.2 in preorbital snout; interorbital space slightly concave; distance from front of eye to rear edge of spiracle about equal to distance between spiracles; spiracles with two moderately strong posterior ridges; nostrils oblique, at about a 57° angle to longitudinal axis of snout; nostrils moderately broad, their width 1.3 in mouth width, 1.9 times internarial space; anterior nasal flaps with medial folds extending onto internarial space but not medial to the excurrent apertures; anterior nasal flap with a long, broad lobe at its midlength; posterior and posterolateral nasal flaps very broad; horizontal distance from lateral edge of incurrent aperture to lateral margin of snout 4.6 in preoral snout; mouth nearly straight, its width 6.7 in distance from snout to vent; first dorsal fin with origin posterior to pelvic bases by distance of 1.5 in interdorsal space, its base 2.5 in interdorsal space, its height about 1.2 times its length; enlarged denticles or thorns obsolete on dorsal surface of body, absent on snout tip and rostral ridges; denticles on scapular region, midline of back, and between and behind dorsal fins minute, blunt, and inconspicuous; rostrum 1.3 times nasobasal length of cranium (from base of rostrum to occipital condyle), its width across nasal capsules 1.3 times nasobasal length; nasal capsules oblique; pectoral fin with 71 radials (including 33 propterygial radials); 179 free vertebral centra behind synarcual; back with regular, symmetrical, wide-spaced, small white spots on head, disc, pelvic fins and tail; no light stripes on snout edge.

DESCRIPTION.—Proportional dimensions of holotype, 705 mm total length, as percentages of total length, are as follows.

Snout to: nostrils, 10.8; eyes, 12.6; mouth 15.9, fifth gill openings, 24.7; pectoral apices, 28.4; pectoral rear tips, 40.9; first dorsal origin, 53.0; second dorsal origin, 72.3; pelvic origins, 35.0; vent, 37.9; upper caudal origin, 64.4.

Distance between: front edge of eye and rear margin of spiracle, 5.4; eyeball to pectoral axil, 18.9; outer edge of nostril to rim of disc, 3.5; first and second dorsal bases, 13.2; pectoral and pelvic bases, 0.6; pelvic and first dorsal origins, 17.7; pelvic and first dorsal bases 14.1; second dorsal

base and upper caudal origin, 7.4; pelvic bases and lower caudal origin, 44.0.

Eye: length of eyeball, 4.0; length of cornea, 3.0; interorbital space, 34.0.

Nostril: diagonal width, 4.5; length, 3.0; internarial, 2.4.

Spiracle: width, 3.3; interspiracular, 5.5.

Mouth: width, 5.7; length, 3.0.

Gill openings: width of first, 1.4; second, 1.6; third, 1.6; fourth, 1.4; fifth, 1.1. Width between first, 12.5; width between fifth, 8.7.

Height of: head at eyes, 3.4; trunk at pectoral insertions, 4.8; trunk at pelvic insertions, 5.0.

Width of trunk at: pectoral insertions, 12.3; pelvic insertions, 8.8.

Pectoral disc width: 33.8.

Pelvic fin: anterior margin length, 10.1; height, 5.5; base length, 9.4; inner margin length, 7.3; length of fin from origin to free rear tip, 16.7.

First dorsal fin: anterior margin length, 11.9; height, 9.5; base length, 5.4; inner margin length, 2.7; length of fin from origin to free rear tip, 8.1.

Second dorsal fin: anterior margin length, 10.8; height, 8.5; base length, 5.5; inner margin length, 2.4; length of fin from origin to free rear tip, 7.8.

Caudal fin: dorsal margin length, 15.2; preventral margin, 7.4.

Snout broadly wedge-shaped, angle in front of eyes 66° ; fifth gill openings about $2/3$ length of first 4; posterolateral nasal flaps extending from posterior margin of incurrent apertures to inner third of excurrent aperture; tooth row counts 76/22 or 37–1–38/34–38; teeth with low, oval, transversely elongated crowns, indistinct cutting edges, no transverse ridges, strong basal ledges and grooves, and small roots, regularly increasing in size from symphysis to mouth corners and not abruptly enlarged in symphyseal region; disc width 87% of disc length; tail from vent to caudal tip 1.6 times snout-vent length, nearly flat below, rounded above, and tapering to caudal fin, its width at pelvic insertions 1.6 times distance between spiracles; tail with lateral dermal folds originating slightly anterior to free rear tips of pelvises and reaching just behind lower caudal origin, widths of folds opposite interdorsal space about $1/7$ of eyeball length.

First dorsal fin slightly larger than second, both triangular, with slightly convex anterior margins, narrowly rounded or pointed apices, concave, nearly vertical posterior margins, angular, slightly pointed free rear tips, and convex inner margins; inner margins of dorsal fins $2/5$ to $1/2$ length of ba-

ses; interspace between second dorsal base and upper caudal origin 1.3 times length of second dorsal; pelvic fins with slightly convex anterior margins, narrowly rounded apices, convex posterior margins, narrowly rounded free rear tips, straight inner margins, and free rear tip angles of about 128°; pelvic lengths from origins to free rear tips 1.8 times base lengths; caudal fin with upper origin slightly anterior to lower origin, dorsal margin convex and with length about 1.2 times interdorsal space, broadly convex preventral margin, broadly rounded ventral apex, undulated postventral margin, and angular dorsal apex; caudal fin without ventral lobe, with axis at about a 16° angle above body axis; epaxial lobe of caudal as high as hypaxial lobe.

Dermal denticles minute, close-set, covering entire body except for area behind posterior nasal flaps on snout, upper lip, and chin, and at pectoral, pelvic, and dorsal fin axils; lateral trunk denticles above the pelvic fin bases with wedge-shaped crowns, low but strong medial ridges, sometimes low lateral ridges, and broad, blunt medial cusps; one or two small, inconspicuous, blunt denticles or thorns present on scapular region; similar denticles at front edges of eyes and along supraorbital ridges.

Rostral cartilage broad, its shaft nearly uniformly wide behind rostral node; rostral appendices broadly expanded and rounded, not angular; rostrum enclosing a broad precerebral cavity that tapers only slightly to rostral node; dorsal edges of precerebral cavity (rostral ridges on surface of snout) broadly separated along their lengths; nasal capsules large, their transverse axes anterolaterally directed; width across nasal capsules 1.3 times nasobasal length of cranium (base of rostrum to occipital condyles); length of nasal capsules about equal to their width; basal plate narrow, its width at anterior ends of orbits 0.2 times in nasobasal length; cranial roof with small, keyhole-shaped frontal fenestra, well behind anterior fontanelle; antorbital cartilage triangular, broad, and wedge-shaped posteriorly, without an anterior lobe extending past nasal capsules; postorbital processes large and bifurcate; preorbital processes poorly differentiated on supraorbital crests; width across postorbital processes 0.6 times nasobasal length; width across otic capsules 0.4 times nasobasal length.

Pectoral fin skeleton with 33 propterygial, 6 mesopterygial, 2 neopterygial, and about 30 metapterygial radials; anteriormost radials of pro-

pterygium reaching in front of base of nasal capsules by about 0.08 of rostral length; pelvic girdle medially arched, with short, broad lateral prepubic processes and narrow, falcate iliac processes; pelvic fin with about 26 radials.

Vertebral column with cervicothoracic synarcual having 15 centrum-free segments and 14 centra (29 total), 27 monospondylous precaudal centra behind synarcual (most with elongate, slender ribs), 104 diplospondylous precaudal centra, and 48 caudal centra; total segments 208 and total centra 193; intestinal valve of spiral type, with 11 turns.

Color in preservative medium brown on dorsal surface of disc and tail, cream below; rostral ridges darker but with a light area on either side of rostrum; small light spots, the largest about 5 mm wide, mostly arranged in sparse, transverse rows on dorsal surface of head, disc, pelvic fins, and tail in front of second dorsal base; underside of preoral snout with a dusky blotch.

DERIVATION OF NAME.—Latin *punctifer*, bearer of spots, for the prominent regular pattern of white spots on the dorsum

COMPARISON WITH OTHER SPECIES OF *RHINOBATOS*.—As noted above *Rhinobatos punctifer* is closest to seven species of Eastern Hemisphere *Rhinobatos* included by Norman (1926, 1930, 1931) in the subgenus *Leibobatos* (= *Rhinobatos*). Of these, *Rhinobatos rhinobatos* occurs in the Mediterranean Sea and eastern Atlantic. It differs from *R. punctifer* in having a more angular, narrow-tipped, bottle-shaped snout; rostral ridges closer together; nostrils smaller, with widths 1.1 to 1.3 times internarial space, 1.7 in mouth width; supraorbital, scapular, and mid-dorsal thorns well developed; distance from first dorsal origin to pelvic bases 1.1 in interdorsal space; and no white spots. Two specimens of *Rhinobatos rhinobatos* BM(NH) 1935.3.5.1, a 487-mm female, and BM(NH) 1936.4.14.44, a 478-mm immature male, were examined for this study.

Two West African species of this group, *Rhinobatos albomaculatus* and *R. irvinei* (descriptions by Norman 1930, 1931), have white spots like *R. punctifer*; the holotypes (*R. albomaculatus*, BM[NH] 1930.3.24.2, 566-mm female; *R. irvinei*, BM[NH] 1930.8.26.3, 569-mm adult male) were examined. These two species differ from *R. punctifer* in having more acutely angular, narrow-tipped snouts; narrower, more closely confluent rostral ridges; smaller eyes, 4 to 4.8 times in pre-

orbital snout; smaller, more widely spaced nostrils, 1.3 times internarial space and 1.7 to 1.9 in mouth width; and first dorsal base 3.1 to 3.3 in interdorsal space. *Rhinobatos irvinei* also differs from *R. punctifer* in having dark spots on the interorbital space and small but prominent supraorbital, scapular, and middorsal denticles. Both *R. albomaculatus* and *R. irvinei* were placed in the genus *Rhynchobatus* by Bigelow and Schroeder (1953) because of their supposedly notched tails with ventral caudal lobes, but both holotypes of these species proved to belong to *Rhinobatos*, having damaged, artificially notched tails.

Rhinobatos holcorhynchus is an Indian Ocean, South African species similar to *R. punctifer* and redescribed by Norman (1926) and Wallace (1967). It differs from *R. punctifer* in having a longer, narrower snout with the preorbital length 2.8 times the interspiracular space; the distance from first dorsal origin to pelvic bases 1.3 in interdorsal space; large supraocular, scapular, and middorsal thorns; and no white spots.

Rhinobatos annandalei and *R. lionotus* are two similar species described by Norman (1926) from the Bay of Bengal. They are close to *R. punctifer* but differ from it in having narrower snout tips; rostral ridges much closer together; nostrils smaller and more widely separated, 1.7 in mouth width and 1.3 times internarial space; and no white spots. *Rhinobatos annandalei* additionally differs by having conspicuous, sharp-tipped superocular, scapular, and middorsal thorns, and *R. lionotus* by having the first dorsal origin posterior to the pelvic bases by a distance equal to the interdorsal space.

Three western North Pacific species, *Rhinobatos schlegelii*, *R. hynnicephalus*, and *R. formosensis* are similar to *R. punctifer*, but all differ in having narrower-tipped snouts with rostral ridges close together; smaller nostrils, 1.2 to 1.5 times internarial space and 1.4 to 1.7 in mouth width; and origin of first dorsal posterior to pelvic bases by 1.0 to 1.3 times in interdorsal space. *Rhinobatos schlegelii* and *R. formosensis* additionally differ in their much longer snouts, with the preorbital snout 3.1 to 3.3 times interspiracular, preoral snout 3.3 to 3.7 times mouth width, and plain coloration; *R. schlegelii* in its more bottle-shaped snout and weak spiracular ridges; and *R. hynnicephalus* in its smaller eyes, 4.7 to 5.8 in preorbital snout, and dorsal color pattern with rosettes of dark spots but no white spots. Apparently, there

are no confirmed records of *R. schlegelii* in the Red Sea or even the Indian Ocean, that of Gohar and Mazhar (1964) from Egypt being based on *R. punctifer* and that of Fowler (1956) from Oman uncertain. According to Norman (1926), *R. schlegelii* has been confused with *R. lionotus*, as well as with the western Pacific *R. formosensis* and *R. hynnicephalus*.

Among other species of *Rhinobatos* in the Red Sea, *R. halavi* was recorded as very common off Egypt (Gohar and Mazhar 1964) and was collected in 1982 by the junior author at Jeddah, Saudi Arabia. *Rhinobatos halavi* differs from *R. punctifer* in its shorter, more acutely angular snout; rostral ridges closely adjacent to each other along their lengths; smaller eyes; lower spiracular ridges; anterior nasal flaps not extending onto the internasal space; enlarged rostral, supraorbital, scapular and middorsal thorns; and plain coloration. The other Red Sea species, *R. thouin*, has not been recently reported from the Red Sea and its presence there requires confirmation. It is easily separable from *R. punctifer* by its extremely elongate, attenuate snout (the preorbital snout 3.3 to 3.7 times the interspiracular space) with laterally expanded tip (unlike that of any other living rhinobatoid). It also has narrow, closely spaced rostral ridges; weak spiracular ridges; narrower nostrils, with very small and narrow anterior, posterior, and posterolateral nasal flaps; anterior nasal flaps not extending medially onto the internarial space; enlarged rostral, supraorbital, scapular, and middorsal thorns; and plain coloration.

NOTES ON THE RED SEA BATOID FAUNA

We preface remarks on the Red Sea batoid fauna with a checklist of species, mostly compiled from available literature (including Fowler 1956; and Gohar and Mazhar 1964). The ray fauna of the Red Sea is poorly known, more so than the shark fauna, and the following list is tentative:

Order RHINOBATIFORMES

Family RHYNCHOBATIDAE

Rhina ancylostoma (Bloch and Schneider, 1801),
Rhynchobatus djiddensis (Forsskål, 1775).

Family RHINOBATIDAE

Rhinobatos halavi (Forsskål, 1775), *R. punctifer* Compagno and Randall, new species, and *R. thouin* (Anonymous, 1798).

Order PRISTIFORMES

Family PRISTIDAE

Anoxypristis cuspidata (Lathan, 1794), *Pristis pectinata* Latham, 1794, *Pristis zijsron* Bleeker, 1851 (note, photos labeled *Pristis pectinata* in Gohar and Mazhar, 1964 apparently are of *P. zijsron*, hitherto not known from the Red Sea).

Order TORPEDINIFORMES

Family TORPEDINIDAE

Torpedo panthera Olfers, 1831, *T. sinuspersici* Olfers, 1831.

Order MYLIOBATIFORMES

Family DASYATIDAE

Himantura gerrardi (Gray, 1851), *H. imbricata* (Bloch and Schneider, 1801), *H. uarnak* (Forsskål, 1775), *Hypolophus sephen* (Forsskål, 1775), *?Taeniura grabata* (St. Hilaire, 1809), *T. lymma* (Forsskål, 1775), *T. melanospilos* Bleeker, 1853, *Urogymnus asperimus* (Bloch and Schneider, 1801).

