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PUNCTAPINELLA (LEPIDOPTERA: TORTRICIDAE), A NEW GENUS FOR THREE PREVIOUSLY KNOWN AND THREE NEW SPECIES FROM SOUTH AMERICA

JOHN W. BROWN

TWO NEW SPECIES OF GEOMETRID MOTHS (LEPIDOPTERA: GEOMETRIDAE: ENNOMINAE) FROM COCOS ISLAND, COSTA RICA

JOHN W. BROWN, JULIAN P. DONAHUE, AND
SCOTT E. MILLER

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PUNCTAPINELLA (LEPIDOPTERA: TORTRICIDAE), A NEW GENUS FOR THREE PREVIOUSLY KNOWN AND THREE NEW SPECIES FROM SOUTH AMERICA

JOHN W. BROWN[1]

ABSTRACT. *Punctapinella,* new genus, is proposed for six species from northern South America: *P. conchitis* (Meyrick), new combination (type species); *P. niphastra* (Meyrick), new combination; *P. chionocarpa* (Meyrick), new combination; *P. braziliana,* new species; *P. scleroductus,* new species; and *P. theta,* new species. Adults of *Punctapinella* are characterized by a unicolorous bronze-brown to dark brown forewing with distinct roundish white spots. Putative autapomorphies for the genus include unique forewing pattern, elongate medial fusion of the gnathos arms, and compound cornutus. *Punctapinella* is morphologically most similar to *Seticosta* Razowski, 1986, and *Anopinella* Powell, 1986, among described genera. The presence of a male foreleg hairpencil confirms the assignment of the genus to Euliini (Tortricinae). The male of only one species, *P. conchitis,* is known. It possesses a row of strong spinelike setae subbasally on the costa of the valva; this character state is interpreted as a synapomorphy for *Punctapinella* and *Seticosta.*

(Additional key words: accessory bursa, Neotropical, *Seticosta, Anopinella.*)

INTRODUCTION

Within the recently redefined tortricid tribe Euliini (Powell, 1986; Brown, 1990), *Seticosta* Razowski, 1986, *Anopinella* Powell, 1986, and *Apolychrosis* Amsel, 1962, form a well defined monophyletic group on the basis of the following putative synapomorphies: labial palpi elongate and porrect, male antennae with extremely long cilia (greater than 1.5 × annular segment diameter), forewing vein CuP absent, valvae narrow and usually subbasally constricted with an apical or subapical region of nondeciduous bristlelike setae (analagous with cucullus), and ductus seminalis from the corpus rather than from the ductus bursae. Females of this group are characterized by the presence of elongate slender apophyses posteriores and anteriores, a moderately long ductus bursae, and the absence of a signum. The latter character states are interpreted as symplesiomorphies because of their widespread distribution in the outgroups (i.e., Chlidanotinae, Olethreutinae, and several tribes of the Tortricinae). In most Euliini the apophyses are comparatively short, and the ductus bursae is greatly reduced and undifferentiated from the corpus.

During recent studies on Neotropical members of the polyphyletic genus *Eulia* Hübner, I discovered a homogeneous group of species that share the above characters states but differ from the above genera in several morphological characters and in facies. *Punctapinella,* new genus, is described to accommodate *Eulia chionocarpa* Meyrick, *Eulia niphastra* Meyrick, *Eulia conchitis* Meyrick, and three previously undescribed species. Females of *Punctapinella* possess a variably developed accessory bursa from the ductus bursae, unassociated with the ductus seminalis, a character state previously considered a synapomorphy for *Seticosta* and *Anopinella* (Brown and Powell, unpubl.). Although accessory bursae are present in Chlidanotini and Hilarographini (Chlidanotinae) and in Cochylini (Tortricinae), these structures are considered independently derived among these phylogenetically distant groups (Horak, 1984; K. Tuck, personal communication). The single male of *Punctapinella* possesses a row of long, strong, spinelike setae subbasally on the costa of valva; this character state is interpreted as a synapomorphy with *Seticosta.* The male of *Punctapinella* also possesses the characteristic euliine male foreleg hairpencil, as do males of *Seticosta* (Brown, 1989, 1990). In *Anopinella* and *Apolychrosis* this structure is apparently secondarily lost. The hypothesized cladistic relationship among these four genera is presented in Figure 1.

MATERIALS AND METHODS

Taxonomic material for this study was obtained through the courtesy of J.F.G. Clarke, National Museum of Natural History, Washington, D.C. (USNM); the late F. Fernandez-Yépez, Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay (IZAV) [currently on loan to USNM]; M. Lödl, Naturhistorisches Museum, Vi-

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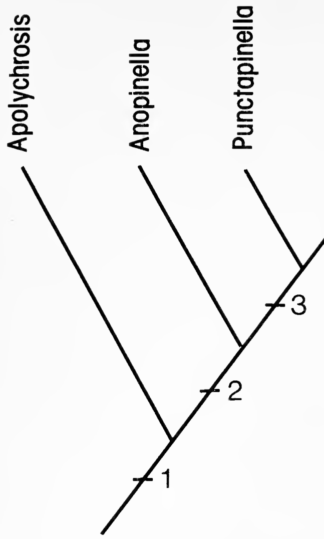


Figure 1. Hypothesized cladistic relationship among *Apolychrosis, Anopinella, Punctapinella,* and *Setocista.* Putative synapomorphies supporting the branching pattern are as follows: 1) Loss of forewing vein CuP; elongate, porrect labial palpi; long antennal cilia in male; valvae narrow; ductus seminalis from corpus bursae. 2) Possession of accessory bursa. 3) Row of spinelike setae on costa of valva.

enna (NHMW); and K.R. Tuck, British Museum (Natural History), London (BMNH).

Dissection methodology followed that presented in Powell (1964). Illustrations of genitalia were drawn using a microprojector. Forewing measurements were made with a standard grid mounted in a dissecting microscope. Terminology for wing venation and genitalic structures follows Horak (1984); FW = forewing; HW = hindwing; DC = discal cell.

SYSTEMATICS

Punctapinella new genus

Eulia Hübner (in part); Meyrick, 1912:681; Meyrick, 1931:151; Meyrick, 1932:257; Clarke, 1958: 120; Razowski, 1964:458, 461.

TYPE SPECIES. *Eulia conchitis* Meyrick, 1912.

DESCRIPTION. *Head:* Antennal setulae (cilia) in male 1.6–1.8 × annular segment diameter. Labial palpus porrect, elongate, broadened distally by scaling; segment II expanded distally to ca 1.5 × its basal diameter, slightly curved; segment III ca 0.4 as long as II, exposed. Maxillary palpus rudimentary. Frons with overhanging crown tuft. Ocelli small. Chaetosema present. *Thorax:* Male foreleg with hairpencil from proximal end of femur, extending to base of coxa. *Forewing:* Venation as in Figure 2. Length 2.3–2.4 × width; length of DC ca 0.6 × FW length; width of DC ca 0.2 × its length; CuA_2 originating ca 0.60 along length of DC; all veins separate beyond cell; R_4 to costa, R_5 to termen; CuP absent; chorda present; M-stem reduced to trace. *Hindwing:* Venation as in Figure 2. Sc+R and Rs separate; Rs and M_1 separate; M_3 and CuA_1 connate; CuP represented by a trace; M-stem a trace. *Abdomen:* Dorsal pits absent. *Male genitalia* (based on *P. conchitis* only): Uncus simple, unmodified, slightly curved. Socii moderately short, digitate, with fine setae; not fused to gnathos. Gnathos well developed with elongate, medial process from fusion of apices of lateral arms. Subscaphium and hami absent. Transtilla membranous mesally; well developed laterally with cuplike subbasal in-

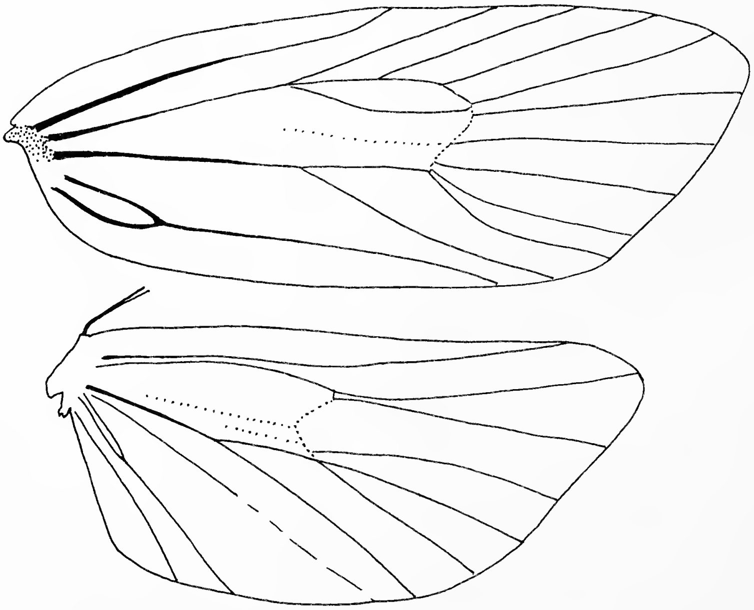


Figure 2. Wing venation of *Punctapinella theta.*

vagination. Valva narrow, moderately elongate; costa with subbasal patch of large spinelike setae; venter weakly excavated ca 0.4–0.7 from base to apex; sacculus simple without free projection, confined to basal 0.5. Vinculum complete. Aedeagus moderately long, straight; a single long slender compound cornutus, attached basally. *Female genitalia* (based on all species): Papillae anales (ovipositor lobes) simple. Apophyses anteriores and posteriores long, slender. Sternum of abdominal segment VIII weakly sclerotized. Sterigma simple; lamella antevaginalis poorly developed; lamella postvaginalis a simple sclerotized transverse band, broadened meso-ventrally, often with narrow scobinate region extending toward or into ostium; ostium displaced anterad of intersegmental membrane between sterna VII and VIII. Corpus and ductus bursae usually differentiated. Ductus bursae narrow, elongate to moderately broad. Corpus bursae narrow, weakly pear-shaped, with little or no spiculae; signa lacking. Accessory bursa variously developed: Short digitate diverticulum (e.g., *braziliana*) to elongate sac from long slender ductus (e.g., *conchitis*), arising from ductus bursae (usually lost in slide-mounted preparations). Ductus seminalis from corpus bursae. Entire apparatus long and narrow. *Sexual dimorphism:* Based on *P. conchitis*, forewing shape, size, and pattern does not differ between sexes. Males can be distinguished by the possession of a foreleg hairpencil and long antennal setulae (cilia).

Punctapinella occurs from Colombia and Venezuela, southeast to Rio de Janeiro, Brazil. The early stages are unknown. The three previously known species were described in the polyphyletic genus *Eulia* and were known only from holotype females.

Members of the genus are characterized by a unicolorous bronze-brown to dark brown forewing with distinct roundish white spots. Forewing pattern in the closely related *Anopinella* and *Seticosta* nearly always features a dark triangular patch bordering the costa approximately 0.33–0.66 from the base and extending about half way to the dorsum. In *Punctapinella* the gnathos are well developed and possess an elongate medial rodlike process formed by the distal fusion of the lateral arms. By contrast, in *Seticosta* the gnathos are reduced; in *Anopinella* each of the arms bears a laterally flattened, usually finely dentate, semicircular process distally. The single male of *Punctapinella* has a moderately long straight aedeagus bearing a single large compound cornutus. Males of *Anopinella* have a comparatively short stout aedeagus bearing a single slender spinelike cornutus; males of *Seticosta* almost always lack cornuti and have a large dorsoanterior process above the opening of the ductus ejaculatoris. Putative autapomorphies for *Punctapinella* include the unique forewing pattern, the elongate medial fusion of the arms of the gnathos, and the unusual compound cornutus.

ETYMOLOGY. The Greek "puncta" means spot or spotted; "pina" refers to feather or wing; the suffix "ella" refers to diminuative in size. The gender of the new genus is interpreted as feminine.

KEY TO SPECIES OF *PUNCTAPINELLA* BASED ON FEMALES

1. FW silver-white with bronze-gray v-shaped transverse band (Fig. 7) .... *conchitis*
1′. FW nearly unicolorous bronze-brown to chocolate brown with roundish white spots 2
2. FW costa with white spot ca 0.65 from base, between large subbasal spot and apical spot(s) 4
2′. FW costa without white spot ca 0.65 from base 3
3. HW chocolate brown, concolorous with FW (Fig. 3) .... *niphastra*
3′. HW light gray-brown, much lighter than FW (Fig. 5) .... *braziliana*
4. Three white spots in medial-tornal area of FW round and equal in size .... *scleorductus*
4′. Three white spots in medial-tornal area of FW irregularly rounded and unequal in size 5
5. Large white spot near base of costa nearly round (Fig. 4) .... *chionocarpa*
5′. Large white spot near base of costa oblong or subrectangular (Fig. 6) .... *theta*

1. *Punctapinella niphastra* (Meyrick) new combination

Figures 3, 8

Eulia niphastra Meyrick, 1931:151; Razowski, 1964:461.

MALE. Unknown.

FEMALE. FW length 6.9 mm (n = 1). *Head:* Frons smooth scaled, white-ocherous below mid-eye, roughened, gray-brown above; vertex gray-brown with white-ocherous tufts medially. Labial palpus white-ocherous, gray-brown laterally. Antenna brown. *Thorax:* Smooth scaled, brown. *Forewing:* Chocolate brown with faint lighter brown transverse striae; small white spot at base along dorsum; large white spot at costa ca 0.20 from base; small white spot at posterior apex of DC; two slightly larger white spots nearly equidistant from the latter, one tornad, the other apicad; a pair of white costal strigulae near apex; faint ill-defined white dots in subterminal region; dorsum with several diffuse short white transverse dashes. Fringe ferruginous-gray. *Hindwing:* Chocolate brown. Fringe slightly lighter brown. *Genitalia:* As in Figure 8 (n = 1; drawn from Razowski slide no. 4339). Lamella postvaginalis a simple transverse curved band, broadened meso-ventrally. Ductus bursae long, fairly broad. Corpus bursae narrow, elongate. Origin of neither accessory bursa nor ductus seminalis detectable.

TYPE MATERIAL. Holotype female: BRAZIL: State of Espíritu Santo, Guanda, December 1920, Fritz Hoffman (NHMW).

ETYMOLOGY. The Greek prefix "nipha" means snow and "astro" or "astrum" means star. Apparently the name "niphastra" refers to the round white spots of the forewing.

2. *Punctapinella chionocarpa* (Meyrick) new combination

Figures 4, 9

Eulia chionocarpa Meyrick, 1932:257; Razowski, 1964:458.

MALE. Unknown.

FEMALE. FW length 9.0 mm (n = 1). *Head:* Frons and vertex white. Labial palpus lacking. Antenna light tan. *Thorax:* White. *Forewing:* Bronze-brown with diffuse darker reticulation; white spot at base along dorsum; large irregularly rounded spot at costa ca 0.25 from base; four smaller white spots in distal 0.5 of wing: one at costa ca 0.65 from base, one directly below latter at posterior apex of DC, one slightly larger, between and distad of latter two, one slightly oblong, at tornus; two pairs of white costal strigulae near apex, forming subconfluent white spot; subtermen with indistinct white dots. Fringe light bronze-brown. *Hindwing:* Light gray with faint darker gray marbling. Fringe gray-white. *Genitalia:* As in Figure 9 (n = 1; drawn from Razowski slide no. 4332). Lamella postvaginalis a simple lightly sclerotized band; ostium indicated by narrow outline of sclerotization. Ductus bursae long, narrow. Corpus bursae irregularly rounded. Origin of accessory bursa and ductus seminails uncertain.

TYPE MATERIAL. Holotype female: COLOMBIA: [Department of Tolima (?)] Central Cordilleras, Guindin, 8500 feet [2750 m], November [no year], Eden (NHMW).

ETYMOLOGY. The Greek "chion" refers to snow and "carpo" or "carpus" means fruit. Apparently the name "chionocarpa" refers to the round white forewing markings.

3. *Punctapinella braziliana* new species

Figures 5, 10

MALE. Unknown.

FEMALE. FW length 6.8–9.0 mm ($\bar{x}$ = 7.5; n = 5). *Head:* Frons and vertex white. Labial palpus white, gray-brown laterally. Antenna bronze-brown. *Thorax:* Yellow-ocherous to silver-white. *Forewing:* Bronze-brown; white spot at base along dorsum; large elongate diagonal white spot from costa ca 0.2 from base; white spot near posterior apex of DC; distal 0.2 of wing with row of three small white spots nearly parallel to termen starting at apex, apical spot formed by coalesced costal strigulae; dorsum with a few scattered tiny white transverse dashes. Fringe bronze-brown. *Hindwing:* Light gray-brown. Fringe gray to dingy white. *Genitalia:* As in Figure 10 (n = 3; drawn from USNM slide no. 69338). Lamella postvaginalis a simple transverse band with a scobinate, broadly v-shaped region meso-ventrally; variable rectangular patch of scobination extending to ostium; sclerotized ridge representing ventral lip of ostium. Ductus bursae moderate with short sclerotized antrum. Accessory bursa a short digitate diverticulum from near junction of ductus bursae and ostium. Corpus bursae oblong. Ductus seminalis from caudal third of corpus.

TYPE MATERIAL. Holotype female: BRAZIL: State of Santa Catarina, Santa Catarina, XI-20-36 [20 November 1936], Fritz Hoffman (USNM).

Four female paratypes as follows: BRAZIL: State of Paraná, Castro, 3♀♀, 1898 (E. Jones, BMNH). No locality data, Paravicini Coll[ection], 1♀, B[ritish] M[useum] [accession no.] 1937-383 (BMNH).

ADDITIONAL MATERIAL EXAMINED. BRAZIL: State of Rio de Janeiro, km 17, 18 km S Teresopolis, 1180 m, 1♀, IV-18/19-77 [18–19 April 1977], C.M. and O.S. Flint (USNM).

REMARKS. The specimen from the State of Rio de Janeiro is smaller in forewing length and has a broader ductus bursae that is not clearly differentiated from the corpus bursae. It is possible that this specimen is not conspecific with *P. braziliana.* Consequently, the specimen is not designated a paratype.