Family GYMNURIDAE

Aetoplatea tentaculata Valenciennes in Müller and Henle, 1841, *Gymnura poecilura* (Shaw, 1804).

Family MYLIOBATIDAE

Aetobatus narinari (Euphrasen, 1790), *Aetomylaeus milvus* (Valenciennes, in Müller and Henle, 1841).

Family MOBULIDAE

Manta ehrenbergi (Müller and Henle, 1841) or *M. birostris* Walbaum, 1792), *Mobula kuhlii* (Valenciennes in Müller and Henle, 1841) or *M. diabolus* (Shaw, 1804).

Like the Red Sea shark fauna, the batoid fauna of the Red Sea is relatively depauperate with fewer species than the western Indian Ocean and with the fauna comprising coastal-benthic, coastal-pelagic, and epipelagic species. There are no deep-water Red Sea rays and no Red Sea members of the order Rajiformes, although deep-sea rays including rajoids occur in the Gulf of Aden. Of the 24 species listed above, 22 are also found in the western Indian Ocean. The ones not known from this region are *Rhinobatos punctifer* and the dubiously recorded *Taeniura grabata* (otherwise known from the Mediterranean Sea and eastern Atlantic). Three of the Red Sea batoids are circumtropical in distribution: *Pristis pectinata*, *Aetobatus narinari*, and *Manta birostris* (providing *M. ehrenbergi* is a junior synonym of it). If the

West African *Urogymnus africanus* is a junior synonym of the Indo-Pacific *U. asperimus*, then it too ranges beyond the Indo-West Pacific region. Compared to the Red Sea shark fauna, the Red Sea batoids have a much lower proportion of epipelagic and circumtropical species and more Indo-West Pacific species. *Rhinobatos punctifer* is currently the only known endemic Red Sea elasmobranch, but it may eventually be collected in the northwestern Indian Ocean. On the other hand, it may prove to be confined to the cooler northern part of the Red Sea. *Taeniura grabata* is a species otherwise known from the Mediterranean Sea and eastern Atlantic, but records of it from the Red Sea are apparently doubtful (Kreffit and Stehmann 1973).

The nature of the Red Sea batoid fauna may be due to restrictive conditions in the Red Sea environment, limiting inshore species that can live there and barring deep-water species. Presumably, the Red Sea batoid fauna originated by dispersal from the western Indian Ocean.

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ADDENDUM

While this paper was in production, an additional specimen of *Rhinobatus punctifer* was collected in the Gulf of Aqaba. We add this specimen here as a paratype for the Hebrew University of Jerusalem (HUJ). It is HUI 11733, 645 mm total length, taken with a gill net off Coral World, Eilat, at a depth of 240 m by Eli Kalmanson on 14 November 1986.

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PROCEEDINGS
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REVIEW OF THE TENEBRIONID TRIBE ANEPSIINI (COLEOPTERA)

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ABSTRACT: The systematics of the 13 known species of Anepsiini is reviewed. Cladistic relationships support recognition of four genera, including the new genus *Batuliomorpha*. Keys, descriptions, and diagnoses are provided for genera and species. New species are: *Anepsius minutus*; *Batuliomorpha comata*, *B. imperialis*, and *B. tibiodentata*; *Batuliodes wasbaueri*, *B. obesus*, and *B. spatulatus*. *Anepsius confluens* (Blaisdell) is newly transferred to *Batuliodes*. In *Anepsius* and *Batuliodes* the more primitive species are surface dwellers, while the more derived ones are strongly modified for a psammophilous existence. *Batulus* and *Batuliomorpha* contain only psammophilous species.

INTRODUCTION

The Anepsiini comprise a small group of little-studied species that occupy arid or subarid habitats in western North America. Aside from the rather brief consideration of higher classification by Doyen and Lawrence (1979), previous systematic treatments have consisted of isolated descriptions of species (LeConte 1851; Casey 1907; Blaisdell 1923) or very superficial analyses of generic interrelationships (LaCordaire 1859; Horn 1970; Casey 1907). During the last few years, a number of undescribed species have been collected from sand dunes in southeastern California and Baja California. Several of these are strongly modified for a psammophilous existence, and significantly increase the morphological variability within Anepsiini. Conversely, a number of names proposed by Casey (1907) need to be placed in synonymy. In addition, this paper reevaluates generic interrelationships and provides keys to genera and species.

MATERIALS AND METHODS

Anepsius delicatulus is commonly found under stones, but other members of Anepsiini are sel-

dom noticed, due to their small size, cryptic coloration, lethargic movements, and nocturnal activity. They are most effectively collected in pitfalls, particularly those left in the substrate for extended periods with a preservative such as ethylene glycol. Dune-inhabiting species may be sifted from the sand about the bases of plants, but several of these species are small enough to pass through the mesh of standard window screening.

Morphological terminology generally follows that in Doyen (1966). Orientation and terminology used in describing the legs follow Doyen (1984). Measurements were made with an ocular micrometer and grid. Elytral length (EL) is the distance from the posterior tip of the scutellum to the elytral apex, measured parallel to a frontal plane through the body. Pronotal length (PL) is measured along the midline; elytral and pronotal widths (EW, PW) are maximum dimensions perpendicular to a sagittal plane.

Type specimens of all described species were examined. Holotypes of species described by Casey (1907) and considered in this paper are located in the United States National Museum; those described by Blaisdell (1923, 1943) are located in the California Academy of Sciences.

BIOLOGY

Life histories of Anepsiini are essentially unknown. Larvae have not been associated with any species. I was unable to obtain eggs or larvae from caged adults of *Anepsioides delicatulus* and *Batuliomorpha comata*, although some adults survived for many weeks or months.

Anepsioides delicatulus, *Batuliodes confluentis*, and probably *A. minutus* and *B. rotundicollis* are surface-dwelling species that hide under stones and in other refuges. *Anepsioides delicatulus* is occasionally encountered on the soil surface at night. All four species appear to be active throughout the year except during the coldest months in the northern portions of their ranges. For example in a pitfall survey of ground-dwelling arthropods at Owens Lake, Inyo County, California *Anepsioides delicatulus* was recorded in all but three months, with peak numbers in May (Fig. 1) (F. Andrews, A. Hardy; personal communication). In warmer portions of its range, such as the San Joaquin Valley and the Los Angeles Basin, specimens have been collected in every month. A similar pattern was found for *Batuliodes rotundicollis* in the Eureka Valley (Mono County, California) (Andrews et al. 1979), where activity was almost entirely restricted to the period between May and September (Fig. 1). Presumably this reflects the relatively severe climate of the Eureka Valley at about 915 m. Once again, in warmer parts of *B. rotundicollis*'s range, collection records exist for most months of the year.

These more generalized, surface-dwelling species range over a variety of sandy and rocky substrates in arid and subarid habitats. In their survey at Owens Lake, Andrews et al. recorded *Anepsioides delicatulus* principally from the *Larrea, Franseria dumosa*, *Atriplex-Franseria*, and *Atriplex confertifolia* associations recognized by Matson (1976). These plant associations occur on alluvial substrates that are not strongly alkaline. Only three of the beetles were recorded from alkali scrub associations, and none were taken from sand dune habitats. However, *Anepsioides delicatulus* is common on the remnant sand hills near Antioch, Contra Costa County, California, and I have taken it from aeolian sand in the Ciervo Hills, Fresno County (J. Doyen Lot #75C4).

In the Eureka Valley *Batuliodes rotundicollis* was common on rocky hillsides and alkali scrub, but was never found on the aeolian dunes. Specimens have been recorded from the Saline

Valley Dunes (Inyo County, California), but appear to be much more abundant on harder substrates.

In contrast to the more generalized group of species discussed above, *Anepsioides montanus*, *Batuliodes obesus*, *B. spatulatus*, *B. wasbaueri*, *Batulius setosus*, and the species of *Batuliomorpha* are all apparently restricted to aeolian sand. Adults shelter beneath the sand surface during the day, sometimes about the bases of vegetation, emerging nocturnally. Available collection records indicate that these species are active during the winter and spring months, but no intensive surveys have been conducted throughout the year. The habits of *A. valens* are unknown.

HIGHER CLASSIFICATION OF ANEPSIINI

In the paper in which he originally described *Anepsioides* and *Batulius*, LeConte (1851) did not use higher level categories. Thus LaCordaire (1859) made the initial tribal placements, including *Anepsioides* in his Triboliides and *Batulius* in his Ulomides vrais. His placement of these genera in tribes possessing defensive glands was based on superficial characters. The fundamental differences in abdominal structure were unrecognized at that time. Separation of *Anepsioides* and *Batulius* was necessary in his classification because of their different mesocoxal configurations. LeConte (1862) included both genera in his Anepsiini, which he placed in his subfamily Tentyriinae. Horn (1870) removed *Batulius* to his tribe Batuliini, which he left in Tentyriinae, but he transferred Anepsiini to the Asidinae. These changes, again based on the differences in mesocoxal structure, were subsequently followed by LeConte and Horn (1883). Casey (1907) recognized the close relationship between *Anepsioides* and *Batulius*, suggesting that all should form a single tribe, probably without subdivisions. He stressed the strong overall similarity, emphasizing especially the unusual elytral sculpture shared by *Anepsioides* and *Batuliodes*, which he split from *Batulius* to receive *rotundicollis* LeConte. Casey was uncertain whether to apply Anepsiini or Batuliini as the proper name, but his comments regarding relationship and classification were essentially correct. Subsequent catalogers (Leng 1920; Gebien 1937; Papp 1961) continued to recognize two tribes, but heeded Casey by giving them adjacent positions in the subfamily Asidinae. Doyen and

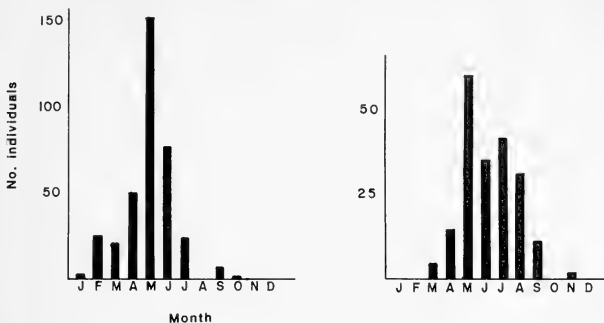


FIGURE 1. Left: Seasonal distribution of *Anepsius delicatulus* at Owens Lake, Inyo County, California. (Based on data from October, 1977 to January, 1979, courtesy of F. Andrews and A. Hardy, California Department of Food and Agriculture.) Right: Seasonal distribution of *Batuliodes rotundicollis* in the Eureka Valley, Mono County, California. (Based on data from October, 1977 to January, 1979, from Andrews, et al. 1979.)

Lawrence (1979) redefined *Anepsiini* to include *Batuliini* and suggested that *Batuliodes* should be placed in synonymy under *Batulus*. That classification is followed here, except that I resurrect *Batuliodes* as a valid name for the reasons detailed below.

Blackwelder (1945), and later Papp (1961), recognized the subfamily *Batuliinae* without formal definition. From their checklists it is impossible to determine which taxa, if any, they intended to include other than *Batuliini*.

Relationships of *Anepsiini* to other groups of *Tentyriinae* are uncertain. The relatively small mentum is shared with tribes such as *Stenosini*, *Coniontini*, *Lachnogyini*, *Cnemoplathiini*, and *Cryptochilini*, as well as difficult to place genera such as *Idisia* Pascoe. Divided eyes are widespread in *Stenosini* (undivided in *Stenosis*) and also occur in *Typhlusechus*, *Alaudes*, and *Boromorphus*. A further character shared by *Anepsiini* and most *Stenosini* is the integration of the elytral bases and the scutellum into the collarlike mesothorax, which is amplexed into the prothorax. The anterior, amplexed parts of the elytra and the scutellum are depressed below the level of the elytral disk. The scutellum is visible only if the prothorax is moved forward, relative to the elytra. In tribes such as *Coniontini* a relatively

small portion of the elytra is incorporated into the mesothoracic collar. In *Cryptoglossini*, a relatively large part of the elytra forms the dorsolateral parts of the collar, but the scutellum remains exposed on the elytral disk. I have not surveyed these complex structures extensively in *Tentyrioid* *Tenebrionidae*, and their taxonomic value is uncertain. Final resolution of the relationships of the *Tentyrioid* tribes will require detailed morphological comparisons across the entire subfamily. At present the *Anepsiini*, *Stenosini*, and probably the *Eurychorini* (Koch 1955) may be considered to comprise a somewhat isolated clade within *Tentyriinae*.

Relationships within *Anepsiini* were assessed by analyzing 27 characters across all the species. Character polarities were determined by out-group comparison with other tribes of *Tentyriinae*. This procedure is rendered difficult by the large size and structural diversity of many of these tribes, which may themselves show more than one state for some characters. Characters and character-state polarities are discussed below and listed in Appendix 1.

Antennal configuration (Characters 1-5). In *Anepsius delicatulus* the antennae are gradually enlarged to the 10th segment (Fig. 9), have no distinct club, and are relatively long. In all other spe-

cies the last 3 or 4 segments are abruptly enlarged as a slight but distinct club (Fig. 7–8). Clavate antennae are commonplace in Tentyriinae and are therefore considered the primitive condition in Anepsiini. The two types of clubs probably developed independently, since the lineages in which they occur differ in numerous other features.

In burrowing species antennae are variably shortened. This derived condition, along with several other features correlated with a strongly psammophilous mode of life, has apparently arisen independently several times. Analogous shortening of antennae occurs in many other psammophilous Tenebrionidae.

It is difficult to assign polarity to Character 5 (shape of apical antennal segment). Probably the subquadrate condition is associated with psammophily and shortening of the antennae.

Tentorial configuration (Character 6). In most Anepsiini the tentorium consists of subvertical lateral laminae, connected posteriorly by a transverse bridge. This primitive condition prevails through a great majority of Tenebrionidae. In *Batuliomorpha*, the posterior space between the transverse bridge and the ventral part of the occipital foramen is closed by a sheet of cuticle (Fig. 2). As far as known, this state is unique to *Batuliomorpha*. Possibly it is correlated to the functioning of the mouthparts, whose muscles attach in part to the tentorium.

Epistomal margin (Character 7). Both truncate and emarginate epistoma are common in Tentyriinae. However, the configuration in *Batuliodes*, with rather prominent lateral lobes and a nearly straight medial portion is distinctive and considered derived.

Submental gland (Character 8). This secondary sexual feature was discussed in some detail and illustrated by Doyen and Lawrence (1979). It is almost certainly a synapomorphy in Anepsiini, but it is unclear whether its absence in *Batuliodes* represents a primitive lack or a secondary loss.