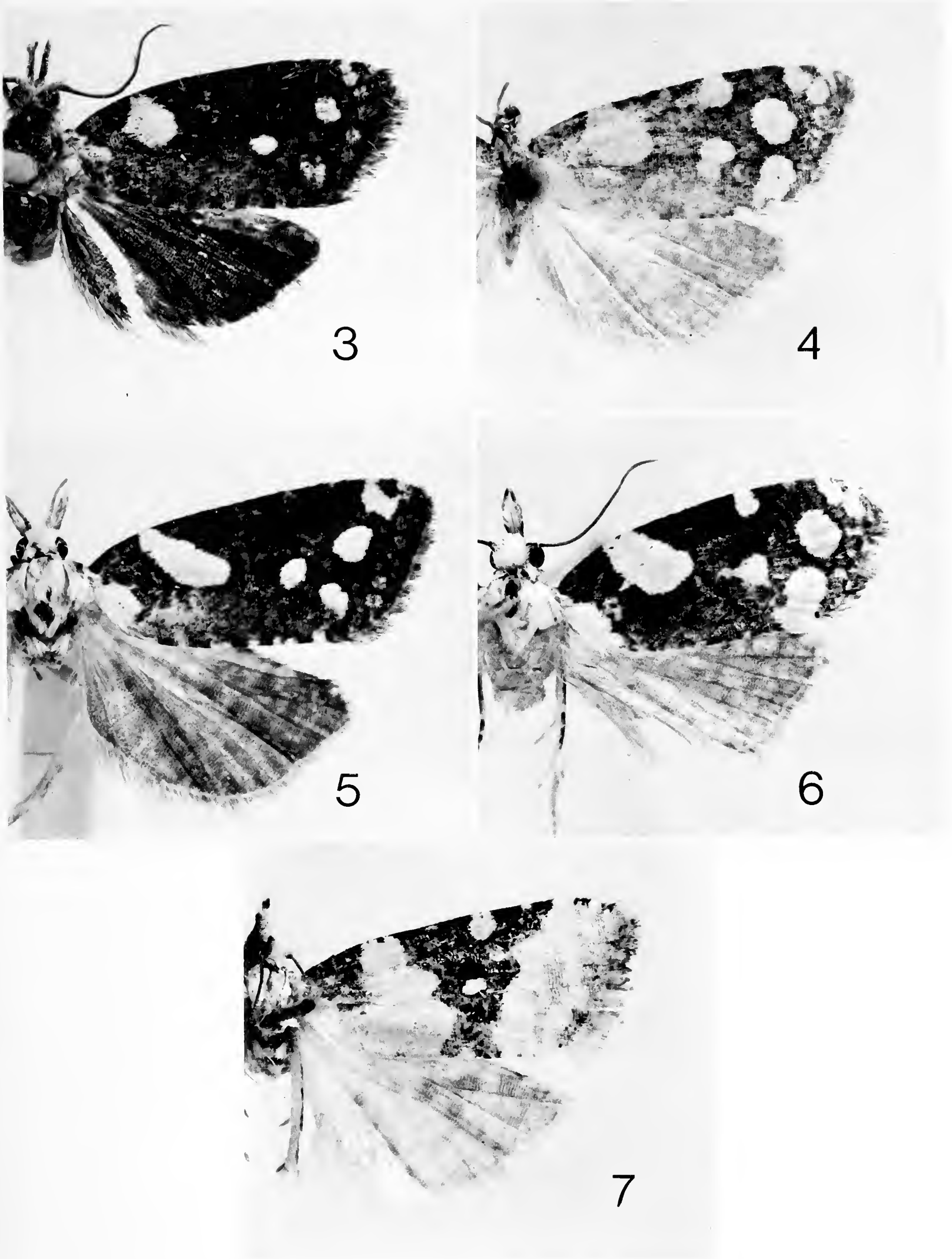
ETYMOLOGY. The name "braziliana" refers to the country of the type locality of this species.

4. *Punctapinella scleroductus* new species

Figure 11

MALE. Unknown.

FEMALE. FW length 9.2 mm (n = 1). *Head:* Frons and vertex white. Labial palpus white, gray-brown laterally. Antenna light brown. *Thorax:* White-ocherous, darker anterad. *Forewing:* Gray-brown with faint sparse red-brown overscaling; small white spot at base along dorsum; diagonal elliptical white spot from costa ca 0.2 from base; four small round spots in distal 0.5: one at costa ca 0.60 from base, one directly below latter near posterior apex of DC, two nearly equidistant from the latter, one tornad, the other apicad; apex with irregular white spot incorporating costal strigulae; subtermen with faint indistinct white dots. Fringe gray-brown. *Hindwing:* Light gray-brown. Fringe concolorous with wing. *Genitalia:* As in Figure 11 (n = 1; drawn from USNM slide no. 69336). Lamella postvaginalis a sclerotized band with dense patch of scobination; edge of abdominal segment VII immediately posterad of ostium with broad patch of scobination and narrow sclerotized ridge; ostium round with sclerotized perimeter. Ductus bursae broad, strongly sclerotized throughout. Corpus bursae narrow with fine ridges ventrally. Accessory bursa from long narrow ductus arising near junction of corpus and ductus bursae. Ductus seminalis from caudal portion of corpus bursae.

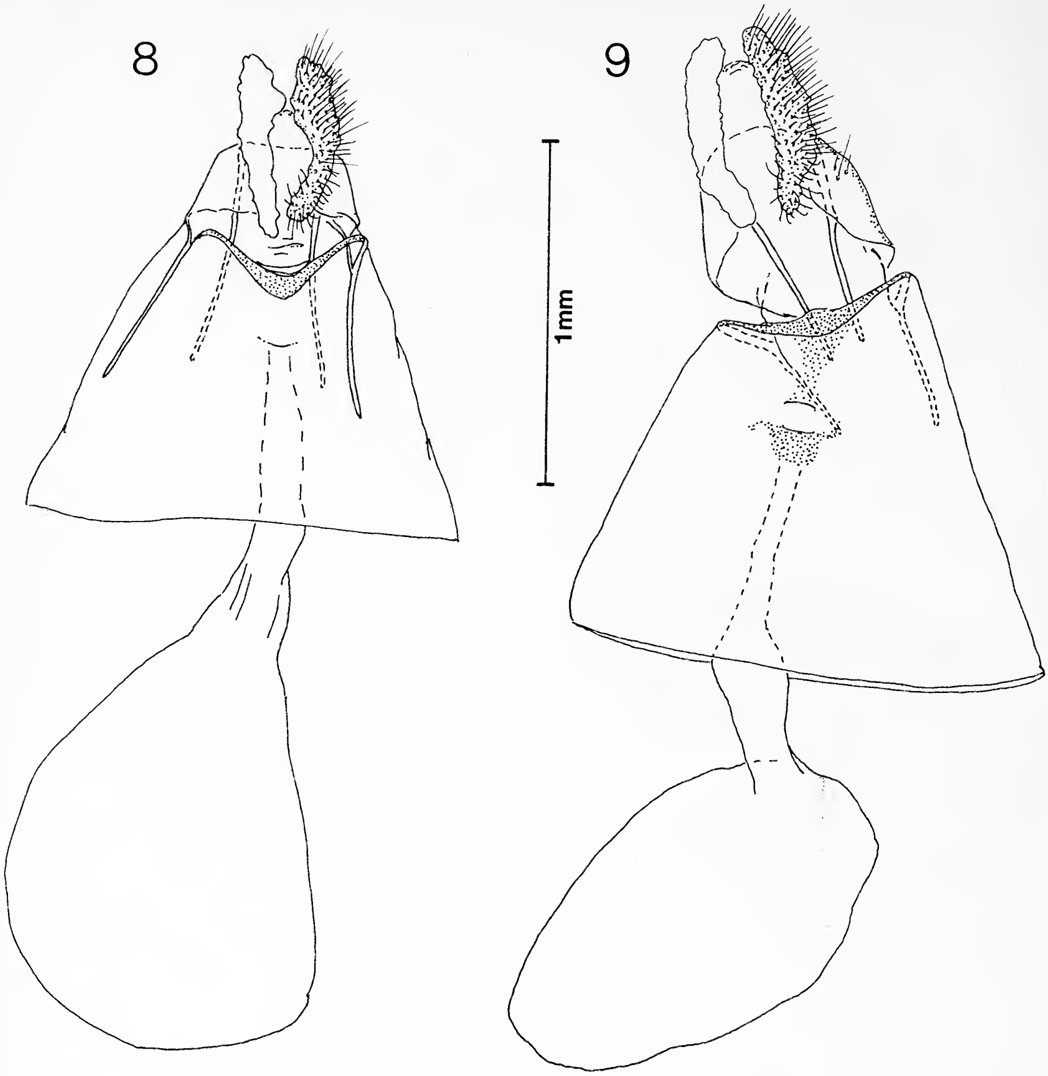


Figures 3–7. Adults of *Punctapinella*. **3.** Holotype of *P. niphastra*. **4.** Holotype of *P. chionocarpa*. **5.** Holotype of *P. braziliana*. **6.** Holotype of *P. theta*. **7.** Female of *P. conchitis*. All photographs courtesy of Victor Krantz (USNM).

TYPE MATERIAL. Holotype female: BRAZIL: State of Rio de Janeiro, Rio de Janeiro, 7/3/29 [3 July 1929], J.F. Zikán (USNM).

REMARKS. The adult of *P. scleroductus* is not illustrated, but it is similar to *P. chionocarpa* and *P. theta*. It can be distinguished from the latter two by the shape and size of the three white spots of the distal half of the forewing; i.e., round and equal in size in *P. scleroductus* (see key to species).

ETYMOLOGY. The name "scleroductus" refers



Figures 8, 9. Female genitalia of *Punctapinella*. **8.** *P. niphastra*. **9.** *P. chionocarpa*.

to the strongly sclerotized ductus bursae of the female genitalia.

5. *Punctapinella theta* new species

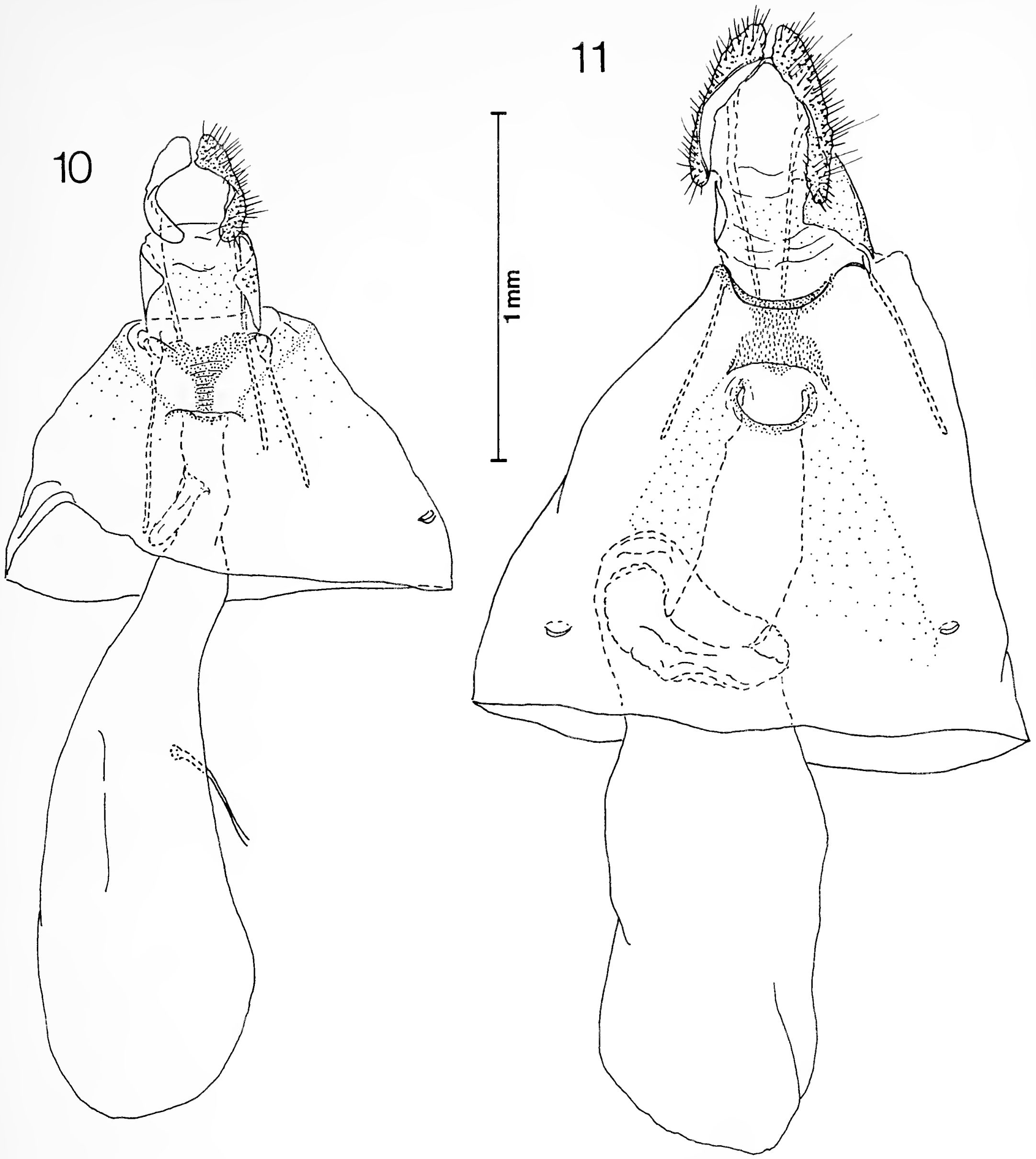
Figures 2, 6, 12

MALE. Unknown.

FEMALE. FW length 8.0–8.2 mm (x̄ = 8.1; n = 2). *Head:* Frons and vertex white. Labial palpus white, bronze-brown laterally. Antenna light brown. *Thorax:* White. *Forewing:* Bronze-brown; white spot at base along dorsum; larger oblong white spot from costa ca 0.2 from base; four roundish white spots in distal 0.5 of wing: one on costa ca 0.65 from base; one at posterior apex of DC; one at dorsum near tornus, the other directly above the latter; apex with irregular white area comprised of coalesced costal strigulae; subtermen with faint white dots. Fringe red-brown. *Hindwing:* White-ocherous with sparse gray-brown overscaling. Fringe white-ocherous. *Genitalia:* As in Figure 12 (n = 2; drawn from USNM slide no. 69334). Lamella postvaginalis a sclerotized transverse band slightly broadened meso-ventrad, with slender digitate band of sclerotization extending anterad into ostium; perimeter of ostium unsclerotized. Ductus bursae moderately broad. Corpus bursae a pear-shaped sac. Ductus seminalis from caudal 0.30 of corpus. Weak, broad ductus of accessory bursa from ductus bursae near ostium.

TYPE MATERIAL. Holotype female: VENEZUELA: State of Aragua, Rancho Grande, 1100 m, VIII-15/21-67 [15–21 August 1967], R. W. Poole (USNM).

One female paratype same locality as holotype, V-15-67 [15 May 1967], J. Salcedo and C. Andara (IZAV).



Figures 10, 11. Female genitalia of *Punctapinella*. **10.** *P. braziliana*. **11.** *P. scleroductus*.

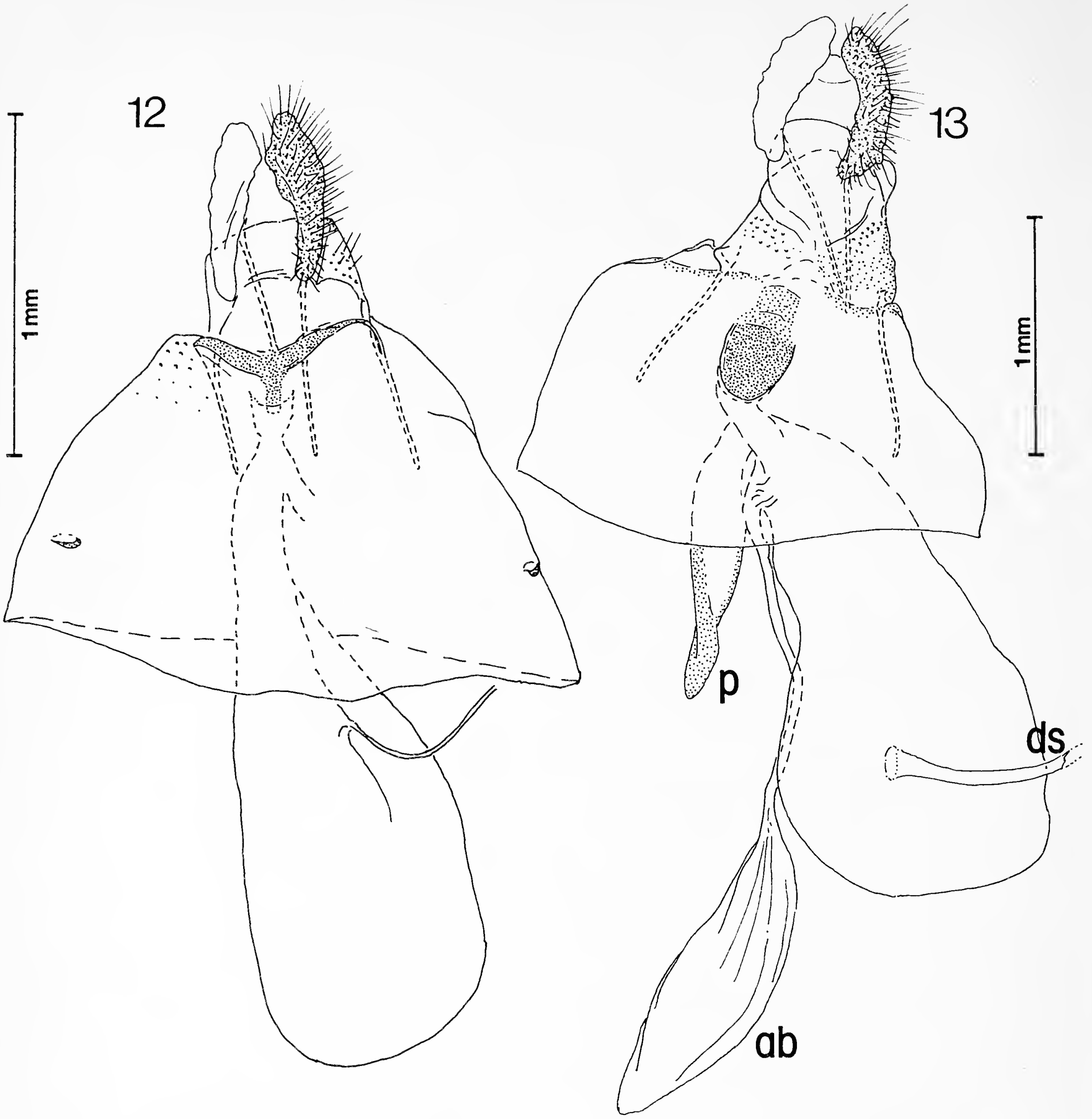
ETYMOLOGY. The specific epithet "theta" refers to the t-shaped sclerotized region of the lamella postvaginalis.

6. *Punctapinella conchitis* (Meyrick) new combination

Figures 7, 13, 14

Eulia conchitis Meyrick, 1912:681; Clarke, 1958: 120.

MALE. FW length 8.0 mm (n = 1). *Head:* Frons and vertex white. Labial palpus white, light brown laterally. Antenna brown. *Thorax:* Silver-white. *Forewing:* Olive green-bronze, with two broad transverse white bands: one from costa ca 0.2–0.3 from base, extending to dorsum, posteriorly contiguous with white basal spot; second band occupying distal 0.3 of wing, with faint, light bronze-olive band at termen; subtermen with poorly defined bronze streak parallel to termen; white spot at costa ca 0.65 from base representing pair of confluent white costal strigulae and a second confluent pair ca 0.9 from base; a small white spot near posterior apex of DC. Fringe tan and cream-ocherous. *Hindwing:* White with gray-brown mottling. Fringe



Figures 12, 13. Female genitalia of *Punctapinella.* **12.** *P. theta.* **13.** *P. conchitis.* ds = ductus seminalis, ab = accessory bursa, p = pouch.

concolorous with wing. *Genitalia:* As in Figure 14 (n = 1; drawn from JWB slide no. 276). Uncus slender, rodlike, curved. Socii simple, short, digitate, setose. Gnathos with strong medial process from apical fusion of lateral arms. Transtilla weak mesally; basal region large, appearing as a strongly sclerotized basal extension of valva; a deep cuplike invagination subbasally. Valva narrow, moderately elongate, attenuate distally; costa with subbasal patch of 10–15 large spinelike setae; venter with rounded excavation ca 0.4–0.7 from base to apex; sacculus confined to basal 0.5 without free projection. Aedeagus moderately long, slender, with a single large compound cornutus.

FEMALE. FW length 9.0 mm (n = 2). As described for male. *Genitalia:* As in Figure 13 (n = 2; drawn from USNM slide no. 68850). Lamella postvaginalis a broad scobinate band; lamella antevaginalis with a strongly sclerotized oval patch at ostium. Ductus bursae moderately short. Corpus bursae simple, elongate. Accessory bursa a membranous attenuate sac from long narrow weakly sclerotized ductus arising on caudal portion of corpus bursae; unusual sclerotized distally attenuate pouch attached to bursa copulatrix at junction of corpus and ductus bursae. Ductus seminalis from anterior third of corpus.