Pronotal configuration (Characters 9–12). In most Tentyriinae the pronotum has distinct angles and carinate lateral margins without fimbriation. This plesiomorphous condition pertains in *Anepsius*. In *Batuliodes*, the posterior angles are strongly obtuse basally but are produced and acute or nearly right angled near the apex. In psammophilous species the pronotal margins become fimbriate, and the lateral carinae may be

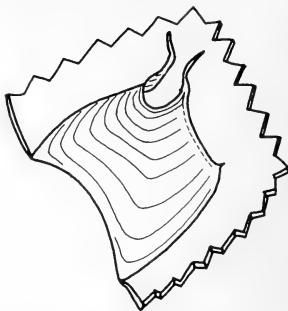


FIGURE 2. Tentorium of *Batuliomorpha comata*, posterior oblique aspect; surrounding cranium removed.

faint or lacking. These latter modifications appear in diverse groups of psammophilous Tentyriinae.

Sculpture of hypomeron (Characters 13–14). Polarity of these characters is uncertain.

Elytral fimbriation (Character 15). The plesiomorphous, glabrous state occurs in nonburrowing forms. Fimbriae very likely developed independently in all psammophilous lineages.

Elytral sculpture (Character 16). As noted by Casey (1907:503), Anepsiinae are characterized by a peculiar pattern of elytral sculpturing. In each row the punctures are intersected anteriorly by a narrow longitudinal carinule. In *Anepsius delicatulus* the anterior edges of the punctures are elevated, producing a characteristic pattern. The same pattern, albeit somewhat modified, is discernable in all except the strongly fossorial species, suggesting that it is primitively present in the anepsiine lineage.

Ventral setation (Character 17). Presence of setae is a derived condition correlated with psammophily.

Mesocoxal closure (Characters 18–20). These characters were discussed in some detail by Doyen and Lawrence (1979). Mesocoxal cavities bounded laterally by the epimeron, with exposed trochantins, are primitive. Those closed by lobes of the meso- and metasterna are derived. However, it should be noted that, even in those Anepsiini where the epimeron reaches the coxal cavity,

the sternite lobes are closely apposed, constricting the epimeron to a narrow strip. In some other groups of Tenebrionidae, notably Diaperini, mesocoxal closure is variable, possibly related to reduction in body size (Doyen 1984). Casey (1907:503) previously realized the instability of this character in Anepsiini.

Metasternum length (Character 21). In flightless Coleoptera, the metasternum commonly becomes much shortened. Although wing loss is pleiomorphic in Anepsiini, the metasternum is relatively long in all genera but *Anepsius*, which is relatively primitive in most other features.

Protibial configuration (Characters 22, 24). Apical expansion of the tibiae is frequently associated with psammophily in Tenebrionidae. Modification of the tibial spurs is often an associated feature, and in extreme cases one spur may be entirely lost, as in *Uniungulum* Koch (1962:113). Likewise, fimbriation of the posterior protibial margin often accompanies these other changes.

Aedeagal configuration (Character 25). The polarity of this character is uncertain. The ventral surface (primitively dorsal in the noninverted aedeagus) of the tegmen is often only lightly sclerotized; the amount of sclerotization sometimes varies among individuals.

Body proportions and setation (Characters 26, 27). Relatively slender, subglabrous bodies are associated with surface dwelling. Obese, fore-shortened bodies and long, projecting setae are associated with psammophilous, burrowing habits in many groups of tenebrionidae. These characteristics have probably evolved independently several times in Anepsiini.

CLADISTIC RELATIONSHIPS

One possible (hand-generated) cladistic arrangement of Anepsiini appears in Figure 3. This diagram includes the distribution of all characters for which the derived state is shared by at least two species even if the character polarity is not absolutely certain. Autapomorphic characters are described in the species treatments. At the outset it should be explained that psammophilous tenebrionidae that burrow in loose sand commonly share a syndrome of morphological specializations. Important modifications, as discussed by Koch (1961), Doyen (1984:15), and others include the following: enlargement of the foretibiae

for digging; shortening of the antennae; increase in body pilosity, especially as lateral fimbriae; and development of obese, rotund body shapes. In addition there is often development of protibial setal fringes, apparently to increase tibial area for digging, and modification of the protarsi or protibial spurs. Parallelism in these characters is particularly evident in the Anepsiini, where most of the same apomorphies characterize psammophilous species of all four genera. Since the generalized body plan is similar throughout Anepsiini, the apomorphic states of these characters are difficult or impossible to distinguish. However, several distinctive structural features, unrelated to psammophily, support the diagram in Figure 3. These are discussed where appropriate below. The characters subject to parallelism should ordinarily be removed before computer analysis. I retain them here to emphasize the extensive level of homoplasy present in Anepsiini.

The primary dichotomy separating *Batuliodes* from the remaining genera is based on differences in the mesocoxal region (Characters 18–20), antennae (Character 2), gular region (Character 8), and epistomum (Character 7). The sculpture of the hypomeron and the configuration of the posterior pronotal angles show derived states in the more generalized, surface-dwelling species. The absence of the derived states of these characters in some of the specialized burrowing species probably represents a secondary absence. Exserted posterior pronotal angles also occur in *Batulus setosus*, but the majority of characters clearly show that *B. setosus* belongs in the *Anepsius* lineage.

Batuliodes rotundicollis and *B. confluens*, the relatively generalized, surface-dwelling species, do not differ in important structural features. However, they differ in several details of cuticular sculpturing and diverge greatly in size and shape of the aedeagus (see species descriptions). The clade comprising *B. wasbaueri*, *B. spatulatus*, and *B. obesus* is united by a series of apomorphic character states related to a psammophilous mode of life. *Batuliodes obesus* is the most specialized member of this clade, having lost the pronotal carina (Character 10), developed dense, long setation on the venter (Character 17), and having entirely lost the elytral carinae (Character 16). In all other characters it is exceedingly similar to *B. spatulatus*. *Batuliodes wasbaueri* lacks apomorphies of the antennae (Character 5) and hypomeral

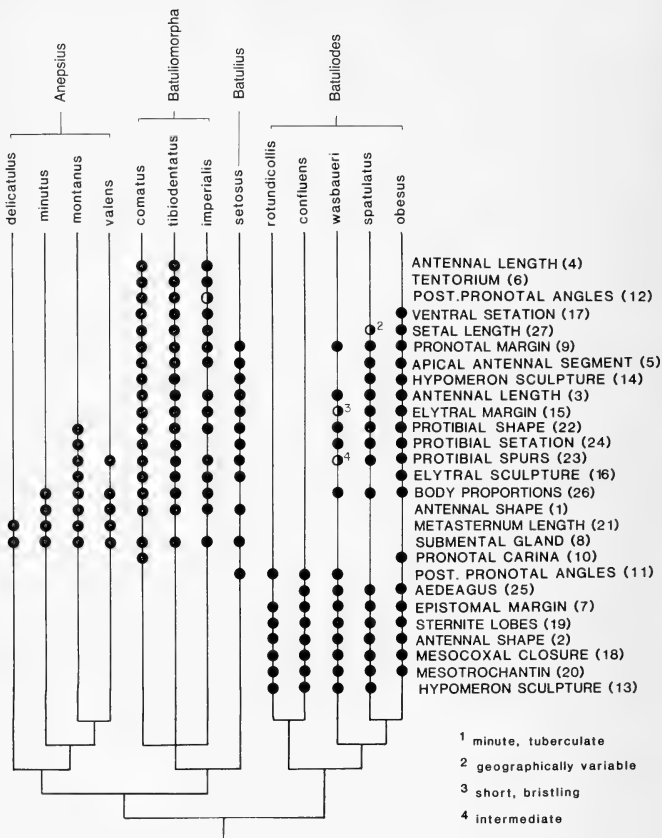


FIGURE 3. Distribution of character states across genera and species of Anepsiini. One possible (hand-generated) cladistic arrangement is indicated by the basal connecting lines. Black dots indicate character states presumed to be apomorphic. Note the numerous parallelisms among features adapted for life in aeolian sand.

sculpture (Character 14), but shares the remaining apomorphies.

The alternate branch, comprising *Anepsius*, *Batuliomorphus* and *Batulius*, of the cladogram is unified by only a single character, the presence of a submental gland (Character 8) in males. This is shown as an apomorphy in Figure 3, but could also be a primitive feature of *Anepsiini* which has been lost in *Batuliodes*.

Anepsius is distinguished by a single apomorphy, the short metasternum (Character 21). Commonly, shortening of the metasternum is correlated with winglessness in Coleoptera. *Anepsiini* are primitively wingless, and in most features *Anepsius* (especially *A. delicatulus*) is the most primitive member of the tribe. Unexpectedly the metasternum is longest in the most specialized burrowing species, and it is possible that the short condition is actually primitive to *Anepsiini*. Within *Anepsius*, *A. valens* and especially *A. montanus* show fossorial specializations of the protibiae and presumably represent a monophyletic clade.

Batulius and *Batuliomorpha*, which constitute the remaining lineage, share numerous apomorphic states of characters involved in psammophilous life. On this basis one might recognize only a single genus. However, *Batuliomorpha* is further characterized by a distinctive, obese body silhouette (Character 26), reduction or loss of the posterior pronotal angles (Character 12), and the uniquely apomorphic tentorium (Character 6). In contrast, in *Batulius* the body shape is not markedly different from that in *Anepsius*, and the tentorium is unmodified, while the posterior pronotal angles are strongly exerted, resembling those of *Batuliodes*. These characters suggest that the apomorphic protibial, setal, and antennal character states shared with *Batuliomorpha* arose by convergence.

An alternative arrangement might derive the lineage containing *Batulius* and *Batuliomorpha* from one of the fossorial species of *Anepsius*. Both *A. montanus* and *A. valens* show a few of the apomorphic features related to psammophilous life. However, such an arrangement would require that metasternal length, presumably derived in *Anepsius*, be reversed in *Batulius* and *Batuliomorpha*. It seems more likely that the specializations obviously related to psammophily arose independently in the two lineages.

Within *Batuliomorpha*, the species *comata* and *tibiodentata* share a single, apomorphic feature, the smooth, subglabrous hypomeron. However, this is a common characteristic of psammophilous forms, and in the *Anepsiini* this characteristic occurs independently in *Batuliodes*. Apomorphies distinguish *B. comata* (loss of pronotal carina, Character 10) and *B. tibiodentata* (coarsely tridentate protibia; unique within *Anepsiini*, not shown in Fig. 3). Furthermore, *B. comata* occurs in the southern Mojave Desert, while *B. tibiodentata* inhabits dunes in central and southern Baja California. Without more convincing evidence, it seems preferable to leave the relationships between the three *Batuliomorpha* species unresolved.

Anepsiini LeConte

Anepsiini LeConte, 1862:215; Horn 1870:276; LeConte and Horn 1883:367; Casey 1907:503; Arnett 1960:670; Doyen and Lawrence 1979:346.

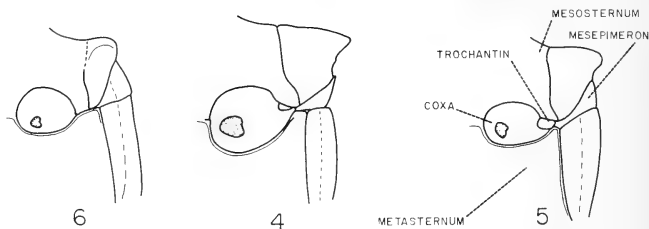
Batuliini Horn, 1870:270; Casey 1907:497; Arnett 1960:670; Doyen and Lawrence 1979:346 (synonymy).

Batulinae Papp, 1961:105.

Batulini Papp, 1961:105.

Wingless Tentyriinae 2–6 mm long with globular prothorax and oval abdomen.

FEMALES.—Lateral epistomal sutures usually distinct, medial suture obliterated. Eye completely divided by epistomal canthus and super-tended by low carina; antenna with 11 segments, clavate or with apical 3 or 4 segments forming club; labrum transverse with long, slender tormae with medial processes directed obliquely posteriorly; mandible with small, smooth mola remote from bidentate incisor lobe; maxilla with galea densely setose; lacinia with bidentate uncus; labium subhexagonal, moderate in size, exposing maxillary articulations; tentorium with sides short, bridge thick, or closed posteriorly (Fig. 2). Prosternal process unmarginated, horizontal a short distance behind coxae, then abruptly declivous; mesosternum scarcely excavated. Elytra constricted basally, collarlike, amplexed into prothorax; scutellum angulate or rounded posteriorly, retracted into prothorax, not visible on elytral disk. Mesocoxal cavities closed by sterna or nearly so; mesotrochantin exposed or concealed. Metasternum about one to two times length of mesocoxa. Metendosternite with short, thick stalk; long stout, tapering arms with tendons apical or subapical; median metasternal sulcus and



FIGURES 4-6. Ventral aspect of pterothoraces, showing variation in mesocoxal structure in Anepsiini. 4) *Batulimorpha comata*, 5) *Anepsius valens*, 6) *Batuliodes rotundicollis*.

internal ridge absent. Femurs stout; foretibia dilated, triangular; tarsi short with few spinose setae beneath. Ovipositor short, thick, with paraproct and coxite subequal; coxite lobes indistinct; gonostyles minute, papilliform, inserted dorsolaterally very near apex of coxite.

MALES.—Aedeagus inverted with paramere 1.1–1.7 times longer than tegmen; median lobe free, its lateral baculi fused proximally (Fig. 12–15). Average length about 10% less than females; submentum perforated by circular opening with tuft of protruding setae (Doyen and Lawrence 1979; Fig. 16–19), except in *Batuliodes*.

LARVAE.—Unknown.

Key to Genera of Anepsiini

1. Middle coxal cavity with trochantin exposed; sternal lobes separated by narrow space laterad of coxal cavity (Fig. 4, 5) 2
- Middle coxal cavity with trochantin concealed; lobes of sternites meeting laterad of coxal cavity (Fig. 6) *Batuliodes* Casey
- 2(1). Metasternum about twice as long as mesocoxa; pronotum and elytra fimbriate along lateral margins; apical antennal segment subquadrate or wider than long (Fig. 7, 8) 3
- Metasternum about one to one and one-half times as long as mesocoxa; pronotum and elytra subglabrous or with short, appressed setae; apical antennal segment longer than broad (Fig. 9) *Anepsius* LeConte

3(2). Posterior pronotal angles obliterated or represented by minute tubercles; antennal club with three segments; lateral fimbriation long, flying (Fig. 31); venter with numerous long setae *Batulimorpha*, new genus

— Posterior pronotal angles strongly angulate; antennal club with four segments; lateral fimbriation short, stiff (Fig. 21); venter with few short setae *Batulus* LeConte

Anepsius LeConte

Anepsius LeConte, 1851:147, 1862:215; Horn 1870:277; LeConte and Horn 1883:367; Casey 1907:503.

TYPE SPECIES.—*Anepsius delicatulus* LeConte; designated by Casey 1907:501.

Relatively slender to moderately obese ($0.55 \leq EL/EW \leq 0.72$) beetles devoid of long flying setae.