TYPE MATERIAL. Holotype female: COLOMBIA: Department of Norte de Santander, San Antonio. 5800 feet [1800 m], November [no year] (BMNH).

ADDITIONAL MATERIAL EXAMINED. COLOMBIA: Department of Norte de Santander, San Antonio, 1♀, "11-07" [November 1907] (USNM);

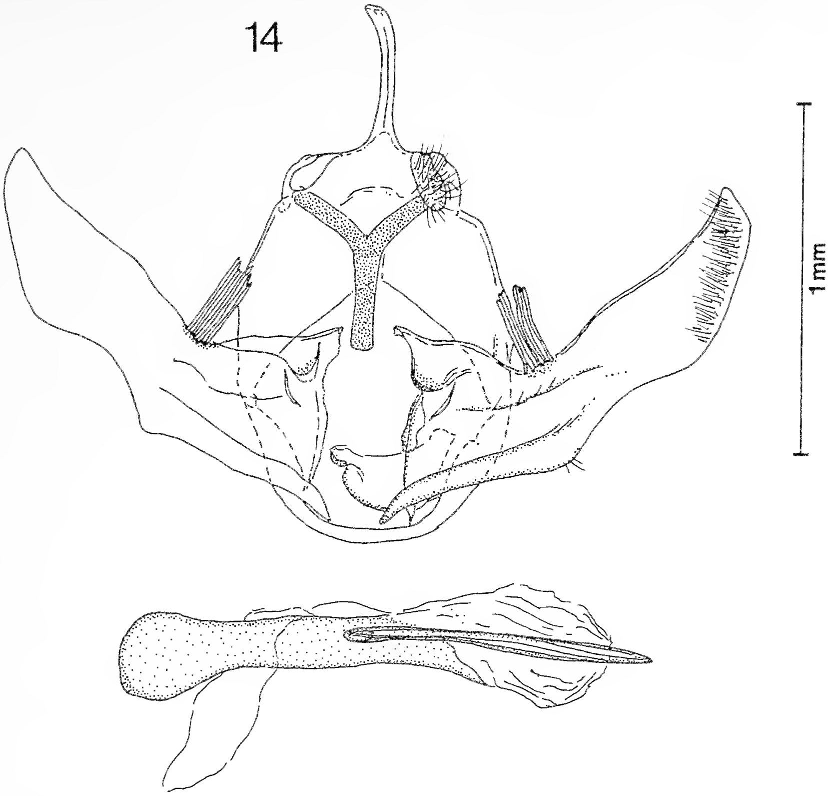


Figure 14. Male genitalia of *Punctapinella conchitis.*

Department of Magdalena, Sierra Nevada de Santa Marta, Hotel Solito, 2300 m, 1♂, VII-24-73 [24 July 1973], 7–8 PM (Oxford Expedition, BMNH).

REMARKS. The forewing pattern of *P. conchitis* probably represents the plesiomorphic state for the genus because it is most similar to that of *Seticosta* and *Anopinella.* Other species of *Punctapinella* exhibit an increase in melanic scaling, reducing the presumed white ground color to small round spots.

ETYMOLOGY. The Greek prefix "conch" means shell; the suffix "itis" means inflammation. The name may refer to the bronze-brown, somewhat triangular-shaped (shell-like?) marking of the forewing.

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TWO NEW SPECIES OF GEOMETRID MOTHS (LEPIDOPTERA: GEOMETRIDAE: ENNOMINAE) FROM COCOS ISLAND, COSTA RICA

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ABSTRACT. Seventy-five species of Lepidoptera are recorded from Cocos Island, Costa Rica, including seven species in the Geometridae. Two of these species in the subfamily Ennominae, *Oxydia hoguei* new species and *Phrygionis steeleorum* new species, are described and figured. *Oxydia hoguei* appears to represent the sister species of the Caribbean *O. lalanneorum* Herbulot, 1985, on the basis of long-bipectinate antennae in the male and an associated long epiphysis and by the configuration and spination of the furca in the male genitalia. The two species can be separated by color pattern, shape of the furca, and size of spines on the gnathos. *Phrygionis steeleorum* can be distinguished from its congeners by the absence of metallic silver scaling on the medial band of the forewing and in the marginal "eye-spot" of the hindwing. The two new species are endemic to Cocos Island. The traditional biogeographic hypothesis of species colonization of Cocos Island and the Galápagos Archipelago by vagrants from the Central and South American mainland is questioned.

(Additional key words: eastern Pacific, vicariance biogeography, Caribbean, *Oxydia hoguei, Phrygionis steeleorum.*)

INTRODUCTION

Cocos Island is a small (46.6 km² [18 mi²]) tropical eastern Pacific island situated midway between Costa Rica and the Galápagos Archipelago (5°32′57″N, 86°69′17″W), approximately 500 km (310 mi) from the Central American mainland. The island is wholly volcanic in origin; the highest point, Cerro Iglesias, reaches 849 m in elevation. The vegetation of Cocos Island is dense and luxuriant with a flora that includes over 200 species (Fosberg and Klawe, 1966). In a recent study of the entomofauna, Hogue and Miller (1981) reported approximately 75 species of Lepidoptera, including seven species of Geometridae. The purpose of this paper is to describe two of these species as new. Both appear to be endemic to this isolated island.

MATERIALS AND METHODS

Although Lepidoptera from Cocos Island were borrowed from all major United States institutions, only the collection of the Natural History Museum of Los Angeles County (LACM) contained specimens of the two new species of Geometridae described here. Holotypes are deposited at the LACM; paratypes are distributed among the following institutions: American Museum of Natural History, New York, New York; United States National Museum of Natural History, Washington, D.C.; The Natural History Museum, London, England (formerly British Museum [Natural History]); and Costa Rican Institute for Biodiversity, San José, Costa Rica.

Dissection techniques followed those presented by Powell (1964). Nomenclature for genitalic structures follows Klots (1970) and Rindge (1973). Figures of the genitalia were drawn with the aid of a microprojector. Measurements were made using a standard grid mounted in a dissecting microscope.

SYSTEMATICS

GEOMETRIDAE: ENNOMINAE

Oxydia hoguei new species

Figures 1–4, 6–9

DIAGNOSIS. Superficially, *O. hoguei* can be distinguished from its congeners by the conspicuous and contrasting yellowish ground color of the anterior half of the dorsal surface of the hindwing, bearing a large solid-blackish and well-marked subapical quadrate spot, and the course of the forewing postmedian line, which is posteriorly concave then abruptly convex at vein M_1 and recurved proximally to the costa (this line is straight and terminates near the apex or is angled more acutely on most, if not

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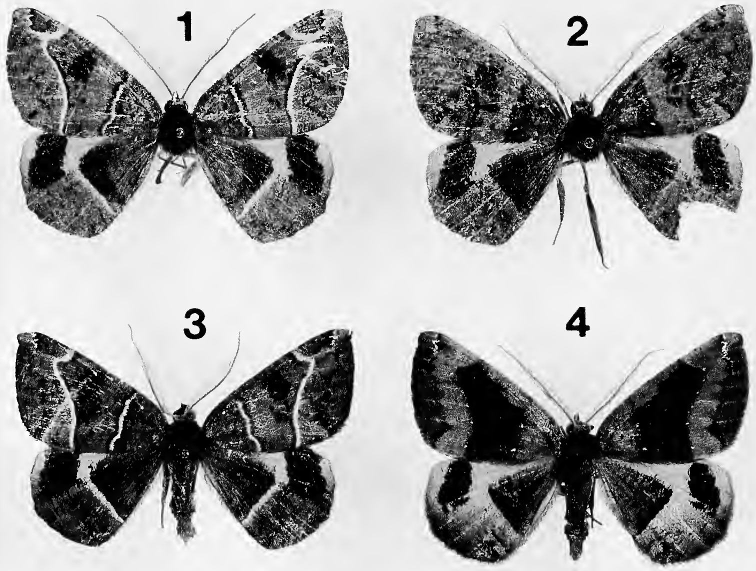
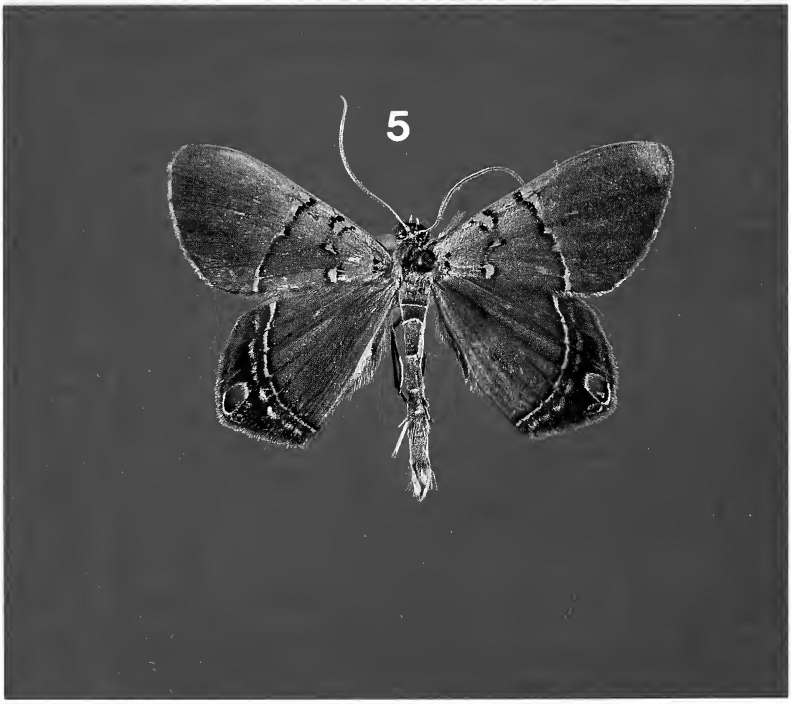
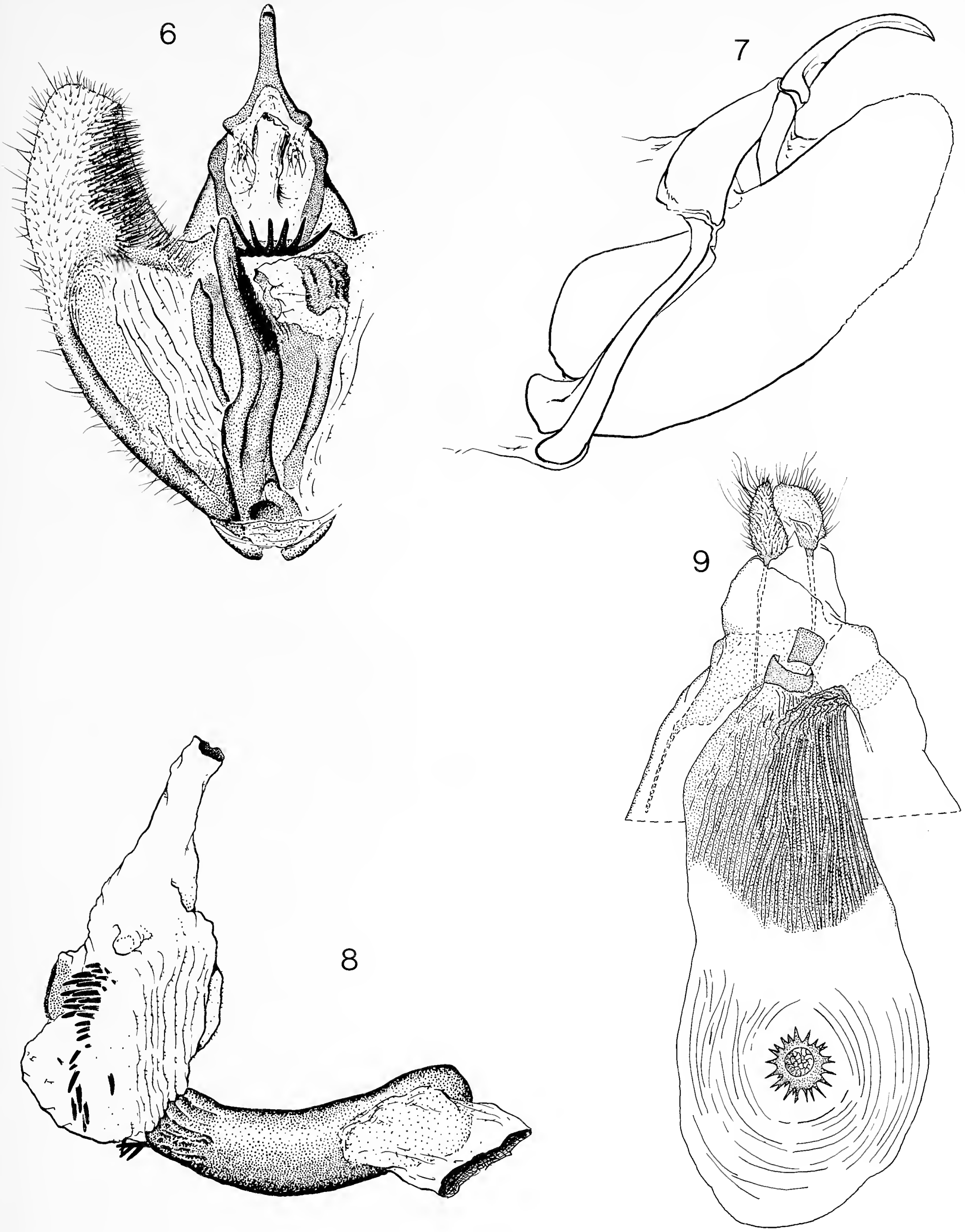




Figures 1–4. Males of *Oxydia hoguei* from Cocos Island, Costa Rica.

Figure 5. Male of *Phrygionis steeleorum* from Cocos Island, Costa Rica.

all, other *Oxydia*). On the basis of the long-bipectinate male antenna and long epiphysis (about as long as the tibia), *O. hoguei* appears to be most closely related to *O. lalanneorum* Herbulot, because all other species of *Oxydia* have short-bipectinate (*O. brevipecten* Herbulot) or simple antennae and short epiphyses (i.e., about one-half the tibia length). The male genitalia of *O. hoguei* are most similar to those of *O. lalanneorum* in the shape of the furca and the size and distribution of



Figures 6–9. Genitalia of *Oxydia hoguei*. **6.** Posterior view of male genitalic capsule, valvae spread, aedeagus removed (right valva omitted). **7.** Lateral view of male genitalic capsule. **8.** Aedeagus. **9.** Ventral view of female genitalia.

the minute brushlike spines that adorn it: in *O. hoguei* the furca is sigmoid and the marginal spines of the gnathos are stout and subequal, whereas in *O. lalanneorum* the furca is evenly curved and concave to the left and the marginal spines on the gnathos are slender and irregular. Females of the two species are easily distinguished by color pattern (the female genitalia of *O. lalanneorum* have not been described).

DESCRIPTION. Adult a large brightly patterned brown and yellow geometrid, with conspicuous bipectinate male antennae. The wing pattern is extremely variable; no two specimens are identical in maculation.

Male. *Head:* Compound eyes well developed, spherical. Antenna bipectinate from distal end of each flagellar segment, the longest rami 4 times the length of segment, each ramus terminating in loosely arranged groups of about six setae; scape, pedicel, few basal segments of flagellum gray (concolorous with vertex), remainder of flagellum light brown. Labial palpus erect, second segment projecting beyond front, third segment short, oblique. Labial palpi, frons, and postvertex dark brown; vertex gray. *Thorax:* Legs simple, only the tarsi bearing spines. Epiphysis nearly as long as tibia. Hind tibia swollen, with long hairpencil arising basally, concealed in a longitudinal mesal slit. Thorax dark brown dorsally, paler ventrally; legs light brown, irrorated with dark brown. *Abdomen:* Sternite III with median transverse row of long bristlelike setae. Abdomen concolorous with thorax dorsally and ventrally, genital scaling paler. Hairpencils and eversible glands absent. *Forewing:* Length 25–28 mm ($\bar{x} = 26$; $n = 12$); apex minutely falcate. Dorsal pattern elements fairly uniform but their expression and coloration extremely variable. Ground color mottled medium brown to blackish brown, costal region paler; costal, basal, and subterminal areas with obscure fine to coarse striations. Transverse lines usually conspicuous: antemedial line white, usually margined both proximally and distally with blackish brown, traversing wing in an irregular but nearly straight path from costa at 0.25 the distance from base to apex of wing, outwardly oblique to cell, then more or less perpendicularly through cell to inner margin at 0.4 the distance from wing base to apex of anal vein, somewhat sinuous: slightly concave through cell, and again through submedian fold, then abruptly convex from anal vein to inner margin. Postmedial line white, usually margined proximally with blackish brown, traversing wing from the base of vein R_5 (adjacent to costa at ca 0.66) then concave and obliquely distad to vein M_1, where it abruptly curves through 90° and is nearly straight to vein Cu_2, then gently concave to anal vein and convex to inner margin; postmedial line occasionally produced distally as a whitish patch in cell R_5–M_1, fusing with subterminal line to set off an irregular subapical costal patch of ground (or darker) color. Subterminal line dentate distally on veins, blackish brown, variable, sometimes macular or widened, most pronounced anterad of vein R_5 where it is blacker and edged distally with white, bearing an extra distally directed tooth in cell R_4–R_5; posterad of vein R_5 roughly parallel to postmedial line to vein Cu_2, then directed abruptly distad to tornus. A single black discal spot at origin of vein M_2 often obscured by large irregular quadrate dark brown patch distad of spot. Fringe concolorous with wing. *Hindwing:* Outer margin minutely scalloped, angulate at vein M_2. Dorsally, cell and inner margin mottled medium brown to solid brownish black, terminating abruptly at the postmedial line, ground color distad of postmedial line varies from dark brown to light brown or yellowish mottled and striate with brown; costal one-third of wing pale yellow, bearing a large black submarginal quadrate spot from (or near) costa to the M_2 fold; postmedial line pale yellow to yellowish white, sometimes obscure, a posterior extension of the costal yellow and evident only from M_1 nearly straight to inner margin at 0.75. Single black discal dot at base of M_2 fold obscured by dark basal ground color. Fringe concolorous with wing. Ventral wing pattern similar, more mottled and less contrasting, ground color pale yellowish, black discal dots more prominent on both wings. *Genitalia:* As in Figures 6–8 ($n = 3$; drawn from C.L. Hogue prep. no. 78-87). Uncus long, slender, gradually curved, apex acute and simple. Gnathos strongly sclerotized with truncate anterior portion bearing a transverse row of 7–11 elongate marginal spines. Valva with costa sclerotized, unarmed, sacculus weakly sclerotized, remainder of valva semimembranous; mesal surface ventrad of costa densely setose (other setae as figured). Juxta complex, asymmetrical: lateral margins convex, revolute (more pronuounced on left side); an elongate digitate sinuous furcal lobe arising basally on left, projecting posteriorly to beyond base of costa of valva, bearing a strip of dense minute brushlike spines on the meso-dorsal surface for most of its length. Aedeagus stout, straight, apex acute ventrally; exserted vesica with a small central oval platelike cornutus bearing slender deciduous setae and two groups of uneven stout setose cornuti: a compact basal group of 7–10, contiguous to apex of aedeagus, and a cluster of smaller ones near the center of the vesica.

Female. *Head:* As in male except antennae simple. *Thorax:* as in male, but hindtibia not swollen and hairpencil lacking. *Abdomen:* Unmodified. *Wings:* Falcate forewing apex more pronounced than in male; length 28–30 mm ($\bar{x} = 29$; $n = 3$). Pattern as in male, dorsal ground color variable, but two of the three specimens with forewing ground color more uniform than in males, median area only slightly darker; discal dots conspicuous, postdiscal and subapical shades absent; ventral ground color variable, forewing pale apical patch prominent, hindwing with broad subterminal dark shade followed by a paler contrasting terminal band. *Genitalia:* As in Figure 9 ($n = 2$; drawn from J. W. Brown slide no. 314). Papillae anales (= ovipositor lobes) simple. Sterigma lightly sclerotized; ostium a sclerotized collar with an irregular quadrate sclerite posterad. Bursa copulatrix not differentiated into distinct ductus and corpus bursae; entire structure with numerous longitudinal creases; posterior one-half slightly more narrow, strongly sclerotized; ductus seminalis from attenuate stout lobe at posterior right side of ductus bursae. Signum a large hollow hemisphere, with numerous pointed projections laterally and internally, a few of them bifurcate.

SPECIMENS EXAMINED. Holotype male: COSTA RICA, Cocos Island, Wafer Bay, 23 March 1978, 15-watt blacklight trap, Station 2, Steele Exped. 1978 (C. Hogue and S. Miller).

PARATYPES. Eleven males and three females as follows: Costa Rica: Cocos Island: 1♂, same data as holotype. Wafer Bay: 1♂, 17–22 April 1975 (C. L. Hogue). Rio Génio: 1♂, 23 March 1978, 15-watt blacklight trap, Station 2, Steele Exped. 1978 (C. Hogue and S. Miller). Mirador: 1♂, 17 February 1984, Malaise trap; 1♂, 26 March 1984, Malaise trap (T.W. Sherry and T.K. Werner). Forest interior: 1♂, 7 January 1984, Malaise trap; 1♂, 1♀, 19 February 1984, at light, elev. ca 200 m (T.W. Sherry and T.K. Werner, 190284-2 and 190284-1, respectively); 1♂, 1♀, 11 February 1984, Malaise trap; 1♂, 2 April 1984, Malaise trap (T.W. Sherry and T.K. Werner). Selva: 1♂, 1♀, 17 February 1984, Malaise trap (T.W. Sherry and T.K. Werner). Wafer Bay/Rio Génio: 1♂, 6–9 March 1980, Malaise trap (T.K. Werner and T.W. Sherry).

REMARKS. Although *Oxydia hoguei* differs considerably from other species in the genus in general appearance and in the possession of bipectinate male antennae (a character state found in only two other recently described Caribbean species of *Oxydia*, *O. lalanneorum* Herbulot, 1985, and *O. brevipecten* Herbulot, 1985), other features of adult morphology agree well with Rindge's (1957) definition of the group. Putative synapomorphies for the genus include the distinctive furca and row of strong sclerotized spines on the gnathos. Other features of *Oxydia* Guénee, 1857, all of which may be found in one or more other genera of Ennominae—often present or absent within the same genus—include the following: male with row of bristles on the ventral surface of abdominal segment III, male with hairpencil concealed in slit of enlarged hindtibia, female genitalia with hemispherical stellate signum, outer margin of hindwing angulate midway, and hindwing with subapical submarginal dark macula (evanescent to distinct).

According to Rindge (1983) and Herbulot (1985), the character state of bipectinate male antennae represents the plesiomorphic condition. On this basis, *O. hogue* and *O. lalanneorum* appear to represent the most primitive members of the genus. The unique configuration of the furca and associated brushlike spines represent a putative synapomorphy supporting the sister status of these two species.

Oxydia lignata (Warren, 1905) from the Galápagos Archipelago (Rindge, 1973) is a diminutive species with similarities to *O. hoguei* and *O. vesulia* (Cramer, 1779) but distinct from both in several characteristics probably correlated with its small size (i.e., male forewing length = 14–16 mm): furcal lobe short, broad, and brushlike; unlobed vesica without distal ovate plate; and nearly unicolorous wing pattern.

ETYMOLOGY. We take great pleasure in naming this species after Charles L. Hogue, who was the first to collect specimens of this striking species in the course of his exhaustive survey of the entomofauna of Cocos Island.

[NOTE: We follow Herbulot (1977:40; 1983:34) and Ferguson (1983:97) in placing *Oxydia* in the Ennominae, characterized by the absence of a tubular M$_2$ vein in the hindwing. We assume that Fletcher's (1979:149) assignment of *Oxydia* to the Oenochrominae was in error.]

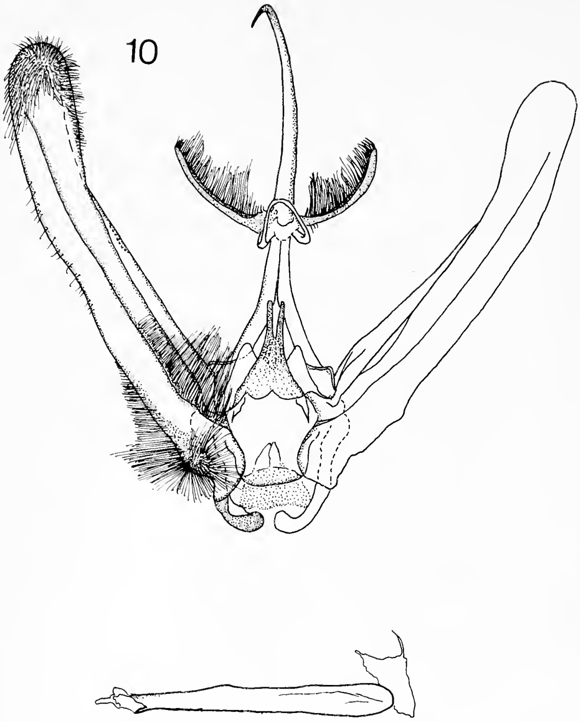
Phrygionis steeleorum new species

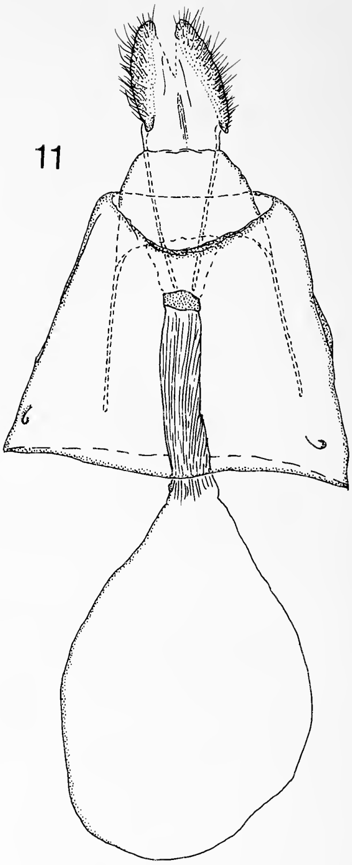
Figures 5, 10, 11

DIAGNOSIS. *Phrygionis steeleorum* can be distinguished from all other species in the genus by the absence of metallic silver edging on the pale medial band of the forewing and the absence of metallic scaling in the marginal "eye-spot" of the hindwing.

DESCRIPTION. *Phrygionis steeleorum* is a medium-sized gray-brown geometrid, with pale yellow antemedial and medial bands and a small marginal "eye-spot" on the hindwing between veins M$_2$ and M$_3$.

Male. *Head:* Scaling on frons smooth, short, fawn brown; scaling on vertex short, suberect, concolorous with frons. Antenna shortly bipectinate, inner rami approximately 0.5 the length of outer rami; basal 12 (more or less) segments of flagellum white-scaled ventrally, width of white line attenuating distally. Compound eyes well developed. Ocelli vestigial, minute, or apparently absent. Labial palpus short, extending slightly above ventral edge of frons. *Thorax:* Fawn brown; legs unmodified. *Abdomen:* Fawn brown; paired subdorsal patches of elongate scales (hairpencil) from posterior edge of segment VI. *Forewing:* Length 15.2–17.2 mm ($\bar{x}$ = 16.2; n = 2). Ground color gray-brown; medial band narrow, diffuse, irregular, transverse, yellow, nearly perpendicular to costa at about half way from base, arched weakly to inner margin at ca 0.8 of distance from base, bordered proximally by irregular thin brown line; antemedial line yellow, irregular, excurved through cell and incurved over fold, bordered internally and externally with brown; antemedial line widest below costa and above inner margin, sometimes incomplete; minute yellow basal dash on costa, and two black basal dots, proximally edged with yellow, perpendicularly arranged between bases of CuP and second A. Fringe concolorous with wing. *Hindwing:* Outer margin angled at M$_3$, without tail. Ground proximally concolorous with forewing, then brown from inner edge of postmedial line to termen. Postmedial line narrow, yellow, evenly excurved, followed by a metallic silver line, interrupted across the veins to form a series of linear spots. Marginal "eye-spot" between M$_2$ and M$_3$ extending slightly into cell M$_1$–M$_2$; a narrow (widened proximally and distally) yellow ring; proximal 0.5–0.66 of area inside of ring orange, distally black, and a similar smaller adjacent "eye-spot" (ca. 0.3 times as large in cell M$_3$–CuP). *Genitalia:* As is Figure 10 (n = 2; drawn from J.W. Brown slide no. 312). Uncus long, slender, with sclerotized attenuate tip. Socii long, narrow, curved,





Figures 10, 11. Genitalia of *Phrygionis steeleorum*. **10.** Posterior view of male genitalic capsule, valvae spread, aedeagus removed. **11.** Ventral view of female genitalia.

densely scaled. Gnathos narrow, arched, u-shaped. Valva long, narrow; a pair of longitudinal creases; ventral base with dense patch of fine non-deciduous setae. Transtilla a triangular plate bearing a distal pair of slender digitate processes. Aedeagus simple, straight; cornuti absent.

Female. *Head, Thorax, and Abdomen:* As in male except antenna simple and abdominal segment VI without hairpencil. *Forewing:* Length 15.6–17.5 mm ($\bar{x}$ = 16.5; n = 10). As described for male. *Hindwing:* As described for male. *Genitalia:* As in Figure 11 (n = 2; drawn from J.W. Brown slide no. 313). Papillae anales (= ovipositor lobes) simple. Sterigma lightly sclerotized, membranous around ostium. Bursa copulatrix differentiated into moderately long narrow ductus and rounded corpus; junction of ductus and ostium indicated by sclerotized collar, open dorsally. Ductus bursae with numerous faint longitudinal creases; corpus bursae simple, unmodified, signa absent.

SPECIMENS EXAMINED. Holotype male: COSTA RICA, Isla de Coco, Cerro Iglesias, 27–31 March 1984, Malaise trap, T.W. Sherry and T.K. Werner.

PARATYPES. Three males and 12 females as follows: Costa Rica: Cocos Island: Mirador: 1♂, 2♀♀, 17 February 1984 (T.W. Sherry and T.K. Werner); 1♂, 19 April 1984, 460 m (D. Thomas). Forest interior: 1♀, 18 September 1984; 1♂, 1♀, 7 January 1984; 3♀♀, 11 February 1984 (T.W. Sherry and T.K. Werner); 1♀, 14 April 1984, 360 m, Malaise trap (D. Thomas); 1♀, 1 August 1984 (T.W. Sherry and T.K. Werner). Wafer Bay/Rio Génio: 2♀♀, 6–9 March 1980 (T.W. Sherry and T.K. Werner). Cerro Iglesias: 1♀, 3 March 1980 (T.W. Sherry and T.K. Werner).

REMARKS. Prout (1933) listed 18 species in his treatment of *Phrygionis* Hübner, 1825, distributed from Florida to northern Argentina, with several species endemic to Caribbean islands (e.g., Jamaica, Cuba, Puerto Rico, Dominica, Martinique). Putative synapomorphies for the genus include male antenna minutely bipectinate in middle (i.e., unmodified at base and tip), legs long and slender, male with paired hairpencil from enlarged base of sixth tergite [lacking in *P. flavilimes* (Warren, 1907) and *P. sumptusaria* (Möschler, 1886)], hindwing angled or tailed at distal end of vein M_3, and frenulum absent. Figures 10 and 11 represent the first published genitalic illustrations of the genus. For comparisons of the adult moth with *P. argentata* (Drury, 1773), illustrations of the latter can be found in Holland (1903:pl. 44, fig. 35), Kimball (1965:pl. 23, fig. 20), and Covell (1984:286, pl. 56, fig. 3).

In the absence of comparative material from throughout the range of *Phrygionis,* it is premature to speculate on the phylogenetic position of *P. steeleorum* within the genus.

ETYMOLOGY. We taken pleasure in naming this species in honor of Richard, Elizabeth, and Patricia Steele, sponsors of the 1978 LACM expedition to Cocos Island.

DISCUSSION

In addition to the two new ennomines described here, five other species of Geometridae have been collected on Cocos Island, one in each of the following genera: *Synchlora* Guenée, 1857 (Geometrinae), *Psaliodes* Guenée, 1857 (Larentiinae), *Eupithecia* Curtis, 1825 (Larentiinae), *Idaea* Treitschke, 1825 (Sterrhinae), and *Tricentrogyna* Prout, 1932 (Sterrhinae). Although these five species have not been studied adequately to render specific determinations (and even the generic assignments are equivocal for the Sterrhinae), it is likely that one or more represent undescribed species. It is possible that all seven geometrids recorded from Cocos Island are endemic to the island. A similar situation is evident on the Galápagos Archipelago, where 12 geometrids have been recorded: nine (75%) are endemic; the other three are common widespread Neotropical species (Rindge, 1973), none of which has been recorded from Cocos Island. Cocos Island and the Galápagos Archipelago share only one genus, *Oxydia,* of which each supports a single endemic species.

In his discussion of the geometrid fauna of the Galápagos Islands, Rindge (1973) suggests that its depauperate nature may be attributable to the relatively limited vagility of many species of geometrids. He suggests that most of the resident species probably were blown out to the islands from the adjacent South and Central American mainland. Although it may seem likely that the fauna of the Central American mainland represents the species pools for the fauna of Cocos Island, phylogenetic affinities of some Cocos and Galápagos Islands insects with Caribbean congeners suggests a more complicated biogeographic scenario than simple colonization by vagrants from the mainland. These islands may have been part of the Eastern Pacific–Caribbean vicariant track created by the Early Cenozoic breakup of the postulated proto-Antilles archipelago (Rosen, 1976:440). However, understanding of the tectonics of the region continues to evolve (Donnelly, 1988), and the place of Cocos Island within the regional tectonic events is unclear. Cocos Island is the summit of a seamount on the submerged Cocos Ridge, a proposed trace of the Galápagos volcanic hot spot. Cocos Island is about 2 million years old, although it lies on a portion of the ridge that is Middle Miocene in age (Castillo et al., 1988).

Thus the fauna of Cocos Island may represent a composite of vicariant relicts and recent invaders from the mainland. Such a hypothesis can be tested by careful phylogenetic analyses of taxa that occur on Cocos Island and the Galápagos Archipelago, the Central and South American mainland, and islands of the Caribbean. For example, Mathis and Wirth (1978) found *Paracanace hoguei* Mathis and Wirth, 1978 (Diptera: Canacidae), which is endemic to Cocos Island, to be the sister group to the species pair *P. aicea* Mathis and Wirth, 1978, and *P. leban* Mathis and Wirth, 1978, which are restricted to the West Indies. A similar biogeographic pattern is illustrated by *Oxydia*; the sister species of the endemic *O. hoguei* from Cocos Island appears to be *O. lalanneorum* from Guadeloupe Island in the West Indies. Further corroboration of this pattern awaits detailed revisions of taxa that have species endemic to Cocos Island, Central America, and the Caribbean regions.

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THOMAS C. LADUKE

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THE FOSSIL SNAKES OF PIT 91, RANCHO LA BREA, CALIFORNIA

THOMAS C. LADUKE[1]

ABSTRACT. The known snake fauna from Rancho La Brea is increased from four species to 12 on the basis of material from recently reexcavated LACM 6909 (=Pit 91). Two taxa, *Masticophis lateralis* and the *Thamnophis couchii* group, are reported as fossils for the first time.

Recognition of intracolumnar vertebral position is necessary for identification. A previously undescribed feature, the subcentral lymphatic fossa, aids in determining vertebral position.

The composition of the fauna suggests that the locality represents a Pleistocene stream site traversing a prairie or scrub habitat. The fauna is similar to the modern Los Angeles region fauna. This common pattern among late Pleistocene herpetofaunas in North America contrasts with known endothermic faunas. It is suggested that the evolutionary stability of the North American herpetofauna, as compared with that of endotherms, may be due to an ability to maintain viable populations during periods of environmental stress that result in extirpation of endotherms.

INTRODUCTION

The most important late Pleistocene fossil vertebrate locality in North America is Rancho La Brea in Los Angeles, California. This site has produced thousands of fossils in a superb state of preservation and has provided one of the most detailed accounts of a late Pleistocene biological community known. Moreover, it is the type fauna for the Rancholabrean Provincial Land Mammal Age (Savage, 1951).

Rancho La Brea is located in the Los Angeles Basin within the city of Los Angeles. The fossil deposits overlie the Palos Verdes Sand, which is partly impregnated with asphalt at Rancho La Brea. Numerous accounts of dates and dating techniques for Rancho La Brea material have been published (Howard, 1960; Berger and Libby, 1966, 1968; Ho *et al.*, 1969; and McMenamin *et al.*, 1982). Estimates vary from about 4,000 to over 40,000 years B.P. (McMenamin *et al.*, 1982). See Stock (1956), Woodard and Marcus (1973), Shaw (1982), and Shaw and Quinn (1986) for detailed discussions of location, age, geology, stratigraphy, and history of excavation.

Early workers postulated that the tar deposits of Rancho La Brea represent previously fluid, viscous pools in which animals were trapped and entombed. These pools were conceived of as dynamic fluid bodies that underwent convective turnover that disarticulated skeletons, wore bone surfaces, and obliterated stratigraphy (Stock, 1956). Woodard and Marcus (1973) have shown that a gross stratigraphy exists in some pits and that some of the material is entombed in stream deposits that were inundated by asphalt. Shaw and Quinn (1986) indicate that most animals were probably entrapped in thin sheets of tar exposed at the surface of the deposits.

Early studies of Rancho La Brea concentrated on its spectacular large mammal and avian faunas (see Stock, 1956, for a review and bibliography) but largely neglected vertebrate microfossils, invertebrates, microbotanical remains, taphonomy, and details of stratigraphy. In the 1940's, D.W. Pierce developed a technique for recovering minute fossils from the asphaltic matrix (Stock, 1956). Pierce's studies were mostly concerned with insect remains, but microvertebrate fossils were also recovered (Brattstrom, 1953b).

Brattstrom (1953b) published the first comprehensive treatment of amphibians and reptiles from Rancho La Brea, based partly on Pierce's collections. Snakes were poorly represented in this collection, and Brattstrom anticipated that greater diversity would be revealed by further collecting.

In 1969, a study was initiated at Rancho La Brea to improve understanding of aspects of the site that were not well documented by previous investigators. Locality LACM 6909 (=Pit 91), originally set aside for display purposes in 1915, is being reexcavated with careful attention to taphonomy, the recovery of microfossils, stratigraphy, etc. (Shaw, 1982; Shaw and Quinn, 1986). Lower levels of this deposit are partly composed of natural stream sediments that may yield some stratigraphic information. Radiocarbon dates on wood and bone collagen from Pit 91 range from 25,100 to over 40,000 years B.P. (Marcus and Berger, 1984), revealing that Pit 91 is relatively old among Rancho La Brea deposits. The present study is based on the snake

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remains from this excavation and documents the diversity that Brattstrom (1953b) anticipated.

OPHIDIAN OSTEOLOGY

Fossilized snake remains are relatively common in Neogene deposits that bear vertebrates. The most important factor contributing to their abundance is probably the large number of skeletal elements per individual. The number of precaudal body segments in snakes typically ranges between 150 and 300. Each of these segments bears three skeletal elements, a vertebra and two ribs. Because of their fragile nature, the ribs and many skull elements are not commonly found as fossils. Other factors affecting the number of snake remains in the fossil record are the relative abundance of individuals in fossil communities and the durability of their solidly constructed vertebrae (Holman, 1981). Articulated snake skeletons are rare in the fossil record. Most snake remains are found in stream deposits and predator accumulated deposits. For these reasons, isolated vertebrae are by far the most frequently encountered and closely studied snake fossils.