Epistomal margin arcuately truncate or very feebly and gradually emarginate; lateral epistomal sutures obscured by sculpturing. Antennal length at least three-fourths head width; flagellum gradually enlarged to 10th segment (Fig. 9) or with terminal 3 segments enlarged to form slight but distinct club (Fig. 10); apical segment longer than broad. Submentum of males perforated by circular opening with tuft of protruding setae. Tentorium consisting of subparallel lateral laminae joined by posterior transverse bridge. Pronotum moderately convex, about one and one-half times broader than long; anterior angles nearly right angled or slightly obtuse, angulate or with apexes briefly rounded; posterior angles broadly obtuse, angulate to briefly rounded, but always

distinct; lateral pronotal carina complete, never fimbriate. Elytra minutely carinate or punctate (*montanus*), with short, appressed setae (*minutus*) or subglabrous. Epipleural carina very narrowly margined; epipleuron narrowed just behind humerus, then subparallel almost to apex. Mesocoxal cavities nearly closed by opposed meso- and metasterna; sternites subequal, not offset (Fig. 5); trochantins exposed. Metasternum length one to one and one-half times length of mesocoxa; venter subglabrous or with short, appressed setae. Foretibia moderately to broadly triangular (Fig. 16-18); protibial spurs subequal or mesal spur enlarged, curved posteriad.

Key to the species of *Anepsius*

- 1. Antenna about as long as greatest head width; anterior tibia narrowly triangular (Fig. 16, 18)2
- Antenna about three-fourths as long as greatest head width; anterior tibia broadly triangular (Fig. 17)
.....*montanus* Casey
- 2(1). Elytra and venter glabrous or nearly so. . . .3
- Elytra and venter sparsely, evenly covered by short but evident setae*minutus*, new species
- 3(1). Antenna with last 3 segments enlarged as distinct club; anterior tibia with lateral margin broadly scalloped; spines in central region of anterior margin separated by four to six spine widths (Fig. 18)
.....*valens* Casey
- Antenna gradually enlarged to segment 10; anterior tibia with anterior margin entire, spines in central region separated by about two spine widths (Fig. 16)
.....*delicatus* LeConte

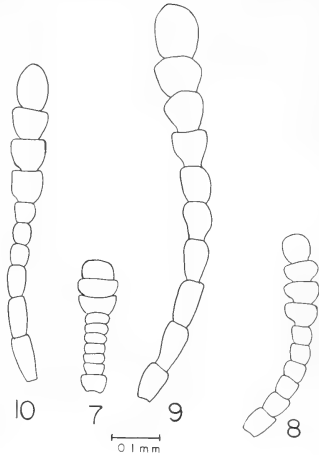
Anepsius delicatus LeConte

(Figure 11)

Anepsius delicatus LeConte, 1851:148.
Anepsius catenulosus Casey, 1907:505. (new synonymy)
Anepsius atratus Casey, 1907:506. (new synonymy)
Anepsius brunneus Casey, 1907:506. (new synonymy)
Anepsius nebulosus Casey, 1907:507. (new synonymy)
Anepsius bicolor Casey, 1907:507. (new synonymy)
Anepsius deficiens Casey, 1907:507. (new synonymy)

Relatively slender, subglabrous, reddish-black to black beetles with narrowly triangular protibiae.

FEMALE.—Cranium with elongate tubercles on epistomum, becoming tuberculopunctate poste-



FIGURES 7-10. Antennal configuration in Anepsiini. 7) *Batuliomorpha comata*, 8) *Batuliodes spatulatus*, 9) *Anepsius delicatus*, 10) *Batuliodes rotundicollis*.

riorly and punctate on back of vertex; postgena shallowly, reticulately punctate; mentum deeply, reticulately punctate. Antenna about as long as head width, gradually enlarged to 10th segment, without distinct club.

Pronotal disk medially with punctures slightly larger than eye facets, separated by about one puncture diameter; laterally punctures becoming attended ectally by short, longitudinal carinules, producing tuberculopunctate appearance. Lateral carina transversely rugulose. Hypomeron sparsely, coarsely tuberculate, finely, longitudinally strigose or scabrous; prosternum and prosternal process coarsely punctate, asetose.

Elytra seriatly punctate with minute carinules intersecting punctures anteriorly; carinules faint, short medially, becoming longer and stronger in lateral two-thirds; interstitial surfaces minutely alutaceous. Metasternum and metepisternum shallowly, coarsely punctate; punctures separated

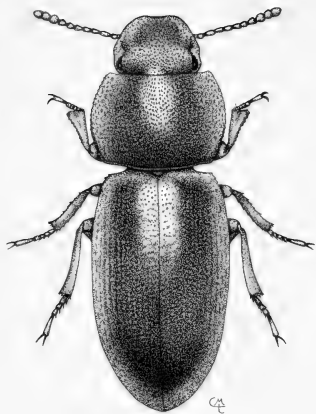


FIGURE 11. *Anepsius delicatulus*, Kern County, California

by about one puncture diameter medially, becoming closer laterally and subcontiguous on episternum. Abdominal sternites sculpted like metasternum; punctures denser on last two sternites.

Femurs with sparse, short, appressed setae; polished or finely scabrous. Protibia narrowly triangular; lateral margin bearing row of coarse, blunt spines, densest near apical angle (Fig. 16); mesial margin with four to five coarse spines; posterior surface scabrous or rugulose, irregularly set with several coarse spines; apical spurs subequal. Meso- and metatibia with short, sharp spines on all but posterior surfaces.

MALE.—Differs as stated in tribal description. Aedeagus as in Figure 12.

MEASUREMENTS.—EL 1.9–3.1 mm, EW 1.20–1.8 mm, PL 0.8–1.2 mm, PW 1.1–1.8 mm

HOLOTYPE.—Sex undetermined; in the LeConte Collection (MCZ).

TYPE LOCALITIES.—Colorado River Valley (*A. delicatulus*); southern California (*A. catenulosus*); San Diego, California (*A. atratus*); southwestern Utah (*A. brunneus*); southern California (*A. nebulosus*); Kern County, California (*A. bicolor*); near San Diego, California (*A. deficiens*).

DIAGNOSIS.—*Anepsius delicatulus* differs from all other species in not having a distinct antennal club. It is most similar to *A. minutus* Doyen, but is nearly devoid of visible setae on the pronotum and elytra, whereas *A. minutus* is sparsely pubescent. In addition, the male genitalia are different in shape (Fig. 12, 13).

The distribution of *A. delicatulus* (Fig. 20) is in arid and subarid habitats from Contra Costa County and northern Inyo County, California south through the Central Valley and Owens Valley to northern Baja, California and east to southwestern Utah, central Arizona, and northern Sonora, Mexico. It occurs on rocky or sandy substrates and sometimes on aeolian dunes, as at the Cervo Hills, Fresno County, California.

The color varies from reddish black to black. Bicolored individuals, corresponding to *A. bicolor* Casey, with reddish prothorax and black abdomen occur in several areas sympatrically with uniformly dark individuals. These color differences are not correlated with differences in other features and may be partly related to age.

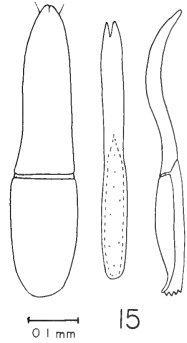
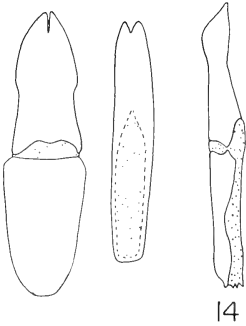
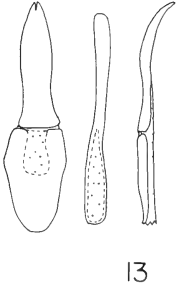
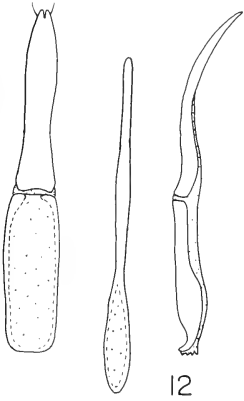
Anepsius minutus, new species

Slightly obese, brown, sparsely pubescent beetles with narrowly triangular protibiae.

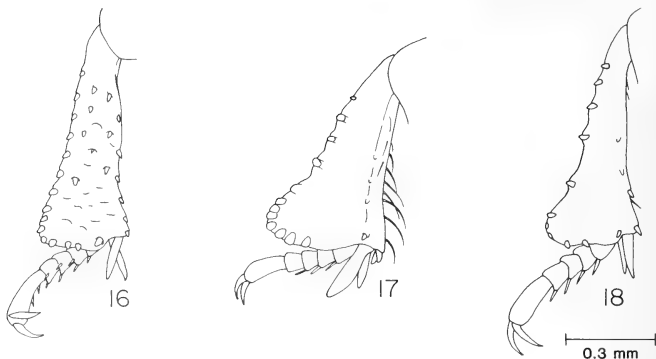
FEMALE.—Cranium set dorsally with nearly round tubercles slightly larger than eye facets; postgena finely scabrous posteriorly, becoming obscurely, coarsely punctate anteriorly; mentum coarsely, shallowly punctate; antenna about as long as head width; apical three segments enlarged as distinct club.

Pronotal disk medially with punctures slightly larger than eye facets, separated by about one to two puncture diameters; laterally punctures attended ectally by short, sharp, longitudinal carinules, producing reticulate appearance; punctures laterally with short, appressed setae. Lateral carina narrowly margined, with sparse row of short, appressed setae. Hypomeron and prosternum finely scabrous with a few coarse, obscure punctures at base of prosternal process; asetose or with two to three short setae.

Elytra with fine seriate punctures, each attended anteriorly by minute tubercle and short, appressed seta; interstitial surfaces minutely alutaceous. Metasternum and metepisternum shallowly, coarsely and sparsely, setosely punctate, the latter obscurely so. Abdomen sculpted like metasternum, punctures denser on fifth sternite



FIGURES 12-15. Male genitalia of species of *Anepsius* (ventral aspect, left; lateral aspect, right; median lobe, center). 12) *A. delicatulus*, 13) *A. minutus*, 14) *A. montanus*, 15) *A. valens*.



FIGURES 16-18. Right foretibiae of species of *Anepsius*, anterior aspect. 16) *A. delicatulus*, 17) *A. montanus*, 18) *A. valens*.

and posteriorly on first four, forming subcontiguous rows near margins.

Femora shining, with few obscure punctures and short, appressed setae. Protibia narrowly triangular; lateroapical margin with row of six to eight coarse, blunt spines, densest along apical angle; mesial margin with few fine setae; posterior surface finely sculpted, without spines; apical spurs subequal. Meso- and metatibia with sparse, short setae.

MALE.—Differs as stated in tribal description. Aedeagus as in Fig. 13.

MEASUREMENTS.—EL 1.6-1.7 mm, EW 1.1 mm, PL 0.6 mm, PW 1.0 mm

HOLOTYPE.—Female from Laredo, Texas, Hubbard and Schwarz, Coll. (USNM)

PARATYPE.—Male from Mexico, Nuevo León, 2 mi NNE China, V-24-1981, J. T. Doyen, on ground at night.

DIAGNOSIS.—*A. minutus* is similar to *A. delicatulus* LeConte in general appearance, but differs in its setose body (subglabrous in *A. delicatulus*).

The holotype is mounted with a specimen of *Myrmecocystus placodops* Forel (Formicidae), but it seems unlikely that *A. minutus* is myrmecophilous, since there are no obvious morphological modifications and no other species of Anepsiini are known to be closely associated with ants.

Anepsius montanus Casey

(Figure 19)

Anepsius montanus Casey, 1907:504.

Moderately obese, dark brown to black, subglabrous beetles with broadly triangular protibiae.

FEMALES.—Cranium with rounded, coarse tubercles on epistomum, becoming tuberculopunctate on vertex or punctate just before pronotum and with tubercles coalescing into carinules above eyes, producing reticulate appearance; postgena and mentum finely, closely punctate or punctatogroove. Antenna about three-fourths as long as head width; apical three segments enlarged as distinct club.

Pronotal disk medially with irregular punctures slightly larger than eye facets, separated by one to three puncture diameters; laterally punctures becoming about twice as large and, in lateral quarters, subcontiguous or contiguous. Lateral carina weakly crenate. Hypomeron finely scabrous with sparse, larger tubercles; prosternum and prosternal process shallowly, coarsely punctate with few long, projecting setae anteriorly.

Elytra with punctures two to three times eye facet in diameter, separated by one to two puncture

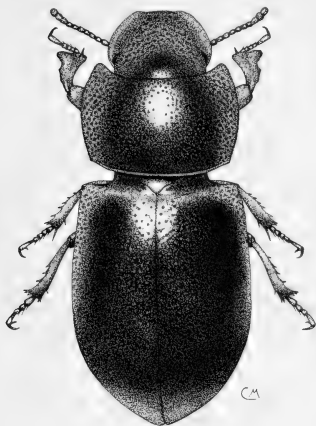


FIGURE 19. *Anepsius montanus*, Lea County, New Mexico.

MALE.—Differs as stated in description of tribe. Aedeagus as in Fig. 14.

MEASUREMENTS.—EL 1.9–2.4 mm, EW 1.4–1.7 mm, PL 0.8–1.0 mm, PW 1.4–1.6 mm.

HOLOTYPE.—Sex undetermined, from Greeley (Weld County), Colorado (USNM).

ADDITIONAL MATERIAL EXAMINED (Fig. 20). **Colorado.** Otero County: La Junta, VI-24/25-1885 (1), VI-15-1896 (1). Fremont County: Florence, 12-10 (1). Larimer County: Fort Collins, 24-4 (2). Las Animas County: Trinidad, 6-25 (1). Pueblo County: Pueblo, VII-II-1934 (1). Weld County: Greeley (1), Nunn, VIII-22-1971 (6). **Montana.** (no additional data) (1). **Nebraska.** Sioux County: Glen, VIII-1903 (1). **New Mexico.** Lea County: just east of Caprock (1). **Wyoming.** Albany County: Laramie, III-18-1894 (1). Laramie County: Cheyenne, IV-23-1888 (2). Niobrara County: Lusk, VII-14-1937 (1); (no additional data) (1). **Mexico.** (no additional data; intercepted with cacti at Nogales, Arizona, II-21-1966) (1).

DIAGNOSIS.—*A. montanus* is superficially similar to *A. valens* Casey, differing as indicated in the diagnosis for the latter.

Very likely *A. montanus* inhabits aeolian sand. This habit is suggested by morphological adaptations such as the enlarged foretibiae, unequal protibial spurs, and shortened antennae. Some of the collection sites are areas of extensive dune formation, as at Caprock, New Mexico.

***Anepsius valens* Casey**

Anepsius valens Casey, 1907:504

Moderately obese, dark brown or black, subglabrous beetles with narrowly triangular protibiae.

FEMALE.—Cranium tuberculate on epistomum, becoming tuberculopunctate posteriorly and punctate on back of vertex; postgena and mentum finely scabrous or rugulose; antenna about as long as head width; apical three segments enlarged as distinct club.