A general guideline for identifying North American Pleistocene snakes is presented by Holman (1981, appendix). Auffenberg (1963), Brattstrom (1967), and Meylan (1982) also treat this topic. Identification of snake skeletal elements to genus or species depends on recognition of ranges of variability of subtle characters and proportions and requires the use of extensive comparative collections (Holman, 1981). Identification is usually simplified by limiting comparisons of Pleistocene fossils to living taxa from a limited geographic area.

The difficulties involved in vertebral identification have been widely recognized, and the practice is often viewed with skepticism because of numerous factors that contribute to the variability of vertebral morphology, not only between taxa but within taxa. Individuals vary both ontogenetically and topographically along the vertebral column. Morphological features change gradually from one character state to another as one proceeds down the vertebral column. In most instances this change is imperceptible in consecutive vertebrae. Furthermore, similar character states may appear in different regions of the vertebral column in different taxa. These factors encumber qualitative description and often force one to rely on comparative terms, using one species as a standard for another. Given ample time and comparative material, however, recognizable patterns in vertebral morphology emerge. Unfortunately, extensive comparative collections are relatively few, and their geographic and ontogenetic representation are often limited.

Some authors have relied on qualitative methods of discrimination to identify snake vertebrae. Others have used ratios of linear measurements as size free discriminators. The use of ratios originated with Auffenberg (1963) and has been continued by Van Devender *et al.* (1977, 1985), Van Devender and Worthington (1977), Van Devender and Mead (1978), and Mead *et al.* (1984). Meylan (1982) has gone a step further by using discriminant analysis to distinguish taxa using populations of ratios of linear measurements.

Although the use of quantitative analysis in conjunction with qualitative characters would be beneficial, most previous workers (using quantitative or qualitative methods) have relied exclusively on the use of mid-trunk vertebrae to identify fossils, while providing little information on how these are distinguished from vertebrae of other regions of the vertebral column. This is unfortunate because, for many characters, the novice may confuse vertebrae from one region of the column of one species with those from a different region in other species. Furthermore, the use of ratios as statistical discriminators has been criticized (Atchley *et al.*, 1976). Unfortunately, quantitative comparisons of characters spanning the entire vertebral column in even a single extant snake species are very few and limited in scope (e.g., Hoffstetter and Gayrard, 1965). The present study relies almost entirely on qualitative comparison.

Although the descriptions of the criteria for identifying snake vertebrae are admittedly cumbersome, qualitative techniques remain the only readily accessible approach to the gross study of entire ophidian paleofaunas. However, taxonomic refinement of fossil snakes will require quantitative study of interspecific, intraspecific, and ontogenetic shape variation in the vertebrae of living and fossil taxa.

DESCRIPTIVE TERMINOLOGY

Auffenberg (1963) provided descriptive terminology for shape variation in snake vertebrae that most subsequent authors have followed. New descriptive terms introduced here require some clarification. Most of these terms refer to shapes of structures and derive from a simple division of shape characters into extremes and intermediates, e.g., elongate, shortened, moderately elongate, etc. In an attempt to provide a quantitative characterization for these shape descriptors, limits for the character states were defined by choosing borderline cases and calculating ratios for measurements of features that strongly affect the shape. The average of these ratios provided approximate limits for character states. Individual fossils were matched with a taxon by visual comparison of these character states. Abbreviations follow Auffenberg (1963) or are described below. Measurements used in this study are illustrated in Figure 1.

Vertebral Length. In this paper, a vertebra is considered *elongate* if CL/NAW (centrum length to neural arch width) is approximately 1.2 or greater (Fig. 1). If 0.8 or less, the vertebra will be considered *short* or *broad* (Fig. 2A). Intermediate values will be referred to as *moderately elongate* (Fig. 5B).

Zygapophyses. These are *produced laterally* if

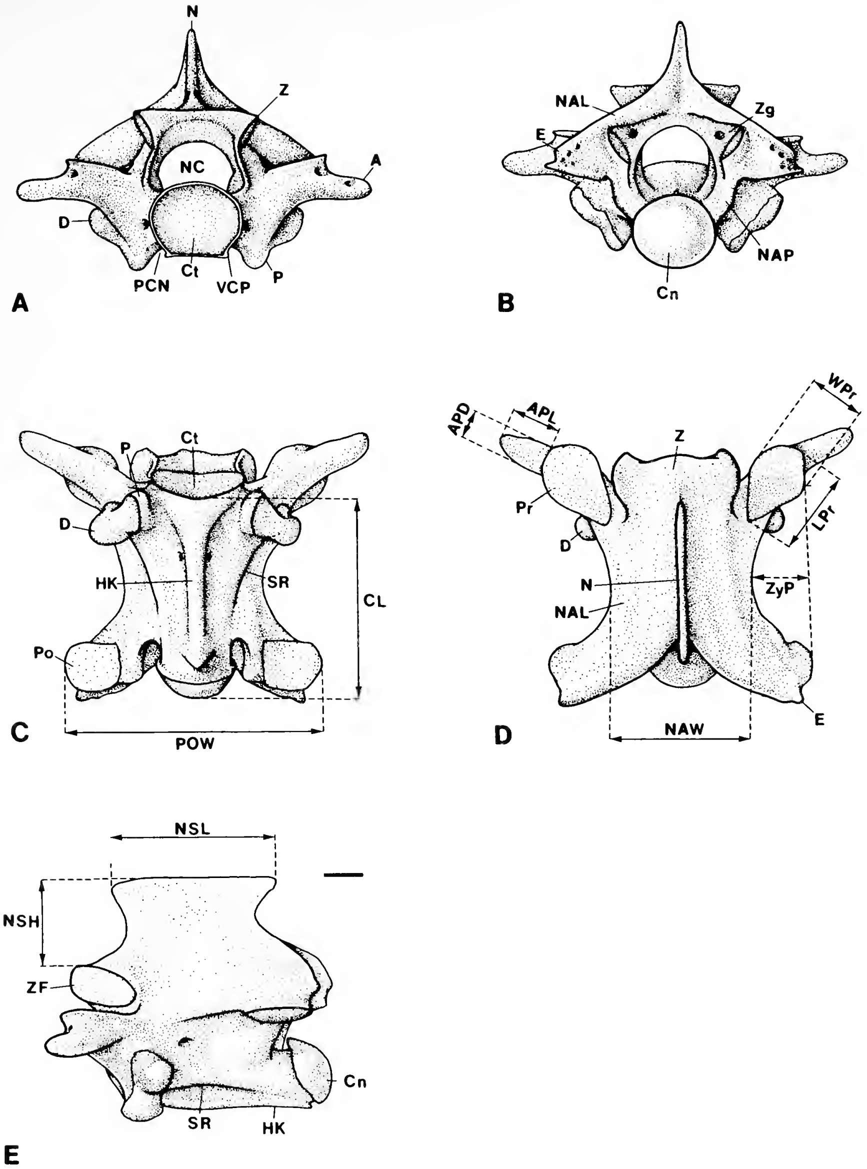

Figure 1. MTV of *Coluber constrictor,* illustrating anatomical terms and measurements used in text. **A.** Anterior view. **B.** Posterior view. **C.** Ventral view. **D.** Dorsal view. **E.** Lateral view. Abbreviations: A = accessory process, APD = accessory process diameter, APL = accessory process length, CL = centrum length, Ct = cotyle, Cn = condyle, D = diapophysis, E = epizygapophyseal spine, HK = hemal keel, LPr = length of prezygapophysis, N = neural spine, NAL = neural arch lamina, NAP = neural arch pedicel, NAW = neural arch width, NC = neural canal, NSH = neural spine height, NSL = neural spine length, P = parapophysis, PCN = paracotylar notch, Po = postzygapophyseal facet, POW = width across postzygapophyses, Pr = prezygapophyseal facet, SR = subcentral ridge, VCP = ventrolateral cotylar process, WPr = width of prezygapophysis, Z = zygosphene, ZF = zygosphenal facet, ZG = zygantrum, ZYP = greatest distance between a lateral tangent to zygapophyses and neural arch. Bar = 1 mm.

the ratio between the greatest distance from a lateral tangent of the zygapophyseal facets to the neural arch (ZyP, Fig. 1D) and CL is 0.40 or greater (Fig. 2A). If less than 0.33, the zygapophyses are *not produced laterally* (Fig. 2B). Intermediate values are moderately produced.

Neural Arch Laminae. These may be either *straight* (Fig. 2E), *convex* (Fig. 2C, 8A), or *convex laterally* (Fig. 2D) in posterior view.

Neural Spine. If the anterior height of this structure (NSH) is approximately half its dorsal length (NSL), then it is considered of *medium height* (Fig.

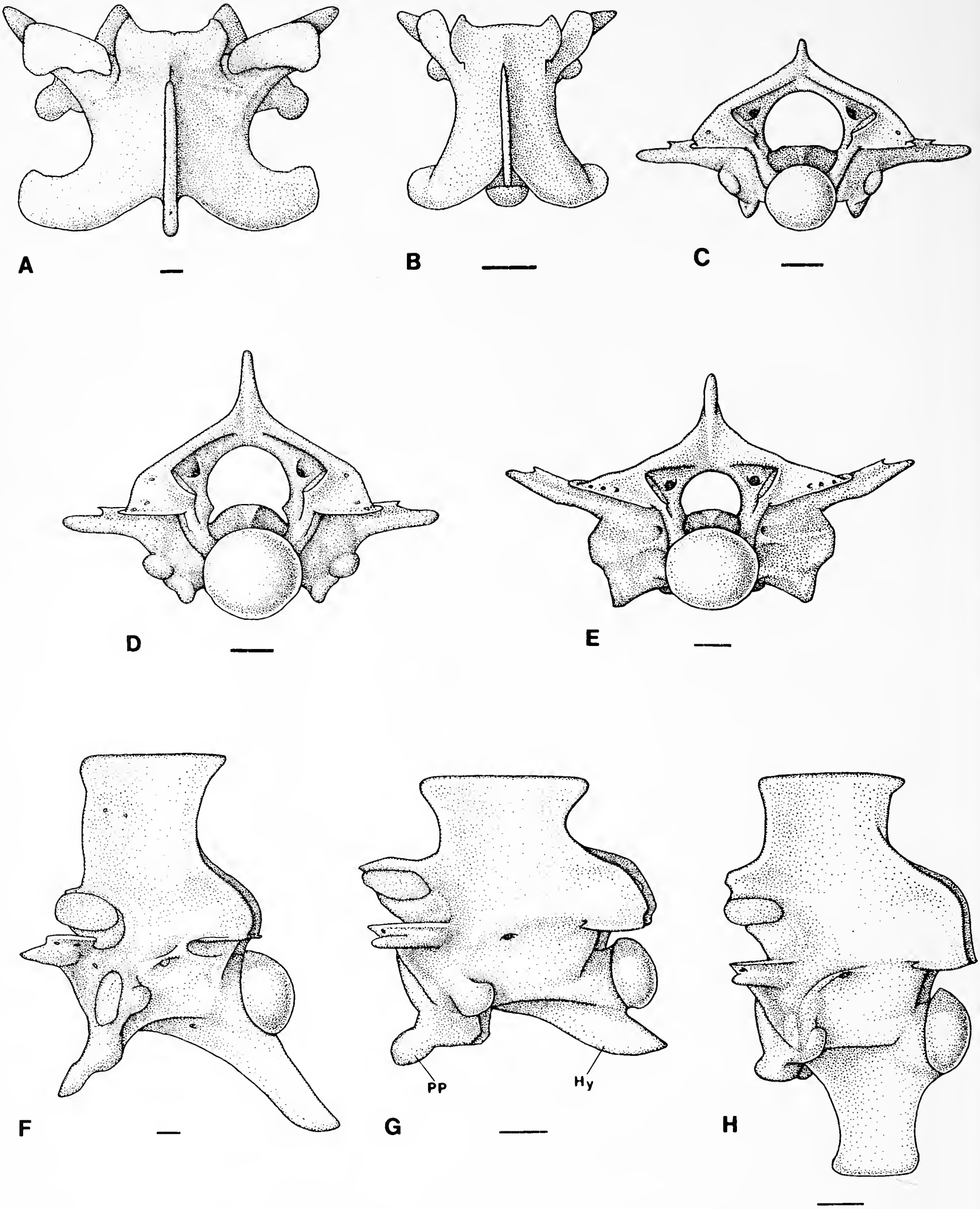

Figure 2. Examples of character states used to describe vertebrae, taken from modern comparative specimens. **A.** Dorsal view of MTV of *Agkistrodon piscivorus,* illustrating zygapophyses produced laterally. **B.** Dorsal view of ATV of *Drymobius margaritiferus,* illustrating nondivergent zygapophyses. C. Posterior view of MTV of *Coluber constrictor,* illustrating a moderately vaulted neural arch with convex laminae. **D.** Posterior view of MTV of *Arizona elegans,* illustrating a moderately vaulted neural arch with laterally convex laminae. **E.** Posterior view of MTV of *Heterodon platyrhinos,* illustrating a depressed neural arch with flat laminae. **F.** Lateral view of *Agkistrodon piscivorus* MTV showing a spine-like hypapophysis. **G.** Lateral view of MTV of *Thamnophis sirtalis,* showing a short, blade-like hypapophysis with a sinuous anteroventral border. **H.** Lateral view of ATV of *Pituophis melanoleucus,* showing a ventrally directed, blade-like hypapophysis, which is squared distally. Abbreviations: Hy = hypapophysis, PP = parapophyseal process. Bar = 1 mm.

2G). If the anterior height is distinctly less than this, it is referred to as *low*. If distinctly greater, it is referred to as *tall* or *high* (Fig. 2F).

Accessory Processes. If the diameter perpendicular to the long axis of this structure (APD) is less than half the greatest width of the prezygapophysis (WPr), they are referred to as *thin* (Fig. 1D). If APD is greater than half, they are referred to as *thick* (Fig. 13A). If the accessory process length (APL) is about half as long or longer than the greatest length of the prezygapophysis (LPr), it is termed *long* (Fig. 1D). If less than this, it is of *medium length* or *short* (Fig. 4B, 4A). The distal end may be *rounded* (Fig. 1D, 13A) or *pointed* (Fig. 4B).

Hypapophysis. The hypapophysis may be *spine-like* (Fig. 2F) (i.e., a cross section perpendicular to its long axis is about as long as wide or slightly longer) or *blade-like* (Fig. 2G), in which case the cross section is considerably longer than wide (as in most natricines). The distal tip of the hypapophysis may be *pointed* (Fig. 2G) or *squared off* (Fig. 2H, 5A). The anterior edge may be *simple* or *straight,* in which case it sweeps back gently to meet the posterior edge (Fig. 2F), or it may be *sinuous,* if its anteroventral border is strongly convex or angular (Fig. 2G).

VERTEBRAL REGIONS

There has been little agreement on how one should refer to the regions of the vertebral column of snakes. Although various authors have used the terms cervical, thoracic, and lumbar (Sood, 1948; Bullock and Tanner, 1966; Brummer, 1980; Szyndlar, 1984), this is clearly improper when applied to snakes because there is no way to determine the homology of snake vertebral regions with those of mammals, for which this terminology was devised (Romer, 1956). Even attempts to compare snake vertebral regions with those of lizards have been unsuccessful (Hoffstetter and Gasc, 1969) because of the variable and gradual nature of the dissociation of limb girdles from the vertebral column in series of lizard taxa with progressive degrees of limb reduction. Homology is further obscured by our general ignorance of the mechanisms by which body segments proliferate phylogenetically in tetrapod taxa.

The terminology of Hoffstetter and Gasc (1969) is the most useful in referring to snake vertebral regions. They specify four general regions.

1) Atlas and axis. These are unique and readily distinguished as in most tetrapods.
2) Trunk vertebrae (Fig. 1, 2). These are generalized vertebrae that lack the processes that distinguish the following regions. Hypapophyses (Fig. 2F, 2G, 2H) are always present anteriorly and may be present posteriorly.
3) Cloacal vertebrae (Fig. 3A, 3B). This region is distinguished by the presence of fused lymphapophyses, hemapophyses may also be present.
4) Postcloacal vertebrae (Fig. 3C, 3D). This and the cloacal region comprise the caudal series of most authors. The postcloacal region is characterized by absence of lymphapophyses and presence of pleurapophyses and hemapophyses.

These regions are readily distinguished, with at most one vertebra with intermediate conditions between regions 2 and 3, and 3 and 4.

The terminology of Hoffstetter and Gasc (1969) does not recognize subregions of the trunk, although a considerable degree of regular but less abrupt morphological change occurs. Assignment of vertebrae to a subregion of the trunk region is helpful and may be crucial to proper identification of isolated vertebrae. In this study, one minor and three major subregions of the trunk are distinguished. These subregions merge gradually into one another, with extensive areas of intermediacy. Assigning isolated vertebrae to subregions is not always clear-cut and is only intended as an aid to identification. Intermediate forms were arbitrarily assigned to one of two adjacent subregions.

The following detailed description of morphological changes between subregions serves as a guide to determine the extent of each subregion in a complete skeleton. These features are best seen in disarticulated specimens in which vertebral order has been preserved. The proportion of the vertebral column occupied by each region varies among taxa. The descriptions are based largely on observations of North American caenophidians and may not apply to other infraorders or caenophidians from other geographic regions. Figures 4–8 illustrate the features described below as seen in representative vertebrae of the three major subregions (ATV, MTV, and PTV below) from a single specimen.

Anterior Trunk Vertebrae (ATV; Fig. 4A, 5A, . . . , 8A). This region excludes the atlas and axis. ATV bear hypapophyses in all snakes examined. The anterior-most vertebrae (not illustrated) are shortened craniocaudally. The zygapophyses are small and are not produced laterally. Zygapophyseal facets are elongate craniocaudally in the first few vertebrae but quickly become rounded. The neural canal is relatively large in this region and has strongly convex laminae. The zygosphene is broad. Parapophyseal processes are large, projecting cranioventrally. Neural spines are moderately high and thin. Hypapophyses are thin and point caudally in the first few vertebrae but quickly become stout, directed ventrally or posteroventrally, and may be squared off distally.

Proceeding caudally through the ATV region (Fig. 4A, 5A, . . . , 8A), overall vertebral size and relative vertebral length gradually increase. Zygapophyses increase in size and extend farther laterally. The neural canal becomes relatively smaller as the vertebrae become larger. The zygosphene becomes relatively narrower, and parapophyseal processes decrease slightly. The neural spine often assumes its

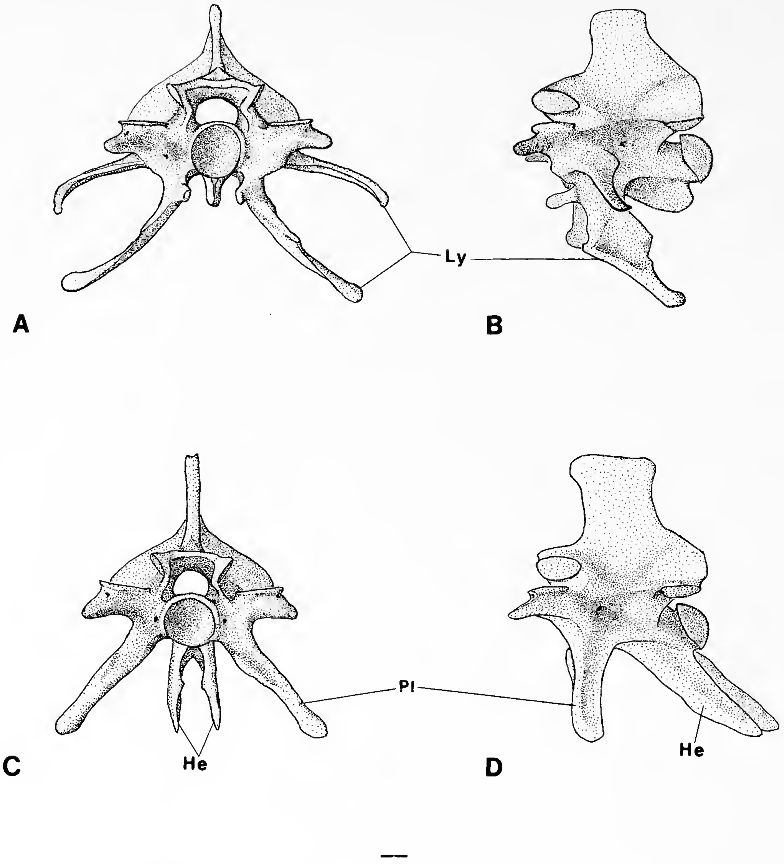

Figure 3. Caudal vertebrae of *Nerodia sipedon.* **A.** Anterior view of cloacal vertebra. **B.** Lateral view of cloacal vertebra. C. Anterior view of postcloacal vertebra. D. Lateral view of postcloacal vertebra. Abbreviations: He = hemapophyses, Ly = lymphapophyses, Pl = pleurapophyses. Bar = 1 mm.

greatest height at the caudal end of this region. Hypapophyses remain approximately the same length throughout most of the region or decrease only slightly posteriorly. In forms that lack mid-trunk vertebral (MTV) hypapophyses, hypapophyseal length decreases rapidly over four to six vertebrae in the zone of transition to MTV.

The caudal end of this zone is readily identified in forms that lack MTV hypapophyses as the point where hypapophyses are no longer distinguishable. In forms that have MTV hypapophyses, the transition from ATV to MTV zones is more subtle but can be detected by relying on the other characters discussed below.

Mid-trunk Vertebrae (MTV; Fig. 4B, 5B, . . . , 8B). These are the largest vertebrae and are the only ones used in identification of fossils by many authors. They become slightly more elongate posteriorly from the cranial to the caudal end of the region. Zygapophyses are produced farthest laterally in this region. The neural canal becomes relatively smaller throughout the rest of the length of the vertebral column. The zygosphene remains approximately the same relative width as the caudalmost ATV throughout this region. Parapophyseal processes are absent in this and following regions in forms that lack posterior hypapophyses. Where posterior hypapophyses are present, parapophyseal processes remain strongly developed throughout (see also Malnate, 1972). Hypapophyses are generally directed caudally and may be somewhat pointed, never squared off. A slight decrease in relative hypapophysis length may occur throughout this and the next region. Neural spines generally decrease in relative height slowly throughout this and the next vertebral regions.

The transition from this zone to the next is always extensive and subtle, but cranial MTV and caudal posterior trunk vertebrae (PTV) from the same individual are always readily distinguishable.

Posterior Trunk Vertebrae (PTV; Fig. 4C, 5C, . . . , 8C). This region has not been distinguished from the MTV in the literature, and it is impossible to tell from published accounts whether PTV have been considered while making identifications. In some species, features that have been considered diagnostic in trunk vertebrae (e.g., neural spine height) have been found to differ in these two

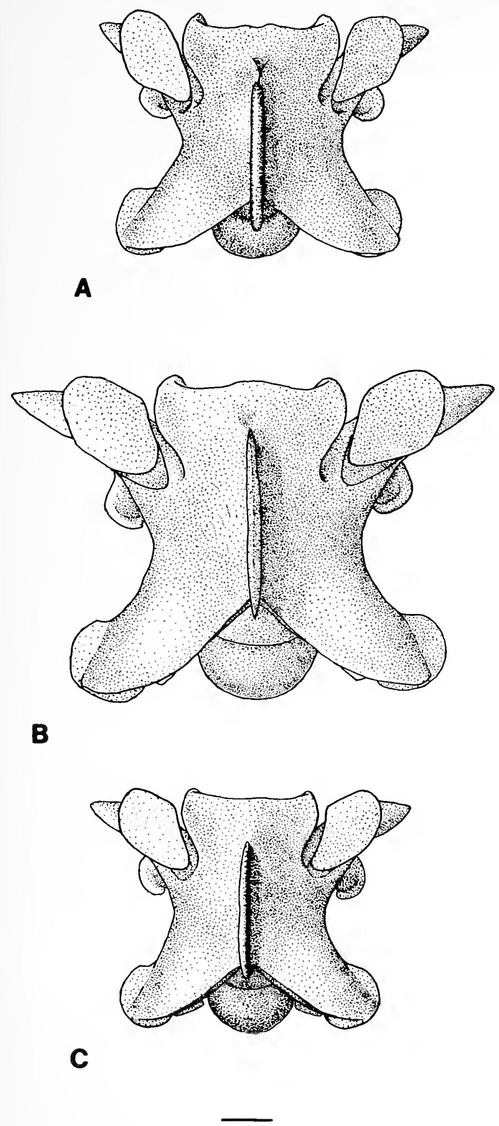

Figure 4. Comparison of the dorsal aspects of three vertebrae from a single specimen of *Pituophis melanoleucus sayi,* a male (snout–vent length 1,039 mm) with 222 precaudal vertebrae, showing changes in shape within a single vertebral column. **A.** ATV (20th vertebra). **B.** MTV (85th vertebra). **C.** PTV (210th vertebra). Bar = 1 mm.

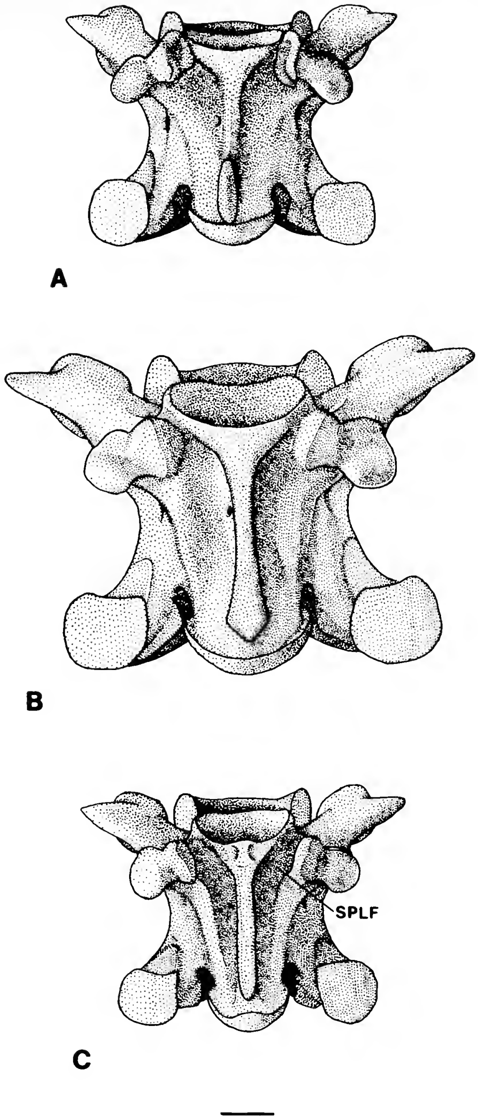

Figure 5. Comparison of the ventral aspects of the three vertebrae illustrated in Figure 4. Abbreviations: SPLF = subcentral paramedian lymphatic fossa. Bar = 1 mm.

regions, such that PTV of one species may be more similar to MTV of a second species than to their own MTV in this character. For example, *Crotalus horridus* Linnaeus, 1758 is said to be distinguishable from *C. adamanteus* (Beauvois, 1799) (as well as many other *Crotalus* species) by its low neural spines (Auffenberg, 1963; Holman, 1967). However, the neural spines of the PTV of *C. adamanteus* may be fully as low as those of the MTV of *C. horridus.* Many similar examples could be cited using other characters and taxa.

The most distinctive aspect of the PTV is a pair of subcentral paramedian lymphatic fossae (Fig. 5C, 13A). This feature has previously received very little attention. Brummer (1980) referred to these fossae as subcentral pits, whereas Hill (1971) called them subcentral excavations. Neither of these authors made any reference to the cause of these structures. Other authors (Auffenberg, 1963; Meylan, 1982) have attributed them to extreme development of the subcentral ridges on otherwise normal centra. This is clearly not the case because these fossae are incised to a level that is well dorsal to the normal level of the ventral face of the centrum with respect to the ventral edges of the cotyle and condyle.

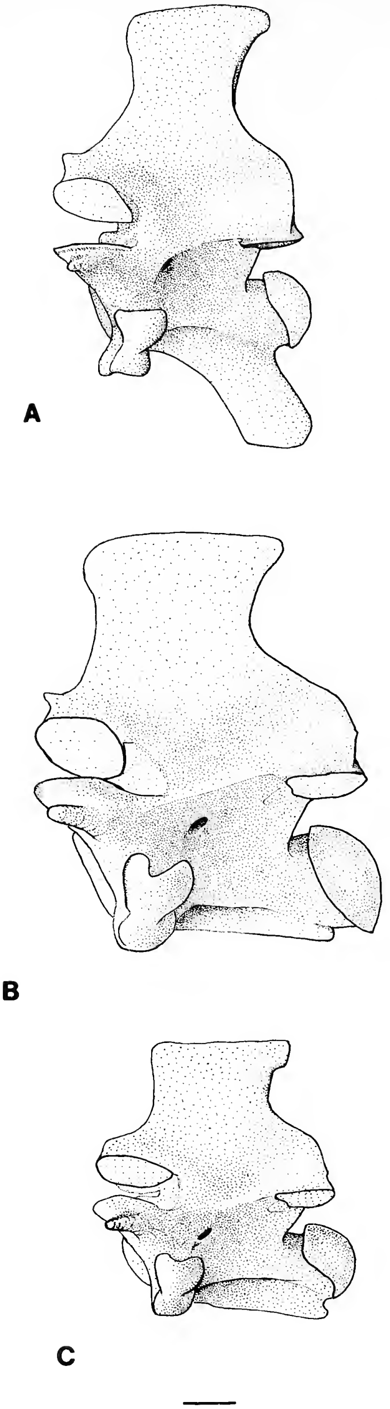

Figure 6. Comparison of the left lateral aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

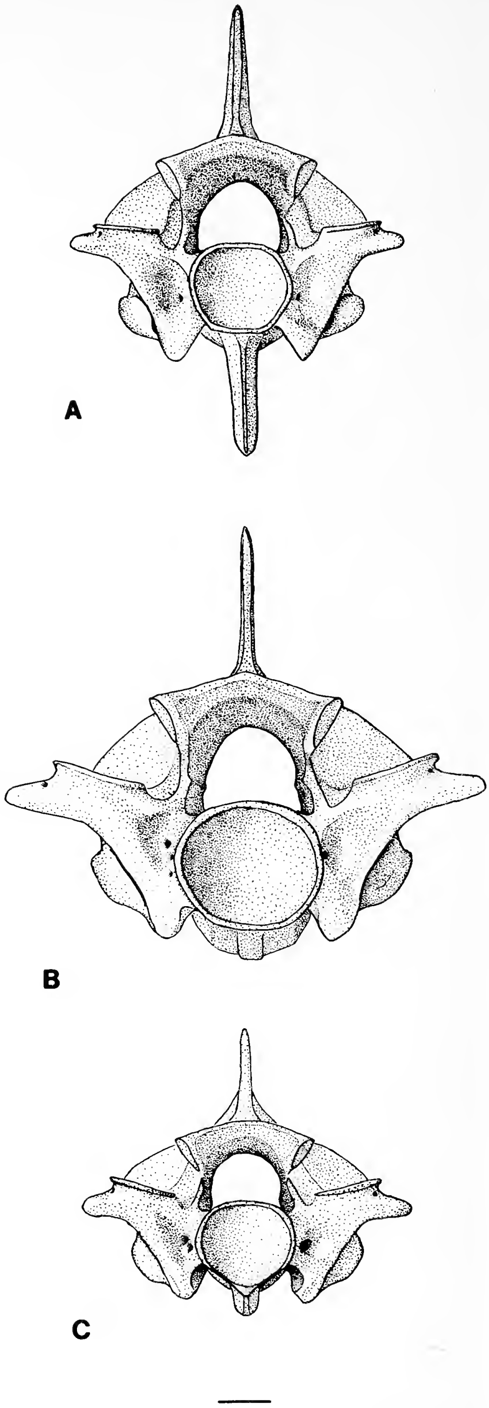

Figure 7. Comparison of anterior aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

Dissection has revealed (pers. obs.) that these fossae accommodate the segmental dilations of the longitudinal paravertebral internal lymphatic vessels described by Hoyer (Ottaviani and Tazzi, 1977). The segmentally dilated portions of these vessels are connected by smaller diameter segments that pass between the parapophysis and the ventrolateral lip of the cotyle. This area is usually notched or grooved for reception of the narrowed segment (Fig. 5C, 7C, 13A, 13B). The notch is bounded ventrally by a ligament that connects the ventral surface of the capitulum of the rib to the ventrolateral lip of the cotyle. A process may be developed on the ventrolateral cotylar lip for the attachment of this ligament in some individuals of certain species, but its presence is unpredictable. In some species, these notches and processes may be found in the posterior MTV series where the fossae are undeveloped. In its most anterior position, the notch is usually faint and of small diameter, but on progressively posterior vertebrae, it gradually increases in size and may even cause the emargination of the ventrolateral lip of the cotyle (Fig. 5C, 7C). The fossa is bounded laterally by the subcentral ridges and medially by the hemal keel (Fig. 5C, 13A). In most snakes the hemal keel is recessed slightly dorsad just posterior to the cotyle (Fig. 6C). This recess allows passage of the transverse anastamosing tracts of the longitudinal paravertebral internal lymphatic vessel. In species that possess PTV hypapophyses, the subcentral lymphatic fossae may be restricted to the anterior portion of the vertebra. Only one species examined in this study, *Lampropeltis getulus* (Linnaeus, 1766), has well developed fossae throughout the column (Fig. 12). Yet, even in this species, paracotylar notches are obviously enlarged in the PTV region.

The PTV tend to be somewhat more elongate than the MTV (Fig. 4B, 4C, 5B, 5C). Their zygapophyses are often produced laterally to a lesser extent. The neural canal and arch generally assume a broadened, more depressed form. The zygosphene may become relatively broadened and crenate in shape, even in forms that have a flat zygosphene in more cranial regions. In species that have high to medium height neural spines in the ATV and MTV, there is usually a significant decrease in height in the PTV that is particularly noticeable in the precloacal region. This decreased neural spine height is slight in species that have lower neural spines cranially. Hypapophyses, when present, are generally shorter and directed sharply caudad.

Precloacal Vertebrae (PCV). In many caenophidian species, there is a very small but distinctive region of three to five vertebrae, which immediately precedes the cloacal series. These vertebrae resemble the cloacal vertebrae in that they are abruptly foreshortened, but they lack the lymphapophyses diagnostic of cloacal vertebrae. PCV have low and short (craniocaudally) neural spines. Their neural arches tend to be more vaulted than those of the PTV. Finally, PCV have very pronounced notches between the parapophyses and cotyle, which usually emarginate the ventrolateral edges of the cotyle. Vertebrae of the cloacal region whose lymphapophyses are not fused greatly resemble PCV. They may be distinguished by their undivided, truncate paradiapophyses.

Cloacal and Postcloacal Vertebrae. The cloacal and postcloacal regions (Fig. 3), which are frequently lumped into the generalized category of "caudal vertebrae," are not easily assigned to species or genera. For this reason, they have not been considered in this study.

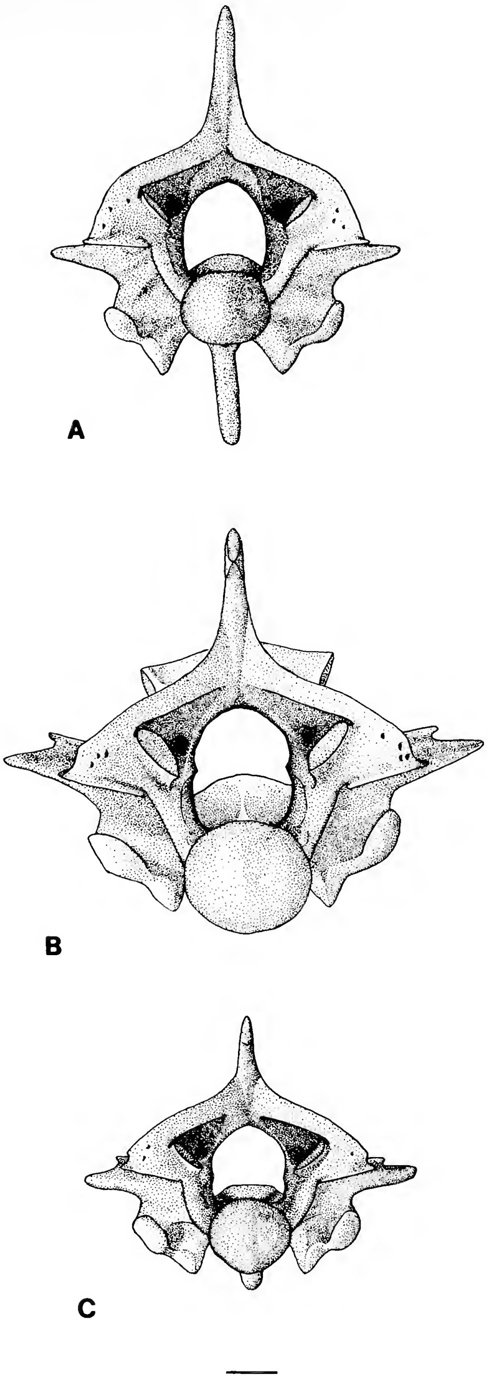

Figure 8. Comparison of posterior aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

Ontogenetic Shape Change. Another category of morphological variability to be considered is ontogenetic shape change. The vertebrae of hatchling and very young snakes are distinctive from those

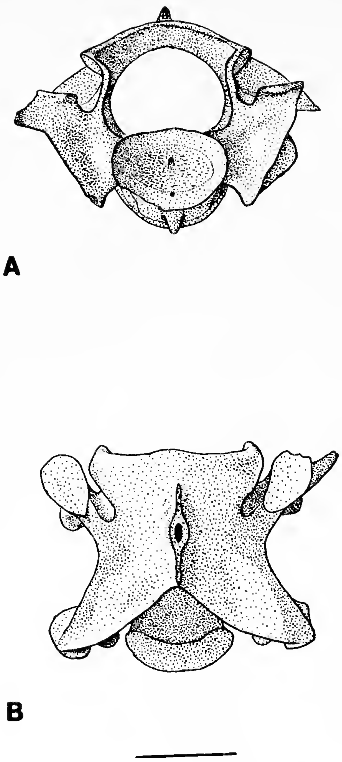

Figure 9. Fossil vertebra (LACMRLP 22109) of a very young juvenile *Pituophis melanoleucus* from Pit 91, Rancho La Brea. Bar = 1 mm.

of adult conspecifics and are easily distinguished from the vertebrae of adults of small species. Identification of hatchling specimens is not ordinarily a concern of the paleoherpetologist because their small, poorly ossified bones rarely fossilize. However, identification of these forms is a concern at Rancho La Brea where the conditions of preservation have allowed the recovery of the bones of several individuals that were very young (Fig. 9). Peculiarities of the vertebral morphology of hatchlings and young are described below in general terms.

Vertebrae of hatchling snakes may be distinguished by the thin, translucent nature of the bone (apparent even in the fossils). At hatching, vertebrae are little more than a thin shell of perichondral bone with some endochondral ossification (Winchester and d'A. Bellairs, 1977). In neonatal through subadult individuals, the endochondral ossification of the ends of the centrum (Winchester and d'A. Bellairs, 1977) can be distinguished as a circular area of ligher color in the center of the cotyle (pers. obs.).