Pronotal disk medially with punctures about one to two times eye facets in diameter, separated by about one puncture diameter; in lateral quarters punctures becoming attended ectally by short carinules, these carinules strongest and punctures shallowest near lateral margins; lateral carina even, punctate. Hypomeron finely scabrous, finely, longitudinally strigose; prosternum and prosteron process finely scabrous, sparsely, obscurely punctate, asetose or nearly so.

Elytra seriatly, somewhat irregularly punctate medially; punctures becoming attended anteriorly by tubercles in lateral thirds, and then by minute carinules in lateral quarters; interstitial surfaces weakly undose. Metasternum shallowly, coarsely punctate; punctures separated by about

ture diameters, arranged in rough striae but confused, especially near suture; interstitial surface smooth, polished. Metasternum shallowly, sometimes obscurely punctate; punctures separated by about two puncture diameters medially, by less than one diameter on metepisternum. Abdominal sternites sculpted like metasternum; punctures denser laterally near posterior margin of sternite four and on sternite five.

Femora smooth, polished, with few small punctures and setae. Protibia broadly triangular (Fig. 17); lateral margin weakly crenate basally, abruptly broadened about two-thirds distance to apex, bearing about 12–14 very coarse, blunt spines, separated by two to three spine widths basally, subcontiguous apically; mesial margin with sparse fringe of inclined setae about half length of tarsus; posterior surface concave, with few small irregularities and minute carina near posterior margin; mesial tibial spur much longer, stouter than lateral. Meso- and metatibia with few stout, sharp spines on lateral and posterior surfaces; slender setae on anterior and mesial surfaces.

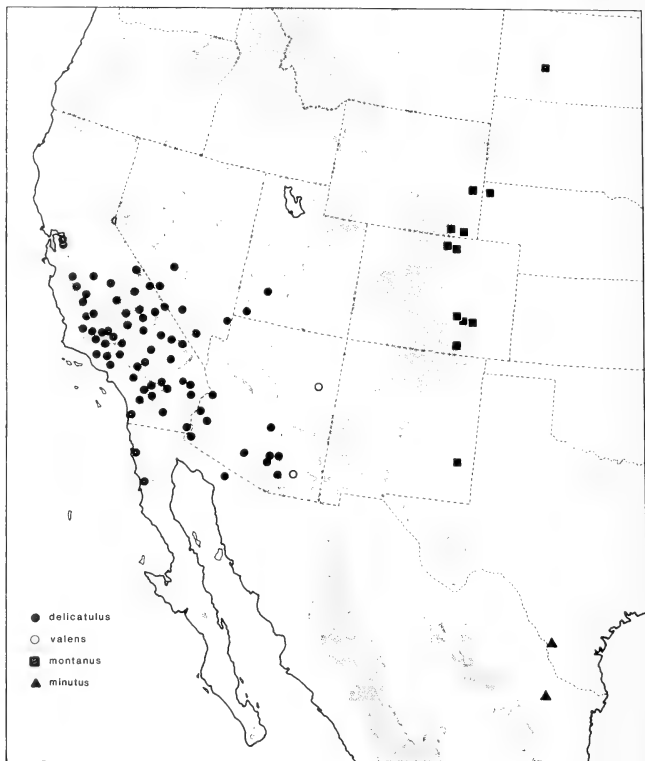


FIGURE 20. Distribution of the species of *Anepsius*.

one to two puncture diameters medially, becoming closer, coarser, and shallower laterally; often obscure on metepisternum. Abdominal sternites sculpted like metasternum; punctures denser along posterior margin of third and fourth sternites and on entire fifth sternite.

Femurs shining, smooth, with few small punctures and appressed setae. Protibia narrowly triangular; lateral margin shallowly crenulate with about seven to eight coarse, blunt spines, densest along apical angle (Fig. 18); mesial margin with few short setae, sometimes with one to two

spines; posterior surface with few irregular carinules or tubercles; mesial tibial spur slightly larger, stouter than lateral. Meso- and metatibia with short, sharp spines set sparsely on all but posterior surfaces; posterior surfaces sparsely setose.

MALE.—Differs as stated in description of tribe. Aedeagus as in Fig. 15.

MEASUREMENTS.—EL 2.2–2.9 mm, EW 1.4–2.0 mm, PL 0.8–1.1 mm, PW 1.3–1.7 mm.

HOLOTYPE.—Sex undetermined, from Holbrook (Navajo County), Arizona, Wickham (USNM).

ADDITIONAL MATERIAL EXAMINED (Fig. 20).—**Arizona.** (no further data) (6). Cochise County: Dragoon (4). Navajo County: Holbrook, VII-17-1940 (1), V-23-1941 (3), (no date) (12).

DIAGNOSIS.—*A. valens* is superficially similar to *A. montanus* Casey, but has much narrower anterior tibiae (Fig. 17, 18). In *A. valens* the antennae are about as long as the head is wide. In *A. montanus* the antennae are no longer than three-fourths the head width.

The habitat of *A. valens* is unknown, but the lack of structural modifications suggests that it is a surface-dwelling or litter-dwelling species, rather than psammophilous.

Batulius LeConte

Batulius LeConte, 1851:148; 1862:215; Horn 1870:270; LeConte and Horn 1883:364; Casey 1907:497, 498; Arnett 1960:670.

Batulius Papp, 1961:105 (misspelling).

TYPE SPECIES.—*Batulius setosus* LeConte [1851]; designated by Casey 1907:497.

Relatively slender to moderately obese ($0.61 \leq EW/EL \leq 0.72$) beetles with pronotum and elytra fringed laterally with stiff, projecting setae.

Epistomal margin truncate or very feebly and gradually emarginate; lateral epistomal sutures moderately impressed. Antennal length subequal to head width; terminal three segments enlarged as distinct club; apical antennal segment subquadrate. Submentum of males perforated by circular opening with tuft of protuding setae. Tentorium consisting of subparallel lateral laminae joined by posterior transverse bridge. Pronotum moderately convex, about 1.65 times broader than long; anterior angles nearly right angled, apices briefly rounded; posterior angles broadly obtuse with apices exserted, slightly obtuse; disk abruptly declivous near margin; lateral carina complete, fringed with stiff, projecting setae. Elytra seriatly tuberculopunctate, epipleural margin fringed with row of stiff, projecting setae about as

long as protarsus. Mesocoxal cavities nearly closed by apposed meso- and metasterna; sternites not offset (as in Fig. 5); trochantins exposed. Metasternum length about twice length of mesocoxa; venter subglabrous except for few setae on prosternum. Foretibia broadly triangular (Fig. 23); mesial protibial spur larger than lateral and strongly curved posteriorly.

Batulius setosus LeConte

Batulius setosus LeConte, 1851:148.

Batulius setosus Papp, 1961:105 (misspelling)

FEMALE.—Cranium tuberculate on epistomum, tubercles becoming elongate posteriorly and anteriorly or anterolaterally attending punctures, producing tuberculopunctate or reticulate appearance on vertex; vertex often simply punctate posteriorly; postgena scabrous; mentum with few large, shallow punctures.

Pronotal disk punctate or weakly tuberculopunctate medially, becoming strongly tuberculopunctate laterally, each puncture attended anteriorly or anterolaterally by elongate tubercle or carinule; lateral carina finely serrate or crenulate, with sparse fringe of stiff setae about as long as protarsus; anterior border narrowly margined and setose but not serrate in lateral quarters. Hypomeron shining, very finely alutaceous with few, scattered setigerous punctures and sparse row of

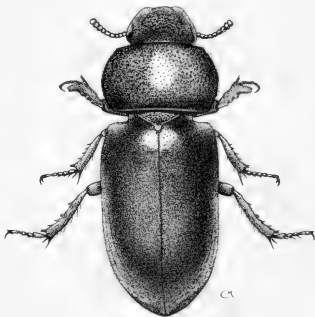


FIGURE 21. *Batulius setosus* from Imperial County, California.

setigerous tubercles just below pronotal carina; prosternum sculpted like hypomeron, setae longest medially; prosternal process becoming more densely punctate, especially along margins.

Elytra seriatly tuberculopunctate, alternate rows more strongly developed; tubercles near suture very small, and punctures very shallow, ill defined; laterally tubercles become larger and punctures become distinct though shallow; disk asetose medially; laterally and on declivity tubercles of alternate rows supertending stiff, inclined setae about one-third to one-half length of protarsus; epipleural carina serrate anteriorly, becoming crenulate posteriorly; epipleuron asetose, smooth or faintly scabrous. Metasternum with sparse, coarse, shallow punctures, densest medially, and each bearing a short, appressed seta and attended anteriorly by a very small tubercle; metepisternum very shallowly, obscurely punctate. Abdominal sternites one to three sculpted like metasternum, but punctures denser laterally; sternite four with punctures crowded near poste-

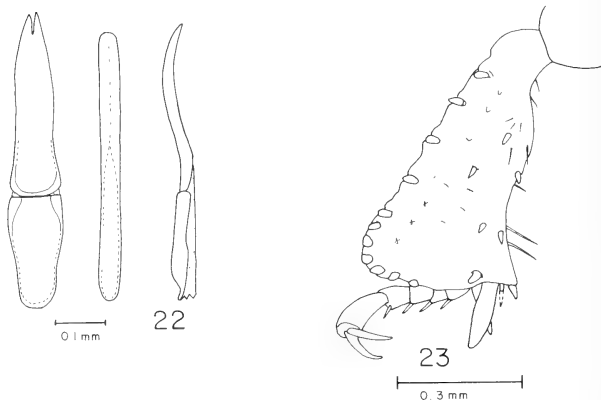
rior margin; sternite five more densely punctate, except near anterior margin. Femora shining, with few small, shallow punctures. Protibia with irregularly crenulate lateral margin, set with about 10-12 coarse, blunt spines, sparse basally, becoming subcontiguous around angle; mesial margin bisinuate, bearing three to five slender setae and one to several coarse spines; posterior surface rough, irregularly set with spines and short setae. Meso- and metatibia flattened, bearing short, sharp spines on anterior surface; slightly longer setae on posterior surface.

MALE.—Differs as stated in tribal description. Aedeagus as in Figure 22.

MEASUREMENTS.—EL 1.9-3.1 mm, EW 1.2-2.1 mm, PL 0.8-1.3 mm, PW 1.1-1.9 mm.

HOLOTYPE.—Male from Gila River valley (MCZ).

ADDITIONAL MATERIAL EXAMINED (Fig. 24).—**Arizona.** Yuma County: Fort Yuma, I-21 (3); 9 mi E San Luis, III-18-1980 (14); Tacna, IV-14 (2). **California.** Imperial County: Brawley, V-17-1967 (1); Glamis, IV-23-1972 (2), V-29-1971 (2); 1 mi N Glamis, IV-27/28-1972 (1); 3 mi N Glamis, IV-12-1973 (9); 7 mi SE Glamis, III-25/IV-8-1979 (18); Algodones Dunes, 2.5 mi NE



FIGURES 22-23. *Batulius setosus*. 22) Aedeagus, ventral aspect (left), lateral aspect (right), and median lobe (center); 23) Right foretibia, anterior aspect.

Coachella Bridge #1, IV-17-1979 (12). Riverside County: Blythe, V-6-1970 (1), III-10-1971 (1), IV-10-1971 (3); 1 mi W Blythe, V-23/24-1970 (6); 3 mi W Blythe, V-27-1971 (1); 18 mi W Blythe, I-29-1965 (1); Thousand Palms, III-12/24-1955 (3); Palen Dunes, IV-27-1978 (3). San Bernardino County: Amboy Crater, IV-24-1960 (1). **Mexico.** Baja California (Norte): Laguna Salada, I-28-1960 (1); San Felipe, II-20-1954 (1).

DIAGNOSIS.—*Batulius setosus* differs from all other Anepsiini in the bisinuate posterior margin of its protibia.

It inhabits aeolian sand dunes or extremely sandy substrates in the southern Mojave and Colorado Deserts. Collection records range from January to late May. Most specimens have been collected in pitfalls.

Batuliomorpha new genus

Relatively obese ($0.70 \leq EW/EL \leq 0.80$) beetles with long, flying setae.

Epistomal margin feebly emarginate to slightly arcuate; lateral epistomal sutures weakly to moderately impressed. Antennal length no more than

one-half head width; terminal three segments enlarged as distinct club (Fig. 7), apical segment subquadrate. Submentum of males perforated by circular opening with tuft of protruding setae. Tentorium consisting of subparallel laminae, closed posteriorly between transverse bridge and occiput (Fig. 2). Pronotum about 1.6–1.7 times broader than long, strongly convex, posterior margin depressed; anterior angles nearly right angled, rounded apically; posterior angles obliterated or marked by slight obtuse irregularity; lateral pronotal carina fimbriate, very narrow, carinate, or rudimentary, hypomeron sparsely setose and tuberculate laterally. Elytra tuberculate to tuberculopunctate, setose; epipleural carina indicated by regular row of closely set, setose tubercles. Mesocoxal cavities nearly closed by apposed meso- and metasterna; sternite lobes subequal or metasternal lobe about twice as broad as mesosternal lobe at apex (Fig. 4); trochanters exposed. Metasternum length about twice length of mesocoxa; venter setose. Foretibia broadly triangular or macrodentate (Fig. 28–30); mesial protibial spur much larger than lateral, strongly curved posteriorly.

TYPE SPECIES.—*Batuliomorpha comata* Doyen.

Key to the species of **Batuliomorpha**

- 1. Anterior tibia with lateral margin scalloped (Fig. 28, 29), bearing row of coarse, blunt spines2
- Anterior tibia with lateral margin produced as two very large, spatulate teeth (Fig. 30); margin without spines
.....*tibiodentata*, new species
- 2(1). Pronotum with lateral carina represented by row of small, discrete tubercles; lobe of mesosternum laterad of mesocoxal cavity much narrower than corresponding lobe of metasternum (Fig. 4) ...
.....*comata*, new species
- Pronotum with lateral margin finely carinate; lobe of mesosternum laterad of mesocoxal cavity subequal to corresponding metasternal lobe
.....*imperialis*, new species

Batuliomorpha imperialis, new species

Obese, dark brown, setose and laterally fimbriate beetles with proximal ends of lateral epistomal sutures subfoveate.

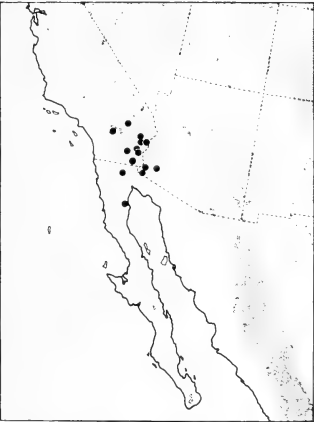
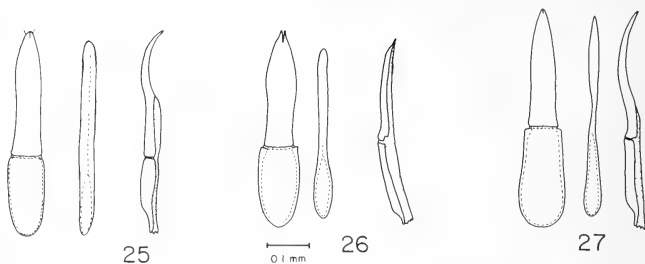


FIGURE 24. Distribution of *Batulius setosus*.



FIGURES 25–27. Male genitalia of species of *Batuliomorpha* (ventral aspect, left; lateral aspect, right; median lobe, center). 25) *B. comata*, 26) *B. imperialis*, 27) *B. tibiodentata*

FEMALE.—Epistomum arcuately convex or briefly truncate in middle; lateral epistomal sutures deeply impressed, subfoveate at proximal ends; epistomum scabrous, sculpture becoming finely, rugosely punctate on vertex; epistomal canthus and postgena asetose; postgena coarsely, shallowly punctate.

Pronotal disk colliculate-punctate, with short, sparse, appressed setae in lateral eighths and along posterior margin; lateral borders narrowly margined, crenulate, bearing sparse fringe of projecting setae about one-half length of protibia; posterior angles very broadly obtuse, angulate; posterior border narrowly margined; prosternum and prosternal process coarsely, shallowly punctate, medially with few setae about one-half length of protibia.

Elytral disk weakly undose and finely, seriatly punctate, becoming more coarsely so laterally; alternate rows with tubercles supertending fine, inclined setae about one-half length of protarsus medially to one-third to one-half length of protibia laterally; epipleuron narrowed abruptly about one-fourth distance from humerus, asetose. Meso- and metasternal lobes subequal laterad of mesocoxal cavity (as in Fig. 5); metasternum with large, shallow punctures, with few setae about one-half length of protarsus; metepimeron with large, shallow punctures; abdominal sternites

sculpted like metasternum, but more densely setose; punctures denser on last two sternites.

Profemur with sparse irregular posteroventral fringe of setae about one-half length of protarsus; meso- and metafemora with sparse anteroventral fringe of slightly longer setae; similar setae scattered on dorsal surface. Protibia with lateral margin coarsely, shallowly crenate, bearing about five coarse blunt spines and about four closely set blunt spines at apical angle (Fig. 28); few coarse spines on posterior surface; row of spinose setae on mesial margin; mesial angle scarcely produced; mesial spur much longer, stouter than lateral. Meso- and metatibia bearing longitudinal bands of sharp, coarse, projecting spines on anterolateral surface; sparse fringe of long, inclined setae on posterior surface.

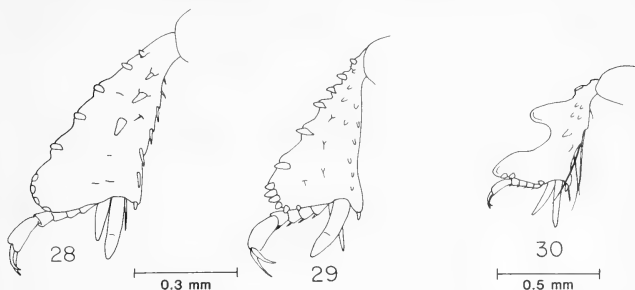
MALE.—Differs as stated in description of tribe. Aedeagus as in Fig. 26.

MEASUREMENTS.—EL 1.7–2.4 mm, EW 1.35–1.8 mm, PL 0.7–0.9 mm, PW 1.2–1.6 mm.

HOLOTYPE.—Female (CAS) and 38 paratypes from California, Imperial County, Algodones Dunes, 3.5 mi SE Glamis, II-26-1978, F. Andrews, A. Hardy.

ADDITIONAL PARATYPES.—Same data, IV-28-1978 (28); Glamis, IV-24-1972, pit trap, M. Wasbauer (1); 7.0–7.4 mi SE Glamis, III-19/IV-14-1979 (33).

DIAGNOSIS.—*Batuliomorpha imperialis* is most similar to *B. comata* Doyen, but has the meso-



FIGURES 28-30. Right foretibiae of species of *Batuliomorpha*, anterior aspect. 28) *B. imperialis*, 29) *B. comata*, 30) *B. tibidentata*.

and metasternal lobes subequal and aligned laterad of the mesocoxal cavities and has the ventral surface shallowly, coarsely punctate (sternal lobes offset in *B. comata*; ventral surface tuberculate).

The distribution of *B. imperialis* (Fig. 32) likely extends into the Gran Desierto, Sonora, Mexico, where some other endemics of the Algodones Dune system occur. Adult activity appears to be restricted to the winter and spring months.

***Batuliomorpha comata*, new species**

(Figure 31)

Obese, dark brown, setose and laterally fimbriate beetles with the sternal lobes laterad of the mesocoxal cavity unequal in width.

FEMALE.—Epistomum shallowly emarginate; lateral epistomal sutures slightly impressed, sometimes subfoveate at proximal ends; epistomum with short, longitudinal carinules, transforming into tuberculopunctate sculpture on vertex; epistomal canthus and postgena near eye with projecting setae about as long as protarsus; postgena faintly scabrous, asetose.

Pronotal disk irregularly tuberculopunctate medially, each crescentic puncture impressed anteriorly by small tubercle; becoming more

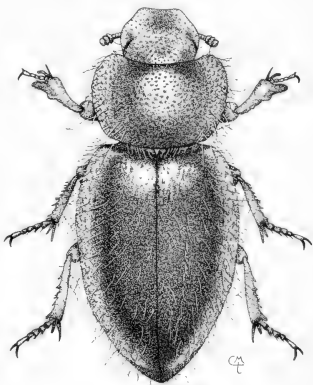


FIGURE 31. *Batuliomorpha comata* from Kelso Sand Dunes, San Bernardino County, California.

coarsely tuberculate in lateral sixths, along posterior margin and lateral two-thirds of anterior margin; tubercles each subtending inclined, fulvous seta about as long as tibia; lateral carina indicated by regular row of setose tubercles; posterior angles obliterated; posterior border narrowly and obscurely margined. Prosternum smooth laterally, finely tuberculate and on prosternal process set with setae about as long as tibia.

Elytra seriatly tuberculopunctate; elongate tubercles antieriad of shallow punctures, larger in alternate rows and supertending declined setae about as long as protarsus; becoming coarser and supertending longer setae laterally; epipleuron abruptly narrowed one-fourth distance from humerus, asetose. Metasternal lobe extending laterad of mesosternal lobe at mesocoxal cavity (Fig. 4). Metasternum regularly set with round tubercles, each supertending long, declined seta set in very shallow puncture. Metepimeron glabrous. Abdominal sternites sculpted like metasternum, but more clearly tuberculopunctate, most densely so on fifth sternite. Femora finely, irregularly tuberculate, tubercles supertending long fulvous setae. Protibia with serrate lateral margin (Fig. 29), each serration bearing large, blunt spine; five to six subcontiguous spines fringing outer apex; mesial margin with row of short, stiff setae; mesial angle prominent; mesial spur much stouter and longer than lateral. Mesotibia bearing irregular double row of long, blunt spines on lateral margin; long, fine, inclined setae on lateral and posterior surfaces. Metatibia bearing long, blunt spines on anterior and lateral surfaces, whorled with long, fine, inclined setae.

MALE.—Differs as stated in description of tribe. Aedeagus as in Figure 25.

MEASUREMENTS.—EL 1.7–2.7 mm, EW 1.2–1.9 mm, PL 0.6–1.0 mm, PW 1.0–1.6 mm

HOLOTYPE.—Female (CAS) and 8 paratypes from California, San Bernardino County, Kelso Sand Dunes (8 mi SW Kelso), II-1-1977, J. Doyen, P. Rude, M. Bentzien (J. Doyen Lot # 77B1.1).

ADDITIONAL PARATYPES.—Kelso Dunes, I-13-1965, M. Irwin (5), IV-16/18-1974, F. Andrews, M. Wasbauer (19), II-8-1974, D. Giuliani (22), II-13-1976, F. G. Andrews, A. Hardy (5); 2 mi S Kelso, XII-18-1977, J. Doyen (J. Doyen Lot # 77L4) (2); 9 air mi SW Kelso, VI-29/30-1978, J. Doyen, P. Rude (J. Doyen Lot # 78F4) (3); 10 air mi SW Kelso, IV-23-1977, J. Doyen (2); 2.5 mi E Kelso, II-13-1965, R. Dickson, M. Irwin (3)

ADDITIONAL MATERIAL EXAMINED (Fig. 32).—California, San Bernardino County: Dumont Dunes, 600', V-1-1974, Creosote Assoc., T. Eichlin and A. Hardy (1), II-21-1974, D. Giuliani (1). Arizona, Mohave County: 3 mi SE Parker, VI-28-78, J. Doyen (J. Doyen Lot # 78F3) (1).

DIAGNOSIS.—The unequal meso- and metasternal lobes and the rudimentary lateral carina of the pronotum distinguish *Batuliomorpha comata* from other *Batuliomorpha*, where the sternal lobes are equal and the carina distinct.

Nearly all specimens of *B. comata* have been collected between December and April, suggesting winter activity of the adults. Most individuals have come from pitfall traps. One large collection was made from about the roots of sparse perennial grass (J. Doyen Lot # 77B1.1). At the Kelso Sand Dunes, where *B. comata* is common, collection sites range from the flat apron of sand surrounding the main dune mass to the highest crests. *Batuliomorpha Comata* is known from three sets of dunes in the northeastern Mojave Desert (Fig. 32).

Batuliomorpha tibidentata, new species

Obese, dark brown, setose and laterally fimbriate beetles with the anterior tibiae produced into two large teeth.

FEMALE.—Epistomum arcuately convex or

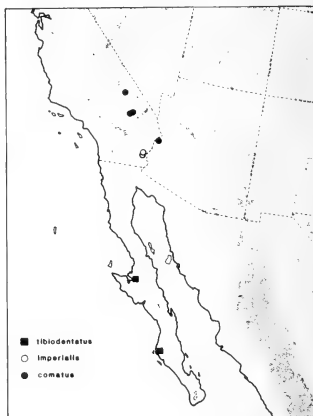


FIGURE 32. Distribution of the species of *Batuliomorpha*.

nearly truncate medially; lateral epistomal sutures lightly impressed; epistomum and vertex with short, longitudinal carinules between eyes, becoming more oblique anteriorly and posteriorly. Epistomal canthus asetose; postgena with few projecting setae about as long as protarsus. Postgena finely tuberculopunctate, bearing a few long setae medially.

Pronotal disk coarsely, closely punctate or weakly tuberculopunctate in medial one-fourth to one-third, becoming tuberculopunctate, then tuberculate laterally and along posterior margin; tubercles in lateral one-sixth to one-third and in posterior one-sixth to one-fifth supertending erect, fulvous setae about two-thirds as long as protibia; lateral carina narrowly margined, finely crenate, bearing fringe of closely set, long, projecting setae; posterior angles obliterated; posterior border very narrowly margined. Prosternum and prosternal process shallowly tuberculopunctate, set with setae about two-thirds as long as protibia.

Elytra very finely, seriatly tuberculate; tubercles supertending inclined, fulvous setae about one-half to two-thirds length of protibia, slightly longer laterally; epipleural carina narrow, crenate, bearing row of closely set long setae; epipleuron gradually narrowed from base to apex, setose. Meso- and metasternal lobes aligned laterad of mesocoxal cavity (as in Fig. 5); metasternum closely set with coarse, shallow punctures bearing setae about one-third to one-half length of protibia. Metepimeron obscurely punctate, asetose; abdominal sternites sculpted like metasternum, but setae slightly longer.

Profemur sparsely set with long fulvous setae on anterodorsal surface; set with shorter setae on basal anteroventral surface; meso- and metafemora sparsely set with long setae on anterior surface. Protibia with small basal, large medial, and very large apical scallop (Fig. 30); few coarse, blunt spines on basal posterior surface, two to three coarse, truncate spines on distal margin; two to three long setae on mesial margin; mesial angle slightly produced; mesial spur slightly larger than lateral. Meso- and metatibia bearing irregular row of long coarse spines on lateral margins; posterior surfaces set with long, inclined setae.

MALE.—Differs as stated in description of tribe. Aedeagus as in Fig. 27.

MEASUREMENTS.—EL 1.6–2.1 mm, EW 1.2–1.5 mm, PL 0.7–0.8 mm, PW 1.1–1.4 mm.

HOLOTYPE.—Female (CAS) and five paratypes from Mexico, Baja California del Sur, 7 mi SE Guerrero Negro, IV-8-1976, J.

Doyen, P. Rude, R. Morrison; on dunes at night, J. Doyen Lot # 76D5. Two paratypes from Baja California del Sur, San Carlos, IX-25-1981, D. Faulkner, F. Andrews, sifted from sand dunes.

DIAGNOSIS.—*Batuliomorpha tibiodentata* is distinguished from all other Anepsiini by its very coarsely tridentate protibiae.

The specimens from near Guerrero Negro were found crawling slowly on the surface of sand hummocks at night. *Batuliomorpha tibiodentata* is known from sand dunes at two localities in south central and central Baja California (Fig. 32).

Batuliodes Casey

Batuloides Casey, 1907:499; Arnett 1960:670.

Batulus Doyen and Lawrence, 1979:347 (in part).

TYPE SPECIES.—*Batulus rotundicollis* LeConte, 1851; designated by Casey 1907:498.

Relatively slender to moderately obese ($0.63 \leq \text{EW/EL} \leq 0.75$) beetles with mesocoxal cavities closed by apposed meso- and metasterna.

Epistomal margin feebly to distinctly emarginate (Fig. 33). Lateral epistomal sutures weakly to not impressed, often faint, obscured by sculpturing. Antenna 0.7–1.2 times longer than head width; terminal four segments enlarged as distinct club; apical segment longer than broad or subquadrate. Tentorium consisting of subparallel laminae joined by posterior transverse bridge. Pronotum moderately convex, about 1.4–1.6 times broader than long; anterior angles nearly right angled or obtuse, angulate to rounded; posterior angles very broadly obtuse basally, usually exerted and nearly right angled or slightly acute just before apex; lateral pronotal carina complete or absent, subglabrous or fringed with setae. Elytra minutely carinate or tuberculate with seta arising behind each tubercle. Mesocoxal cavities closed by apposed meso- and metasterna; metasternal lobe laterad of coxal cavity broader than mesosternal lobe (Fig. 6); trochantins concealed. Metasternum length about twice length of mesocoxa; venter subglabrous or sparsely setose. Foretibia moderately to very broadly triangular (Fig. 39, 40); protibial spurs subequal or mesial spur slightly larger, curved posteriad.