Vertebrae of all recent hatchling snakes observed were relatively shorter than those of adults of the same species. This condition is most obvious in species such as *Coluber constrictor* Linnaeus, 1758, where vertebrae of adults are elongate, and less obvious in species that have relatively short vertebrae as adults, e.g., *Arizona elegans* Kennicott, 1859 or *Elaphe obsoleta* (Say, 1823). Other features characteristic of hatchling snakes include a relatively enormous neural canal, a broad zygosphene, small zygapophyses that are not produced laterally, and a wide, shallow posterior notch in the neural arch (Fig. 9). Furthermore, some small or detailed features found in adults may not be apparent in hatchlings (i.e., epizygapophyseal spines). Regional differentiation of many characters is much less noticeable in hatchlings and may be almost obscured in some cases.

Vertebral shape change is rapid in young snakes and appears to decrease at about the same rate as growth. Vertebrae of young adults approach the characteristic shape of larger individuals but retain many vestiges of juvenile form, such as relatively shorter centra. Vertebral shape change appears to be continuous throughout life, although slow in mature individuals. Very large individuals of a species may appear hypermorphic (i.e., have very thickened bone, relatively small neural canals and foramina, exaggerated processes such as epizygapophyseal spines and accessory processes) when compared with smaller individuals.

SYSTEMATIC DESCRIPTIONS

Every attempt has been made to include as great a taxonomic and geographic diversity of comparative material as possible to identify potentially exotic or extinct forms. A list of comparative specimens used may be obtained from the author. Anatomical terminology of vertebrae is derived largely from Auffenberg (1963) and Hecht (1982); that of skull elements is from Cundall (1981) and Szyndlar (1984). Cranial muscle terminology follows Varkey (1979) (Fig. 10).

The systematic arrangement of subfamilies approximates that of Dowling and Duellman (1978). This arrangement was chosen because it provides a reasonable approximation of osteologically similar groups. Below the subfamily level, genera are divided into osteologically similar groups arranged in decreasing order of fossil abundance within groups. This arrangement is used to facilitate comparison and is not intended to reflect an opinion on phylogenetic relationships.

The species accounts provide descriptions of material that is definitively identifiable, including all skull elements, MTV, and PTV. Accounts are followed by descriptions of allocated material (i.e., ATV, PCV, and immature vertebrae), which is material that compares favorably with the assigned taxon but would not be definitively identified if considered in isolation.

Most vertebrae were assigned to the MTV subregion (the traditional standard of identification) unless they had distinct features of another subregion. Therefore, the MTV subregion is overrepresented in the materials listed below because of the inclusion of intermediate forms, and the ATV

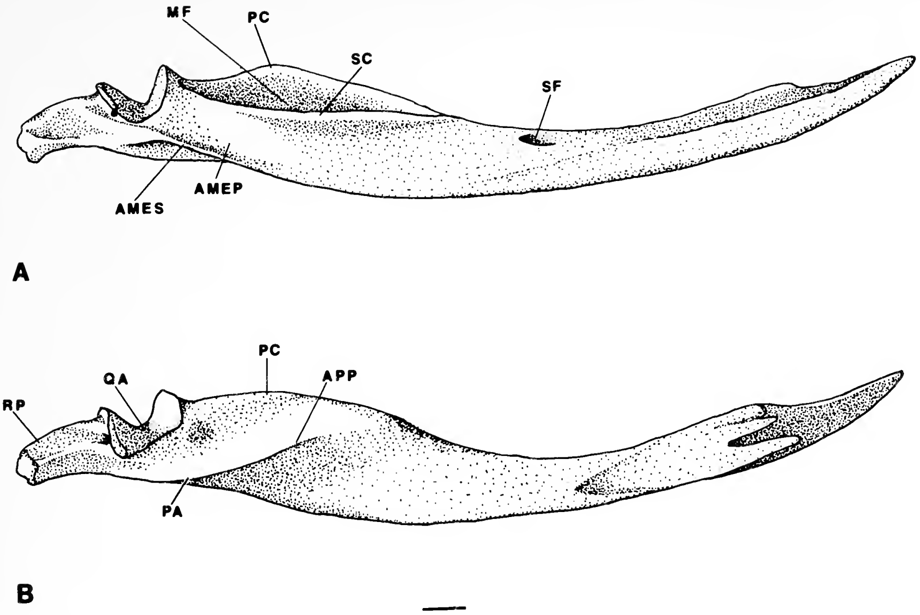

Figure 10. Right compound bone of *Nerodia sipedon sipedon,* illustrating terms used in text. **A.** Labial surface. **B.** Lingual surface. Abbreviations: AMEP = insertion of *M. adductor mandibulae externus profundus,* AMES = insertion of *M. adductor mandibulae externus superficialis,* APP = insertion of *M. adductor posterior: pars profundus,* MF = mandibular fossa, PA = insertion of *M. pterygoideus accessorius,* PC = prearticular crest, QA = quadrate articular facet, RP = retroarticular process, SC = surangular crest, SF = supraangular foramen. Bar = 1 mm.

and PTV subregions correspondingly are underrepresented. Vertebrae that were clearly immature are listed separately for each species with the subregion designation prefixed by the letter "I" (e.g., IMTV, etc.). Vertebrae representing specimens that are little differentiated from the condition in hatchlings were simply designated by "H" because regional differentiation is rudimentary at that stage. All fossil material is deposited at the Natural History Museum of Los Angeles County (LACMRLP).

Class REPTILIA Laurenti, 1768
Subclass LEPIDOSAURIA Romer, 1945
Order SQUAMATA Oppel, 1811
Suborder SERPENTES Linnaeus, 1758
Family COLUBRIDAE Cope, 1886
Subfamily XENODONTINAE Cope, 1893
Genus *Diadophis* Baird and Girard, 1853

Diadophis punctatus (Linnaeus, 1766)

(Fig. 11, 12A)

REFERRED MATERIAL. Maxilla: 47445 (L); Compound bone: 52172 (R); MTV: 15694, 18293, 20278, 21562, 24307, 44507, 51928, 51961 (11), 52051, 52052, 52058, 52063 (5), 52071, 52076 (4), 52186 (2), 52192, 52195 (3), 52212 (10); PTV: 15554, 51578, 51961, 52051, 52063, 52076, 52195 (2), 52212 (4).

COMPARISONS. The maxilla of *Diadophis* (Fig. 11A) has a posterior diastema followed by two compressed, blade-like teeth that lack grooves or ducts. The shaft of the maxilla is bent laterally near the anterior end of the ectopterygoid process.

Sonora and *Chionactis* have shorter maxillary diastemata and weaker lateral bending. Other small colubrids examined lack a similar combination of diastema and lateral bending.

The shaft of the compound bone is bent slightly medially rostral to the mandibular fossa in *Diadophis* (Fig. 11B). The retroarticular process is directed medioventrally. The prearticular crest is highly arched, whereas the surangular crest is flat dorsally. The labial surface of the surangular crest is occupied by a distinct fossa that is bordered ventrally by a ridge. The fossa receives the insertion of the *M. adductor mandibulae externus profundus.* The ridge is continuous ventrally with the ventral surface of the compound and is the insertion of the *M. adductor mandibulae externus superficialis.* In large adults, a second ridge is located on the lingual surface running from near the ventral surface below the quadrate articulation, rostrally and dorsally, ending rostral to the prearticular crest. The anterior portion of this ridge is the insertion of the *M. adductor posterior: pars profundus.* The posterior portion of the ridge, which may be drawn into a tubercle (Fig. 11B) is the insertion of the *M.*

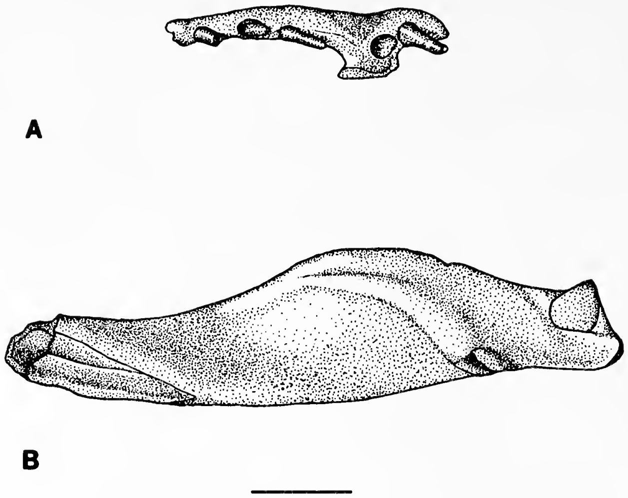

Figure 11. Fossil skull elements of *Diadophis punctatus* from Pit 91. **A.** LACMRLP 47445, left maxilla. **B.** LACMRLP 52172, right compound bone. Bar = 1 mm.

pterygoideus accessorius. The supraangular foramen (Szyndlar, 1984) is located a short distance rostral to the mandibular fossa.

Two other small North American snake species examined, *Hypsiglena torquata* (Gunther, 1860) and *Contia tenuis* (Baird and Girard, 1853), have the prearticular crest more highly arched than the surangular crest. However, the prearticular crest is more highly arched in *Diadophis.* Also, *Contia* lacks the fossa of insertion for the *M. adductor mandibulae externus profundus,* whereas in *Hypsiglena* this fossa is reduced to a shallow horizontal groove. The ridge receiving the insertion of the *M. adductor posterior: pars profundus* and the *M. pterygoideus accessorius* was not observed in any specimens of *Hypsiglena* or *Contia.* Finally, the supraangular foramen is displaced rostrally in *Hypsiglena* and *Contia* relative to *Diadophis.*

The MTV of *Diadophis* (Fig. 12A) have been described by Auffenberg (1963). They are elongate with depressed neural arches. The neural arch laminae are convex in posterior view. The neural arch notch is usually acute. The zygapophyses are moderately divergent. The accessory processes are short and blunt distally in large individuals. Auffenberg (1963) describes the hemal keel as oblanceolate or subspatulate. However, most comparative specimens observed had broader and flatter keels. The lateral edges of the hemal keel are often sloping and indistinct. *Diadophis* hemal keels may thus be better described as cunate or oblong *sensu* Auffenberg (1963:153). The neural spine is low and long but not obsolete posteriorly.

In *Diadophis* PTV, the centrum becomes relatively shorter than that of the MTV. Also, zygapophyses are less divergent, and the neural arch notch is more rounded in progressively posterior vertebrae. PTV cotyles and condyles are distinctly smaller than those of MTV. The sharpness of the edges of the hemal keel is accentuated by the sub-

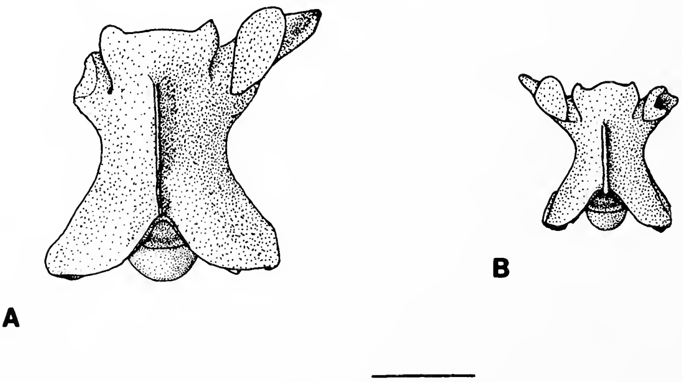

Figure 12. Comparison of dorsal aspects of fossil *Diadophis punctatus* LACMRLP 51961 (**A**) and *Tantilla* sp. LACMRLP 44374 (**B**) from Pit 91, Rancho La Brea. Bar = 1 mm.

central lymphatic fossae. The anterior region of the keel, just posterior to the ventral edge of the cotyle, is usually recessed dorsally to allow for the passage of the transverse anastomosing lymphatic duct. In some specimens, the neural spine becomes obsolete posteriorly in the PTV series.

Auffenberg (1963), Holman (1967, 1977b), Hill (1971), and Meylan (1982) discuss differences between the vertebrae of *Diadophis* and *Carphophis, Rhadinaea, Stilosoma,* and *Tantilla. Carphophis* MTV and PTV may generally be distinguished from those of *Diadophis* by their more depressed neural arches and lower neural spines that may be obsolete posteriorly, particularly in PTV. In *Rhadinaea* and *Stilosoma,* the accessory processes are directed approximately 90 degrees from the long axis of the centrum, whereas in *Diadophis* they are usually directed obliquely anteriorly. Meylan (1982:45) stated that the accessory processes of *D. punctatus* "... are hooked anteriorly and are not markedly pointed." However, examination of a broad geographic and ontogenetic series of individuals has shown these characters to be variable. Furthermore, several other genera have "hooked" accessory processes to some extent. Although there is some overlap, *Tantilla* (Fig. 12B) may often be distinguished from *Diadophis* by a lower neural spine that may be obsolete posteriorly (especially in the PTV), postzygapophyses that are distinctly longer than wide (only slightly longer than wide in *Diadophis*), and the obtuse posterior notch of its neural arch (acute notch in *Diadophis* MTV, Fig. 12A). The angle of this notch increases posteriorly in the PTV of both *Diadophis* and *Tantilla* such that they may still be distinguished by this character. Finally, the PTV of *Tantilla* are more elongate than those of *Diadophis.* The MTV and PTV of *Contia tenuis* may be distinguished from those of *Diadophis* by the relatively shorter centrum, the lower and thicker neural spines, and the more broadly rounded postzygapophyses of *C. tenuis.* Also, the distal tips of the laterally directed accessory processes tend to be more strongly hooked in *Contia* than in *Diadophis.*

The fossil material does not differ noticeably from modern *Diadophis punctatus.* It differs from the extinct *D. elinorae* Auffenberg, 1963 (material not seen) in its longer vertebrae with more depressed neural canals, weaker subcentral ridges, lower neural spines, and broader hemal keels. The neural spine of *D. elinorae* lacks an anterior overhang, a variable character in *D. punctatus.*

ALLOCATED MATERIAL. ATV: 52195; PCV: 52212; IMTV: 52063 (2), 52188; IATV: 52100, 52188.

COMPARISONS. The neural spine of ATV of *Diadophis punctatus* increases only slightly in height anteriorly. ATV hypapophyses are spine-like and directed caudally in the posterior region of the series. However, in the anterior region they become blade-like with a sinuous anterior edge.

Immature *Diadophis* vertebrae are generally less depressed and have hemal keels that are neither so broad nor as flattened ventrally as those of adults. The accessory processes are relatively more elongate and acute in immatures.

DISCUSSION. This is the first record of *Diadophis punctatus* from the Pleistocene of California. *Diadophis punctatus* prefers relatively moist habitats, ranging from forest and woodland through chaparral and prairie, and inhabits arid habitat only along riparian corridors (Stebbins, 1985; Van Devender and Worthington, 1977). This species occurs in Los Angeles County today (Stebbins, 1985).

Genus *Tantilla*
Baird and Girard, 1853
Tantilla sp.

(Fig. 12B)

REFERRED MATERIAL. MTV: 43748, 44374, 44617, 51965, 52059, 52210 (4); PTV: 52210 (2).

COMPARISONS. The vertebrae of *Tantilla* (Fig. 12B) are similar in shape to those of *Diadophis.* The MTV are usually elongate with convex neural arch laminae. The neural spines are low and may be obsolete posteriorly. The zygosphene is usually strongly crenate. Accessory processes are generally thin and elongate. The hemal keel is broad, has sloping edges, and is often flattened ventrally.

Intracolumnar variability in *Tantilla* is essentially the same as noted for *Diadophis,* except the PTV tend to be more elongate in *Tantilla.*

In addition to the features mentioned under *Diadophis punctatus, Tantilla* may be distinguished by the smaller size of its vertebrae. Although there is size overlap between adult *Tantilla* and small *Diadophis* vertebrae, the latter usually have the distinctive features of young snakes, such as the enlarged neural canal, broader appearance, smaller zygapophyses, etc.

DISCUSSION. This genus is comprised of many widely scattered species that often have restricted ranges (Wilson, 1982). Many of these species are rather poorly known. No attempt was made to assign the fossil specimens to species because of the high degree of morphological similarity in this large genus and the lack of sufficient comparative material. The fossils do not differ noticeably from *Tantilla planiceps* (Blainville, 1834) known from southwestern California today.

This is the first record of *Tantilla* from the California Pleistocene. *Tantilla planiceps* is the only species found in the vicinity of Rancho La Brea today (Stebbins, 1985) and is found in woodland, grassland, chaparral, and desert habitats.

Genus *Hypsiglena* Cope, 1860
Hypsiglena torquata (Gunther, 1860)

REFERRED MATERIAL. MTV: 14794, 20135, 35943, 39061, 51962 (4), 52064 (3), 52077 (2), 52088, 52211 (7); PTV: 52077, 50143.

COMPARISONS. *Hypsiglena torquata* vertebrae were described by Van Devender and Mead

(1978), Mead *et al.* (1984), and Van Devender *et al.* (1985). The MTV are relatively short and wide. The neural arch is depressed and has convex laminae. The neural canal is broad. Zygapophyses are produced laterally with unusually large, round facets. The neural spine is medium to low, with strong anterior and weaker posterior overhangs. The hemal keel is moderately narrow, strong, and rounded or flattened ventrally. Accessory processes are fairly elongate but blunt distally. They may be slightly hooked anteriorly.

Hypsiglena PTV have only moderate subcentral lymphatic fossae, yet the parapophyses are separated from the ventral edge of the cotyle by a pronounced notch. In the PTV, neural spines are lower and their cotyles and condyles are smaller than in the MTV.

Hypsiglena vertebrae are much shorter, their neural spines are less elongate and higher, and the hemal keel is less flattened and wider than in *Diadophis* or *Sonora. Hypsiglena* may be distinguished from *Phyllorhynchus* and *Rhinocheilus* by a more depressed neural arch. The zygapophyses of *Hypsiglena* are larger and are produced laterally more than those of *Sonora, Chionactis, Contia, Gyalopion, Chilomeniscus,* or *Ficimia.* The vertebrae of *Coniophanes fissidens* (Gunther, 1858) are similar to those of *H. torquata* but may usually be identified on the basis of the more pronounced interzygapophyseal ridge and lack of an anterior overhang on the neural spine.

ALLOCATED MATERIAL. ATV: 31214, 52081, 52152, 52194; PCV: 52093; IMTV: 52098; IPTV: 26260.

COMPARISONS. ATV postzygapophyses are even more laterally divergent than those of the MTV. The ATV neural arch laminae are convex, and their neural canal is large and rounded so that the ATV lack the overall depressed appearance of the MTV.

The zygosphene of the PCV is very broad, its anterior edge arching strongly downward laterally, and its shape is strongly crenate. The zygapophyses are not produced laterally as strongly as in the MTV or PTV. The cotyles and condyles are very small.

In immature specimens, the hemal keel is gently rounded in transverse section. Large, rounded zygapophyses are evident even here.

DISCUSSION. Fossil material assigned to *Hypsiglena torquata* falls well within the range of variability noted above for the species. However, relative vertebral length was greater in some of the comparative material than in the fossils. Assignment to this species is based in part on geographic range because no other species of *Hypsiglena* were examined. The specific designation must therefore be regarded as tentative.

Pleistocene records of *H. torquata* from California include Redtail Peaks and Whipple Mountains (Van Devender and Mead, 1978). The habitat of this snake ranges from desert to woodland, including chaparral, creosote, sagebrush, grasslands, and grass–sedge meadows (Wright and Wright, 1957; Stebbins, 1985; Conant, 1975). *Hypsiglena torquata* is found in the Los Angeles area today (Stebbins, 1985).

Subfamily COLUBRINAE Cope, 1895

Genus *Coluber* Linnaeus, 1758

Coluber constrictor Linnaeus, 1758

REFERRED MATERIAL. Maxilla: 41901 (L); Compound bone: 14208 (R); MTV: 10066, 14304, 16976, 19474, 22040, 22241, 22565, 29148, 37999, 39737, 41241, 47324, 51941, 51966, 52070, 52074, 52082 (6), 52108 (2), 52111 (2), 52116, 52162, 52180 (2), 52216 (8); PTV: 51917, 51941, 52082, 52092, 52111 (4), 52216 (6).