Key to the Species of *Batuliodes*

1. Anterior tibia narrowly triangular (Fig. 39); epipleural carina appearing glabrous or nearly so. 2
- Anterior tibia broadly triangular (Fig. 40);

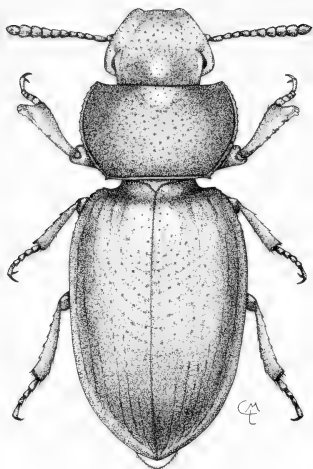


FIGURE 33. *Batuliodes rotundicollis* from Inyo County, California

- epipleural carina sparsely fimbriate with moderate to long setae, at least anteriorly. 3
- 2(1). Pronotal disk punctate in lateral quarters; intercarinal areas of elytra near epipleuron impunctate or nearly so; aedeagus with paramere attenuate in apical one-third; much longer than tegmen (Fig. 34) *rotundicollis* LeConte
- Pronotal disk reticulate or reticulopunctate in lateral quarters; intercarinal areas of elytra distinctly punctate, even near epipleuron; aedeagus with paramere gradually attenuate to very acute apex; subequal in length to tegmen (Fig. 35) *confluens* (Blaisdell)
- 3(1). Antenna about three-fourths as long as head width; pronotum with lateral fringe

- of setae; pronotum with posterior angles strongly obtuse or rounded, ill defined. 4
- Antenna about as long as head width; pronotum without lateral fringe of setae; pronotum with posterior angles exerted at apex, nearly right angled. *wasbaueri* new species
- 4(3). Pronotum with lateral carina absent; hypomeron with lateral row of setae about as long as protarsus. *obesus* new species
- Pronotum with lateral margin finely, narrowly carinate; hypomeron with lateral row of setae about half as long as protarsus. *spatulatus* new species

***Batuliodes rotundicollis* (LeConte)**

(Figure 33)

Batulius rotundicollis LeConte, 1851:148.

Batuliodes rotundicollis Casey, 1907:499.

Slender, pale to dark brown, subglabrous beetles with finely carinate elytra.

FEMALE.—Epistomum with lateral lobes prominent, medial portion truncate (Fig. 33); set with nearly round to elongate tubercles anteromedially, these becoming short carinules laterally and posteriorly; vertex tuberculopunctate; postgena and mentum with very shallow, obscure, nearly contiguous, coarse punctures. Antenna about as long as head width; apical segment longer than broad.

Pronotal disk medially with punctures slightly larger than eye facets, separated by one to two puncture diameters; in lateral quarters ectal rims of punctures becoming raised as slight tubercles; lateral carina crenulate, asetose; posterior angles acute or nearly right angled, exerted at apex; anterior angles angulate, nearly right angled. Hypomeron with coarse, exceedingly shallow, often obscure, subcontiguous punctures, sometimes becoming reticulate; prosternum shallowly, coarsely punctate; prosternal process with punctures mostly along margins.

Elytra seriatly, shallowly punctate, punctures interrupting fine, longitudinal carinae; near suture rows of coarser punctures with lower carinae alternating with rows of smaller punctures with more prominent carinae; laterally rows of coarser punctures becoming shallower, obscure or absent

near epipleuron; carinae becoming less pronounced laterally, obscure or absent near epipleuron. Epipleural carina weakly crenulate anteriorly, becoming nearly straight posteriorly; supertergites with irregular row of shallow punctures, these disappearing in posterior third. Metasternum with coarse punctures separated by about one puncture diameter; metepisternum glabrous; abdominal sternites more finely punctate than metasternum; sternites four and five with punctures mainly confined to posterior margins.

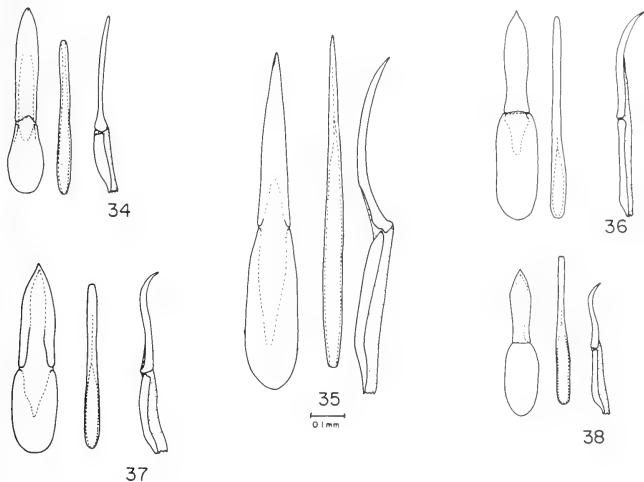
Femora finely, sparsely tuberculate. Protibia (Fig. 39) rather narrowly triangular with about 8–10 coarse, blunt spines along lateral margin; mesial margin with few coarse spines and setae; posterior surface with irregular ridge and row of spines near mesial margin; tibial spurs subequal. Meso- and metatibia each with sparse row of sharp spines along lateral margin, few setae on anterior and posterior surfaces.

MALE.—Differs as stated in description of tribe. Aedeagus as in Figure 34.

MEASUREMENTS.—EL 1.3–2.0 mm, EW 0.1–1.4 mm, PL 0.5–0.8 mm, PW 0.8–1.2 mm

HOLOTYPE.—Sex not determined; from Gila River valley (MCZ).

ADDITIONAL MATERIAL EXAMINED (Fig. 41).—**Arizona.** Maricopa County: Buckeye, 2-4-1942 (1); Phoenix, II-9/III-16-1941 (5), II-2-1945 (1); 18 mi W Tonopah, IX-5-1978 (3). Mohave County: 3 mi N, 7 mi E Littlefield, Virgin River, III-28/X-1-1982 (3). Pima County: Lukeville, X-26-1969 (2); Tucson, April (1) Yuma County: Ehrenberg, II-8-1939 (1), II-15-1940 (1); Fort Yuma, I-28 (2); Quartzite, II-27-1940 (4). **California.** Imperial County: Cargo Muchacho Mtns, Mesquite-Creosote, 480', IV-19/V-27-1979 (3); 3.9 mi N Walter's Camp (1). Inyo County: Eureka Valley, 1978, March, (4), April, (13), May, (58), June, (36), July, (40), August (31), September (13), November/December (1); Eureka Valley, 8 mi N, 4 mi W dunes, 3300', IX-1-78 to V-5-1980 (77); Saline Valley, VI-21-1978/V-18-1979, 1100' (6), 1200' (37), 1360' (28); Grapevine Canyon, IV-20-1978/V-18-1979, 2500' (4), 2700' (5), 3800' (1); NW end Saline Valley, Sand Dunes, 1150', VI-6-1976 (1); Saline Valley Dunes, VI-6-1976 (14), IV-20-1975 (4); Inyo Mountains, Lead Canyon,



FIGURES 34–38. Male genitalia of species of *Batuliodes* (ventral aspect, left; lateral aspect, right; median lobe, center). 34) *B. rotundicollis*, 35) *B. confuens*, 36) *B. wasbaueri*, 37) *B. spatulatus*, 38) *B. obesus*.

3300' V-5/VIII-13-1982 (12). Riverside County: Painted Canyon, IV-15-1974 (3), various dates, V-18-1978/I-7-1979 (4); Riverside Mountains, Crest, Riverside Pass Rd., IV-27/VII-18-1978 (71). San Bernardino County: Daggett, X-17-1951 (1). San Diego County: Borrego, II-3-1939 (5); Carter Lake, III-23-1959 (1). Nevada: Nye County: Rock Valley, IV-11-1975 (1).

DIAGNOSIS.—*Batuliodes rotundicollis* is most similar to *B. confluens* (Blaisdell). In *B. rotundicollis* the lateral areas of the pronotal disk are punctate and the intercarinal areas of the elytra near the epipleuron are impunctate or nearly so. In *B. confluens*, the lateral areas of the pronotum are irregularly set with short carinules, causing a reticulate appearance and the intercarinal spaces of the elytra are distinctly punctate, even laterally. In addition, the aedeagi of these two species are different in shape and very different in size (Fig. 34, 35).

Batuliodes rotundicollis occupies arid habitats from east central California and southern Nevada south to extreme southern California and east to central Arizona (Fig. 41). No collection records exist, but the beetles undoubtedly inhabit extreme northern Baja California and Sonora.

Many collections are from aeolian dunes, but

others are from sandy washes, areas of desert pavement, or stoney regions. Nearly all specimens have been collected in pitfalls. In contrast to the predominantly winter activity of most of the species inhabiting dunes, *rotundicollis* is most abundant during the warm season.

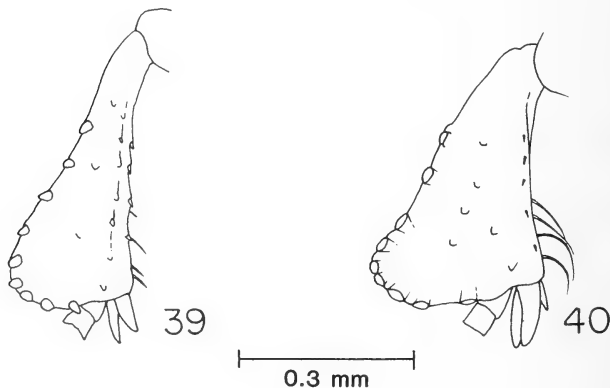
Batuliodes confluens (Blaisdell) (new combination)

Anepsius confluens Blaisdell, 1923:243; 1943:218.

Anepsius angulatus Blaisdell, 1923:244; 1943:218. (new synonymy)

Slender, brown to black beetles with finely carinate elytra.

FEMALE.—Epistomum truncate anteriorly or with lateral lobes slightly more prominent than middle; sparsely set with round or elongate tubercles anteriorly, becoming tuberculopunctate posteriorly on vertex and tubercles becoming short, sometimes anastomosing carinules, producing reticulate appearance, especially laterally above eyes; postgena and mentum with shallow, nearly contiguous, coarse punctures. Antenna about as long as head width; apical segment longer than broad.



FIGURES 39–40. Right foretibiae of species of *Batuliodes*, anterior aspect. 39) *B. rotundicollis*, 40) *B. spatulatus*.

Pronotal disk medially with punctures about two eye facets in diameter, separated by about one puncture diameter or less; laterally, ectal rims becoming raised as low carinules, these becoming strong and anastomosing in lateral thirds, producing reticulate surface; lateral carina crenulate, asetose. Posterior angles acute or nearly right angled, exerted at apex; anterior angles angulate, nearly right angled. Hypomeron scabrous, longitudinally strigose, with scattered, coarse, shallow punctures, often obscure; prosternum and prosternal process shallowly, coarsely, subcontinuously punctate.

Elytra seriatly punctate; in alternate rows punctures interrupting fine longitudinal carinae; carinae weakest near suture, becoming very distinct laterally, where anterior rims of punctures are raised; rows between carinae with each puncture attended anteriorly by slight tubercle, anterior rim slightly raised laterally; intercarinal areas becoming more weakly sculpted posteriorly and usually smooth on declivity. Epipleural carina weakly serrate or crenulate near humerus, becoming nearly straight posteriorly, bearing sparse line of short, appressed setae; supertended by irregular row of obscure, shallow punctures. Metasternum with coarse, setigerous punctures separated by about one puncture diameter; setae short, appressed or declined; metepimeron obscurely, shallowly, and coarsely punctate; abdominal sternites sculpted as metasternum, sometimes more finely so; sternites four and five usually with punctures mostly near posterior margin.

Femora with few fine tubercles or obscure punctures. Protibia nearly as in *Batuliodes rotundicollis* (Fig. 39), posterior surface with scattered tubercles, ridge near mesial margin usually indistinct; meso- and metatibia with few short spines and scattered tubercles on ectal surface and sparse, short, appressed setae.

MALE.—Differs as stated in description of tribe. Aedeagus as in Figure 35.

MEASUREMENTS.—EL 1.6–2.4 mm, EW 1.0–1.4 mm, PL 0.6–0.9 mm, PW 0.9–1.2 mm.

HOLOTYPE.—Male in the California Academy of Sciences, San Francisco.

TYPE LOCALITIES.—Mexico, Baja California Sur, Isla Partida, (*B. confluens*); Mexico, Baja California Sur, Loreto, Arroyo Gua (*B. angulatus*).

ADDITIONAL MATERIAL EXAMINED (Fig. 41).—Mexico, Baja California (Norte): Tijuana, IV-14-1942 (2); Arroyo Catavina, 35 mi S El Progreso, IV-2-1976 (1); 2.7 mi SE Catavina, VII-4-1979 (8); 6.2 mi W Bahía de Los Angeles (31); 10 mi S Punta

Prieta, VI-21-38 (2); 6.2 mi NE Rosarito, VII-10-1979 (20); 57 mi E El Rosario, 2 mi E San Fernando Velicata, VII-2-1979 (2); 2 mi NW Rancho Santa Ynez, III-27-1973 (3). Baja California Sur: 2 mi E San Ignacio, VII-6-1979 (6); Rancho Mesquital, 21.4 mi E San Ignacio, VII-9-1979 (11); Rancho Tablon, 13 km S Guillermo Prieto, IV-16/18-1983 (11); 12 mi S Guillermo Prieto, IV-7-1982 (1); 34.4 mi SE Guerrero Negro, IX-22-1981 (1); Isla Mejia, IV-20-1921 (1); Isla Carmen, V-23/VI-6-1978 (7); Isla Estanque, VII-1-1921 (1); Isla Monserrate, VI-11/23-1978 (3); Isla Raza, IV-21-1921 (1).

DIAGNOSIS.—*Batuliodes confluens* is very similar to *B. rotundicollis* LeConte, differing as stated in the discussion of the latter. The habits of *B. confluens* seem to be similar to those of *B. rotundicollis*, with occupation of many different substrates and adult activity through the hot part of the year.

Batuliodes wasbaueri new species

Moderately obese, brown, subglabrous beetles with very broadly triangular protibiae.

FEMALE.—Epistomum with lateral lobes prominent, usually extending well beyond truncate middle; sparsely, evenly set with round tubercles

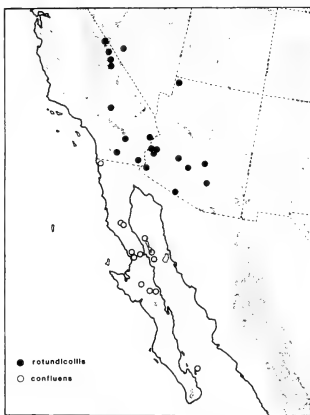


FIGURE 41. Distribution of *Batuliodes rotundicollis* and *B. confluens*.

slightly larger than eye facets; tubercles becoming elongate posteriorly and carinulate posterolaterally near eyes; postgena coarsely, subcontiguously punctate; mentum scabrous; antenna about as long as head width; apical segment longer than broad.

Pronotum medially with punctures about 1.5 times diameter of eye facets, separated by one to several puncture diameters; becoming denser laterally; punctures attended ectally by longitudinal carinules, strongest in lateral quarters; lateral carina distinct, fine, immediately subtended by row of asperities, producing thickened appearance; posterior angles nearly right angled, exserted at apex; anterior angles angulate, slightly obtuse; hypomeron, prosternum, and prosternal process coarsely punctate; punctures separated by less than one puncture diameter.

Elytra confusedly set near suture with shallow, ill-defined punctures about as large as eye facets; punctures attended anteriorly by small, slightly elongate tubercles; laterally punctures becoming smaller, very poorly defined, and tubercles becoming more elongate, then carinulate in lateral thirds; carinules and punctures becoming obsolete in alternate one to two rows adjacent to epipleuron; epipleural carina evenly margined, forming prominent, explanate humerus; sparsely fringed by short, declined setae; metasternum with coarse punctures separated by about one puncture diameter or less; metepisternum with few coarse punctures; abdominal sternites more finely punctured than metasternum; punctures mostly on posterior margins of sternites four and five.

Femora finely, sparsely punctate: Protibia very broadly triangular (as in Fig. 40) with about 9–11 very coarse, blunt spines along lateral margin, subcontiguous around angle; mesial margin with four to five slender setae about one-fourth to one-third length of protarsus; posterior surface sparsely tuberculate; tibial spurs subequal. Mesotibia with row of 2–4 stout spines along ectal margin, scattered spinose setae; metatibia with few smaller spines on ectal margin, scattered spinose setae.

MALE.—Differs as stated in description of tribe. Aedeagus as in Figure 36.

MEASUREMENTS.—EL 1.7–2.4 mm, EW 1.2–1.7 mm, PL 0.7–0.9 mm, PW 1.1–1.4 mm.

HOLOTYPE.—Female (CAS) and one paratype from California, Imperial County, 5 mi N Glamis, IX-10-1974, M. Wasbauer, R. McMaster, pit trap. Additional paratypes as follows.

California. Imperial County: Glamis, IV-24-1972, M. Wasbauer, pit trap (3), V-29-1971, M. Wasbauer, pit trap (11); Algodones Dunes, 12.4 mi ESE Holtville, IV-13-1979 (1); Algodones Dunes, 2.5 mi NE Coachella Bridge #1, IV-17-1979 (1); Seeley, V-8-1970 (1) Paddock, Flock and Johnson. Mexico. Baja California (Norte), 20 mi S Palacio [= Palaco?], IV-4-1939, E. Ross (2).

DIAGNOSIS.—*Batuliodes wasbaueri* is similar to *B. confluent* (Blaisdell), but has the protibiae very broadly triangular (much narrower in *B. confluent*) (Fig. 39, 40). *Batuliodes wasbaueri* is similar to *B. spatulatus* Doyen, differing as indicated in the discussion of the latter. *Batuliodes wasbaueri* appears to be endemic to the Algodones Dunes, although it lacks most of the morphological specializations that distinguish the truly psammophilous species such as *Batuliodes obesus* and the species of *Batuliomorpha*.

Batuliodes spatulatus new species

Brown, strongly convex, obese beetles, with inconspicuously setose elytra and very broadly triangular protibiae.

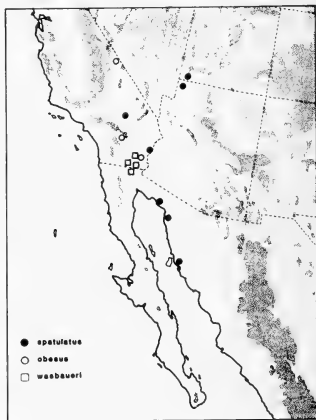


FIGURE 42. Distribution of *Batuliodes spatulatus*, *B. wasbaueri*, and *B. obesus*.

FEMALE.—Epistomum with lateral lobes slightly more prominent than middle, which is truncate or concavely arcuate; set with round tubercles slightly larger than eye facets, these becoming elongate posteriorly on vertex and often carinulate; postgena and mentum shallowly, coarsely punctate. Antenna about three-fourths as long as head width; apical segment about as long as broad.

Pronotum medially with shallow punctures slightly larger than eye facets, separated by one to several puncture diameters; attended ectally by low tubercles, these becoming stronger and longitudinally elongate laterally and forming short carinules near lateral margins; lateral carina very fine, narrow and even; posterior angles strongly obtuse but definitely angulate; anterior angles rounded. Hypomeron glabrous except for few punctures on coxal cowl and band of setigerous tubercles just below pronotal carina; setae stiff, slightly curved, about one-third to one-half as long as protarsus; prosternum with few setigerous punctures medially with anterior rims tuberculate raised; setae about as long as protarsus; prosternal process with few marginal punctures.

Elytra seriatly tuberculate, tubercles anteriorly attending shallow, ill-defined punctures; tubercles smaller, ill defined, less regular near suture, often appearing confused, becoming slightly stronger, more elongate laterally, sometimes forming interrupted carinules; punctures disappearing near epipleuron and on declivity; alternate rows of tubercles larger, especially laterally; sometimes supertending short, declined setae, especially laterally; rows of smaller tubercles becoming obsolete laterally and posteriorly, disappearing near epipleuron and on declivity; epipleural carina narrow, weakly crenate, bearing row of slightly curved setae about one-third to one-half length of protarsus. Metasternum with coarse, shallow, setigerous punctures separated by about one puncture diameter; setae exceedingly fine, very short; metepisternum with few obscure punctures; abdominal sternites one to two sculpted like metasternum, but more finely, sparsely so; punctures sparser medially and on last three sternites mostly on posterior margins.

Femora polished, with scattered minute setae. Protibia very broadly triangular (Fig. 40), with row of very short, blunt spines along lateral margin, becoming subcontiguous around angle; mesial margin with row of about five curved setae about two-thirds length of protarsus; posterior

surface with few scattered tubercles, short spinose setae; mesial tibial spur longer, stouter than lateral; strongly curved. Meso- and metatibia with row of three to four coarse, spines on ectal margins; posterior surfaces sparsely, irregularly set with inclined setae about one-half to two-thirds length protarsus.

MALE.—Differs as stated in tribal description. Aedeagus as in Figure 37.

MEASUREMENTS.—EL 1.6–2.2 mm, EW 1.1–1.6 mm, PL 0.6–0.9 mm, PW 0.9–1.3 mm.

HOLOTYPE.—Female (CAS) and six paratypes from California, San Bernardino County, 9 air mi S Baker, VII-1-1978, J Doyen, P. Rude (J. Doyen Lot # 78F5).

ADDITIONAL PARATYPES.—Same locality IV-27-1977, J. Doyen (J. Doyen Lot # 77D2) (2). Riverside County: Sand dunes 1 mi W Blythe, V-23/24-1970, pit trap, J. Johnson, M. Wasbauer (19). Utah, Washington County, 2 mi E Washington, V-20/VI-8-1980, R. Hardy (3).

ADDITIONAL MATERIAL EXAMINED (Fig. 42).—**Arizona.** Mohave County: 3 mi N, 7 mi E Littlefield, Virgin River, III-28/X-1-1982 (2). **Mexico.** Sonora: Cholla Bay, 6 mi N Puerto Penasco, III-18/19-1980 (1); El Desemboque, III-22-1980 (6); 1 mi W Bahia de San Carlos, III-23-1980 (7).

DIAGNOSIS.—*Batuliodes spatulatus* is very similar to *B. obesus* Doyen, differing as described in the discussion of the latter. It is also similar to *B. wasbaueri* Doyen, but *B. wasbaueri* entirely lacks the fringe of pronotal setae present in *B. spatulatus* and has the antennae as long as the head width (about three-fourths head width in *B. spatulatus*).

Batuliodes spatulatus is geographically variable. Specimens from California and Utah have the elytral disk very sparsely setose or subglabrous; if setae are present, they are only about as long as the basal protarsal segment. The pronotal and epipleural setae are about one-third the length of the protarsus. Specimens from Sonora have the elytra setose and the pronotal and epipleural setae are about one-half the length of the protarsus.

Batuliodes obesus new species

Pale tan, strongly convex, obese beetles with setose elytra and with pronotal carina obliterated.

FEMALE.—Epistomum with lateral lobes prominent, extending well beyond truncate middle; sparsely, evenly set with round tubercles slightly larger than eye facets, occasionally becoming carinulate posteriorly on vertex; postgena and mentum nearly smooth with few, obscure punctures. Antenna about three-fourths as long as head width; apical segment about as long as broad.

Pronotum medially with shallow punctures about twice eye facet diameter, separated by about one puncture diameter; becoming denser,

smaller, and less well defined laterally and attended ectally by slightly elongate tubercles in lateral thirds of disk; few short, declined setae near margins of disk; lateral carina absent; posterior angles rounded, strongly obtuse, scarcely indicated; anterior angles rounded. Hypomeron polished, glabrous except for few punctures on coxal cowl and somewhat irregular band of posterodorsally curved setae about as long as protarsus near dorsal margin and on lateral sixths of anterior margin; prosternum and prosternal process glabrous except for few long, curved setae.

Elytra seriatly tuberculate; rounded tubercles anteriorly attending shallow, ill-defined punctures near suture, these becoming smaller laterally and posteriorly and virtually disappearing near epipleuron and on declivity; alternate rows of tubercles larger, setigerous; setae about one-half length of protarsus, inclined, slightly curved; rows of smaller tubercles becoming obsolete laterally and posteriorly and disappearing near epipleuron and on declivity; epipleural carina scarcely elevated, indicated by row of small, round setigerous tubercles anteriorly, becoming carinate in anterior and posterior one-fifth but not prominent; tubercles separated by about one tubercle diameter; setae about as long as protarsus, slightly curved posterodorsad. Metasternum with coarse, very shallow, setigerous punctures, separated by one to several puncture diameters; setae about as long as basal metatarsal segment; metasternum with few obscure punctures; abdominal sternites sculpted like metasternum, except for setae being about one and one-half to two times longer; punctures sparser medially and on sternites three to five mostly near posterior borders. Legs essentially as in *spatulatus* (Fig. 40).

MALE.—Differs as stated in tribal description. Aedeagus as in Figure 38.

MEASUREMENTS.—EL 1.4–1.8 mm, EW 1.0–1.4 mm, PL 0.5–0.8 mm, PW 0.9–1.2 mm

HOLOTYPE.—Female (CAS) from California, Imperial County, 1 mi S Glamis, III-31-1978, J. Powell, in pitfall. Paratypes: Imperial County: 2 mi N Glamis, 1-27-1977, J. Doyen, on sand at night (1); Glamis, V-29-1971, pit trap, M. Wasbauer (1); 5.5 mi SE Glamis, VII-19-1978, A. Hardy, F. Andrews, pit trap (1); 7 mi SE Glamis, III-25/IV-8-1979, pit trap (1). Riverside County: 5 mi NW Indio, III-4-1972, F. Andrews, E. Kane, A. Hardy (1). Inyo County: Death Valley, Stovepipe Wells Sand Dunes, IX-14-1972, D. Giuliani

DIAGNOSIS.—*Batuliodes obesus* is very similar to *B. spatulatus* Doyen. In *B. obesus* the lateral pronotal carina is absent and the hypomeral setae

are about as long as the protarsus and curve strongly posterodorsad. In *spatulatus* the pronotal carina is fine but complete, and the hypomeral setae are about half as long as the protarsus.

Batuliodes obesus is restricted to aeolian sand dunes, with morphological adaptations for a psammophilous mode of life similar to that of *Batuliomorpha*. All specimens have been collected during the winter months, save that from Death Valley, which is badly abraded, lacking setae, and may have been found dead.

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Of special note is the material housed in the collection of the California Department of Food and Agriculture. This is the largest collection of sand dune Coleoptera from western North America, and contains more than one-half the known specimens of Anepiini. About a quarter of the known specimens are housed in the Essig Museum of Entomology, University of California, Berkeley.

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APPENDIX 1

Characters and Character States

Plesiomorphic character states are listed first, apomorphic states last. Some characters, such as antennal shape (1, 2), posterior pronotal angles (11, 12) and hypomeron sculpture (13, 14) are listed twice because more than 2 character states are recognized. A double listing allows such characters to be coded in an additive binary fashion.

1. Antennal shape: a) clavate (or four-segmented club); b) three-segmented club.
2. Antennal shape: a) clavate (or three-segmented club); b) four-segmented club.
3. Antennal length: a) at least as wide as head; b) three-fourths as wide as head or less.
4. Antennal length: a) at least three-fourths as wide as head; one-half as wide as head or less.
5. Apical antennal segment: a) apical segment much longer than wide; b) apical segment subquadrate or nearly round.
6. Tentorium: a) open posteriorly; b) closed posteriorly between bridge and occiput (Fig. 2).
7. Epistomal margin: a) shallowly emarginate or truncate; b) lateral lobes prominent; middle recessed, \pm straight (Fig. 33).
8. Submental gland: a) present; b) absent.
9. Pronotal margin: a) glabrous or with short, appressed setae; b) fimbriate.
10. Pronotal lateral carina: a) distinct, carinate; b) absent.
11. Posterior pronotal angles: a) obtuse (or rounded, absent); b) exerted, about 90° or acute.
12. Posterior pronotal angles: a) angulate, distinct; b) absent.
13. Hypomeron sculpture: a) scabrous, rugulose, or smooth; b) coarsely punctate.
14. Hypomeron sculpture: a) scabrous, rugulose (or punctate); b) smooth polished.
15. Elytral margin: a) glabrous or with short, appressed setae; b) fimbriate.
16. Elytral sculpture: a) carinae interrupted by punctures; b) tuberculate, punctate.
17. Ventral setation: a) subglabrous or short, sparse setae; b) long semi-erect setae.
18. Mesocoxal closure (Fig. 4-6): a) narrow space between lobes of meso- and metasternites; b) sternite lobes touching.
19. Sternite lobes (Fig. 4-6): a) mesosternal and metasternal lobe subequal in width laterad of coxal cavity; b) metasternal lobe much broader than mesosternal.
20. Mesotrochantin (Fig. 4-6): a) exposed; b) concealed.

21. Metasternum length: a) about twice mesocoxal length; b) about mesocoxal length (occasionally 1.5 times mesocoxal length).
22. Protibial shape: a) narrowly triangular (Fig. 18); b) broadly triangular (Fig. 17).
23. Protibial spurs: a) subequal, straight; b) mesial spur much larger than lateral, curved posteriad (Fig. 17).
24. Protibial setation: a) posterior margin glabrous or with short, appressed setae; b) posterior margin with three to seven long, erect or semi-erect setae (Fig. 17).
25. Aedeagus: a) Tegmen entire (Fig. 14); b) tegmen with membranous or submembranous central region on ventral surface (Fig. 13).
26. Body proportions: a) slender ($EW/EL \leq 0.65$); b) obese ($EW/EL \geq 0.72$).
27. Setal length: a) pronotal and elytral fimbriae short (or absent); b) setae long, projecting.

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NH

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Additions to Index, *Proceedings* vol. 44 (nos. 13–15, pp. 283–372)

New names

Anepsius minutus
Batuliodes obesus
Batuliodes spatulatus
Batuliodes wasbaueri

Batuliomorpha comata
Batuliomorpha imperialis
Batuliomorpha tibiodentata
Rhinobatos punctifer

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