COMPARISONS. *Coluber* has 13–17 maxillary alveoli (n = 36 maxillae, 20 individuals) and lacks a diastema.

The maxilla of *Coluber* may be distinguished from that of *Masticophis* by its shorter palatine process that spans roughly two alveoli. *Masticophis* has 16–20 maxillary alveoli (n = 30, 16 individuals, five species) and a palatine process that generally spans two and one-half to three alveoli. Differentiation from *Pituophis* and *Arizona* is described under *Pituophis. Rhinocheilus, Diadophis,* and *Salvadora* all possess diastemata.

The compound bone of *Coluber* has prearticular and surangular crests of roughly equal height. The ventral surface of the bone is rounded in the vicinity of the quadrate articulation.

Masticophis, Rhinocheilus, and some *Lampropeltis getulus* also have prearticular and surangular crests of approximately equal height. In *Rhinocheilus,* the crests are lower than in *Coluber.* The ventral border of the compound bone of *Masticophis* narrows to a keel below the quadrate articulation but is wider and rounded in *Coluber. Lampropeltis getulus* has a narrower mandibular fossa than does *Coluber.*

The vertebrae of *Coluber* have been discussed by Holman (1962), Auffenberg (1963), and Meylan (1982). I have found that the MTV of *C. constrictor* are geographically variable; however, some features are shared by all specimens examined. The MTV are elongate, with a moderately vaulted neural arch. Neural arch laminae range from strongly convex to nearly flat. The neural canal may be rectangular in outline or narrowed dorsally. Epizygapophyseal spines are moderately developed to very strong. The neural spine is elongate, medium to low in height, and often has moderate anterior and posterior overhangs. Accessory processes are long, thin to thick, and acute or blunt distally. Subcentral ridges are usually strong. The hemal keel is well developed and spatulate. Vertebrae of smaller forms are usually more elongate and gracile, with smaller epizygapophyseal spines.

The PTV of *Coluber* are more depressed than the MTV. The accessory processes remain long and are usually thick and blunt distally. Subcentral lymphatic fossae may be very strongly developed or only moderately developed and restricted to the anterior half of the centrum. Subcentral ridges may vary from strong (in forms with strong subcentral lymphatic fossae) to weak and restricted to the anterior region of the centrum. The hemal keel is thick, it may be produced from the centrum, and its cross-sectional outline is squared.

Coluber and *Masticophis* have very similar vertebrae, but as a group they may be separated from most other North American colubrid genera by their relatively greater vertebral length. *Opheodrys* and *Salvadora* also have relatively elongate vertebrae, but *Opheodrys* lacks epizygapophyseal spines (Holman, 1962), whereas *Salvadora* has slightly shorter vertebral centra and relatively smaller condyles (Holman, 1970, 1976). *Drymarchon corais* (Boie, 1827) and *Spilotes pullatus* (Linnaeus, 1758) are readily differentiated from *Coluber* and *Masticophis* by their more robust appearance. Neither the *Drymarchon* nor *Spilotes* examined were as elongate as *Coluber* and *Masticophis*. Furthermore, the neural spine of *D. corais* is usually beveled anterodorsally (Auffenberg, 1963; Meylan, 1982), whereas *S. pullatus* lacks epizygapophyseal spines. *Drymobius margaritiferus* (Schlegel, 1837) is quite similar to racers in its vertebral morphology. However, *D. margaritiferus* consistently has a larger, rounded neural canal and a zygosphene that is correspondingly broader. The zygapophyses have smaller facets and are not produced laterally in *Drymobius* as extensively as in *Coluber* and *Masticophis*.

Several authors (see Holman, 1981:266) have indicated that the similarity between *Coluber* and *Masticophis* is too great to reliably distinguish between them. However, examination of a large series of specimens of broad geographic scope has indicated that there are enough consistent differences, at least on a regional basis, to allow reliable differentiation. *Coluber constrictor mormon* Baird and Girard, 1852 of the western United States appears to be particularly distinctive. It is a relatively small subspecies, but its vertebrae are not as elongate as those of other small racers. Furthermore, its zygapophyses are not produced as far laterally as in most *Masticophis* species. Its epizygapophyseal spines are small, and the neural arch is somewhat depressed. The subcentral ridges are strong and convex laterally in ventral view, giving the centrum a flattened ventral surface. The postzygapophyses are generally elevated above the level of the dorsal edge of the condyle. Finally, the accessory processes are directed nearly laterally.

The smaller, more gracile forms of *Masticophis* [e.g., *M. taeniatus* (Hallowell, 1852) and *M. lateralis* (Hallowell, 1853)] are similar to *C. constrictor mormon* but differ as follows: vertebrae more elongate, zygapophyses produced laterally to a greater degree, neural arch more vaulted, subcentral ridges not as strongly developed and smoothly converging posteriorly, postzygapophyses not (or barely) elevated above condyle, accessory processes directed anterolaterally.

Larger racers (e.g., *C. c. constrictor, C. c. foxi* Baird and Girard, 1853, *C. c. priapus* Dunn and Wood, 1939, and *M. flagellum* ssp.) are readily distinguished from smaller racers. They have more robust vertebrae with highly vaulted neural arches, zygapophyses produced farther laterally than in the smaller racers, and higher neural spines.

Obviously, the vertebral morphology of racers needs a great deal more attention. Although the discriminant analysis of Meylan (1982) was partly successful, I believe that a more detailed morphometric analysis among recognized taxa will provide improved results.

ALLOCATED MATERIAL. ATV: 51953, 52085, 52096, 52145.

COMPARISONS. The anterior ATV of *Coluber* are shorter than the MTV, yet more elongate than ATV of many other genera (e.g., *Arizona, Pituophis, Elaphe,* etc.). The prezygapophyses are small and ovoid, with their long axes craniocaudally directed. Postzygapophyses are small and rounded. Accessory processes are very short, acute, and craniolaterally directed. Neural spines are of moderate length and may have posterior overhangs. The hypapophyses are long, ventrally directed, and squared distally. In the posterior ATV series, most characters are intermediate between anterior ATV and MTV. Here the hypapophysis becomes more posteriorly directed, its anteroventral surface approximates the sinuous condition, and its distal tip becomes obtusely pointed. *Coluber* ATV were distinguished from those of *Masticophis* largely on the basis of their shorter length and laterally convex subcentral ridges.

Because of much greater interspecific similarity and a general lack of comparative material, the vertebrae of immature racers were assigned to the category "*Coluber* or *Masticophis*," below.

DISCUSSION. Fitch *et al.* (1981) have suggested that *Coluber constrictor mormon* should be restored to full species status on the basis of differences in its morphology and various reproductive parameters from other *C. constrictor* subspecies. Yet, other authors (Greene, 1984; Corn and Bury, 1986) have provided evidence of intergradation between *C. constrictor flaviventris* and *C. constrictor mormon* in certain areas in the Rocky Mountains region. The species is here interpreted in the broad sense for convenience. Because the fossil vertebrae represent a population quite similar to modern *C. c. mormon,* which inhabits the Los Angeles region today, and are less similar to observed morphological variants of other *Coluber* or *Masticophis,* it is reasonable to assign these fossils to the more inclusive taxon, *C. constrictor*.

Brattstrom (1953b:376) identified "one partly damaged lower jaw . . ." from Rancho La Brea as "*Coluber* sp. (*sensu latu*)." Here he implies the inclusion of *Masticophis* within *Coluber*. Vertebrae from Rancho La Brea were later assigned to *Coluber constrictor* by Brattstrom (1958). The only other record of *Coluber* from the California Pleistocene is a single vertebra from the Carpinteria asphalt deposits (Brattstrom, 1955). Stebbins (1985) indicates that western forms of this species prefer semiarid to moist open habitats such as meadows, prairies, and thin brush, but they avoid xeric habitats.

Genus *Masticophis*
Baird and Girard, 1853
Masticophis lateralis
(Hallowell, 1853)

REFERRED MATERIAL. MTV: 12166, 15887, 16126, 21016, 48181, 52178, 52217; PTV: 25869, 52184 (2).

COMPARISONS. The MTV of *Masticophis* are discussed by Auffenberg (1963), Hill (1971), Meylan (1982), and Mead *et al.* (1984). MTV are elongate. Neural arches are moderately vaulted to moderately depressed. Neural arch laminae are flat or convex. The neural canal is generally large and subquadratic in outline from anterior, with the dorsal border only slightly narrower than the ventral. Zygapophyses tend to be relatively small, rounded, and divergent. The neural spine is long and varies from moderately high to low. Accessory processes are elongate, thick to moderately thick, and blunt distally. Subcentral ridges are moderate to strong. The centrum is smoothly tapered posteriorly. The hemal keel is low or produced ventrally, thin, and generally spatulate.

Intracolumnar variability is similar to that described for *Coluber constrictor.* Immature racer vertebrae were assigned to the "*Coluber* or *Masticophis*" category. Identification of *Coluber* and *Masticophis* to the generic level is discussed under *Coluber.*

Masticophis lateralis may often be distinguished from *M. taeniatus* by its narrower neural canal, slightly smaller epizygapophyseal spines, and thicker neural arch laminae.

DISCUSSION. Jennings (1983) mentions this first known fossil record of *Masticophis lateralis.* Stebbins (1985) describes this species as an inhabitant of the foothills and, occasionally, forested regions and mountains. It prefers chaparral associations but also frequents grassy, brushy, or rocky areas, especially areas near freshwater (Wright and Wright, 1957; Stebbins, 1985). *Masticophis lateralis* occurs in Los Angeles County today (Stebbins, 1985).

Coluber sp. or *Masticophis* sp.

REFERRED MATERIAL. ATV: 20893, 52145, 52198 (2), 52203, 52219; MTV: 11439 (fragment), 15508, 15992, 17701, 17768, 33437 (fragment), 41386, 51948, 51954 (3), 51966 (3), 52198, 52219 (6); PTV: 25007 (fragment), 48935, 51948 (2), 52060 (2), 52187; IMTV: 24608, 30800, 48094, 51966 (2), 52103, 52181 (2), 52190, 52198, 52203 (2), 52219 (3); IPTV: 52065, 52206, 52219 (2); H: 39745, 52136, 52219.

COMPARISONS. These vertebrae represent *Coluber* or *Masticophis* but are either too fragmentary to assign to species or fall within the range of overlap of both.

Vertebrae of immature racers were all assigned to this category because of a lack of immature comparative material. Vertebrae of immature racers are not quite as short as those of most other immature colubrids. Accessory processes are moderately long and pointed distally. Cotyles and condyles are relatively small. Hatchling racers have vertebrae that are nearly as short as those of any other colubrid species, but they may usually be distinguished by their broad and shallow posterior neural arch notch, small and divergent postzygapophyses, and a broad centrum with subcentral ridges apparent but subcentral lymphatic fossae lacking. The hemal keel in hatchling racers is generally broad and indistinct.

Genus *Pituophis* Holbrook, 1842
Pituophis melanoleucus
(Daudin, 1803)

(Fig. 9)

REFERRED MATERIAL. Maxilla: 42641 (L), 51945 (IL), 51958 (IL); Pterygoid: 51922 (fragmentary R); Compound bone: 24461 (R); MTV: 14266, 14923, 15419, 16307, 17607, 18047, 18786, 18865, 19178, 20048, 21208, 21401, 22018, 23008, 23160, 23652, 23935, 24471, 24645, 25957, 25978, 26982 (fragment), 27718, 30214, 30447, 32393, 37225, 38570, 39618, 42025, 47713, 48877, 51926, 51934, 51950, 51964, 52123 (4), 52164 (fragment), 52215 (8); PTV: 14971, 16405, 16584, 16852, 17704, 18907, 20048, 21436, 21825, 23505, 23848, 30930, 33306, 34743, 37716, 42621, 50543, 51921, 51927, 51940 (2), 52123, 52215 (8).

COMPARISONS. The maxilla of *Pituophis* has 17 (rarely 16) alveoli, a posteriorly placed palatine process, and a long ectopterygoid process. The only other genera examined with similar alveolar counts are *Masticophis* and *Coluber* with 17–19 and 14–16 alveoli, respectively. *Pituophis* may be separated from these by the length of its ectopterygoid process, which spans four alveoli. In *Masticophis* and *Coluber,* it spans only two or two and one-half. The maxilla of *Pituophis* is also distinctive in that the palatine process occurs at a point about two-fifths down the length of the bone. This character is shared with *Arizona,* but here the process lies opposite the sixth alveolus, whereas in *Pituophis* it lies opposite the eighth or part of the seventh and eighth alveoli. The *Arizona* maxillae examined had lower alveolar counts (14) than *Pituophis.*

In *Pituophis,* the pterygoid tooth row extends less than half the length of the bone. *Arizona* is the only other genus observed that shares this feature with *Pituophis.* The two differ in that the dorsal crest is much better developed in *Arizona.*

In *Pituophis,* the prearticular crest of the compound bone is more elevated than the surangular crest but is only moderately arched. The crests are about equal in *Coluber, Masticophis, Rhinocheilus,* and some specimens of *Lampropeltis getulus. Thamnophis, Salvadora,* and *Arizona* have an elevated prearticular crest as in *Pituophis,* but it is more arched. In some specimens of *Lampropeltis getulus,* the prearticular crest is elevated, but the dorsal opening of the mandibular fossa is always narrower than in other large colubrids.

The MTV of *Pituophis* are moderately short to moderately elongate. The neural arch is moderately vaulted, and its laminae are convex. The neural canal is higher than wide from anterior view and usually wider ventrally than dorsally. Zygapophyses are moderately divergent. The zygosphene is usually convex dorsally. Neural spines are of medium height in the western subspecies examined but higher in eastern subspecies (especially *P. m. mugitus* Barbour, 1921). Accessory processes are short and acute. Epizygapophyseal spines are obsolete to absent. The hemal keel is low, narrow, and spatulate to gladiate. Subcentral ridges are weak to moderate.

PTV are noticeably more elongate than MTV. The neural arch retains approximately the same degree of vaulting as in MTV but has less convex laminae. The hemal keel is produced ventrally and may become gladiate.

Criteria for identification of *Pituophis* vertebrae have been discussed by Auffenberg (1963), Holman (1965), Van Devender and Mead (1978), Meylan (1982), and Mead *et al.* (1984). Among western colubrids, *Pituophis* vertebrae are most readily confused with *Arizona, Elaphe,* or *Lampropeltis getulus.* The MTV of *L. getulus* have distinct lymphatic fossae ventrally. This character is only present in the PTV of *Pituophis.* The PTV of *Pituophis* are readily distinguished from those of *L. getulus* by their vaulted neural arches and thin accessory processes. Weaker subcentral ridges will distinguish *Pituophis* from most species of *Elaphe. Pituophis* vertebrae are generally more elongate than those of *Arizona.* However, this character varies with age such that very young specimens overlap strongly with mature *Arizona.* Finally, immature *Pituophis* condyles are much larger than those of similar sized *Lampropeltis, Elaphe,* or *Arizona.* This character appears to change ontogenetically, large specimens not sharing the exaggerated condyle.

ALLOCATED MATERIAL. ATV: 15041, 18490, 50295, 51636, 51929, 52189 (2), 52208, 52215 (4); IATV: 52140, 52189 (2), 52202, 52204; IMTV: 10504, 15419 (6), 20301, 51919, 51921, 51923 (3), 51931 (7), 51933, 51934, 51939, 51964, 52122, 52179 (4), 52196 (2), 52202, 52208, 52215 (6); IPTV: 23847, 25652, 51956, 52087, 52189; H: 15419, 16475, 22109, 35979, 52087.

COMPARISONS. Anterior ATV have a highly vaulted neural arch. Accessory processes are short and acutely pointed. Cotyles and condyles are small. The hypapophysis is long, ventrally directed, and squared distally. The hypapophysis regresses in length posteriorly in the ATV series but remains ventrally directed and squared distally.

Vertebrae of hatchlings (Fig. 9) are extremely short. The neural arch is moderately vaulted with laminae that are slightly convex laterally. The neural canal is higher than wide and wider ventrally than dorsally. Postzygapophyses are elevated above the condyle, and prezygapophyseal buttresses are very high. The zygosphene is convex dorsally. Accessory processes are long, thin, and sharply pointed. Condyles and cotyles are relatively larger in this species than in any other observed at this stage of development.

DISCUSSION. Brattstrom (1953b) reported *Pituophis melanoleucus* (as *P. catenifer*) from Rancho La Brea. Other late Pleistocene localities in California include the McKittrick Asphalt (Brattstrom, 1953a) and Costeau Pit (Hudson and Brattstrom, 1977).

Pituophis melanoleucus is known from most habitat types and to relatively high elevations throughout its wide range. It is found in Los Angeles County today (Stebbins, 1985).

Genus *Arizona* Kennicott, 1859
Arizona elegans Kennicott, 1859

REFERRED MATERIAL. MTV: 51932, 52163, 52214; PTV: 52214.

COMPARISONS. MTV of *Arizona* have been described by Van Devender and Mead (1978) and Mead *et al.* (1984). They are short and broad with a moderately vaulted neural arch and a wide neural canal. Neural arch laminae are distinctly convex laterally. The neural spine is medium in height. Accessory processes are of medium length and relatively thin. The condyle is moderately wide and the subcentral ridges are moderately developed. The hemal keel is distinct, low, and spatulate.

PTV of *Arizona* are not distinctly more elongate and do not have noticeably lower neural spines than MTV. The notch between parapophyses and ventrolateral cotyle is minimally developed except near the PCV series. However, subcentral lymphatic fossae are well developed on the anterior portion of the centrum, and the hemal keel is deep and narrow.

Arizona vertebrae most closely resemble those of *Pituophis.* The criteria used to distinguish these two genera are discussed under *Pituophis.* Holman (1963) discussed the distinction between *Arizona elegans* and several species of *Lampropeltis. Arizona* vertebrae differ from those of *Elaphe* in that they are shorter and have weaker subcentral ridges in the MTV series. Also, the neural arch laminae are convex laterally in *Arizona,* whereas they are simply convex in *Elaphe.*

ALLOCATED MATERIAL. H: 46221.

COMPARISONS. Immature *Arizona* vertebrae are only slightly shorter than those of adults. Their

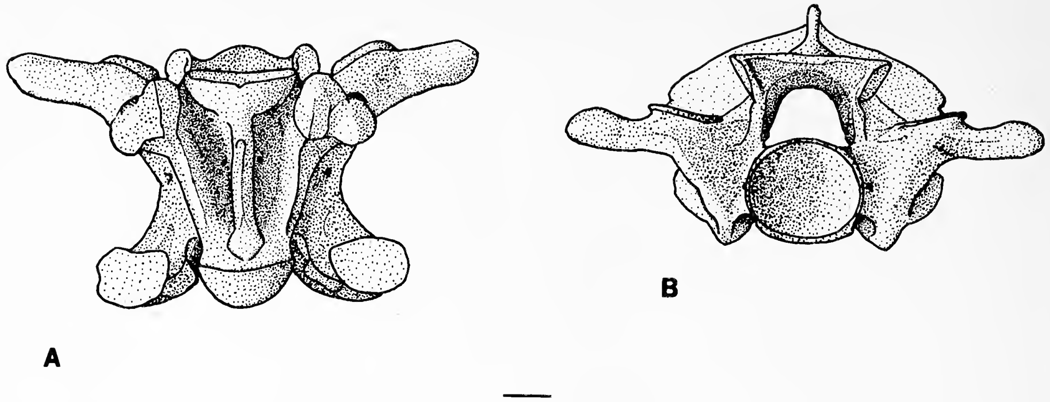

Figure 13. Fossil vertebra (LACMRLP 51960) of *Lampropeltis getulus* from Pit 91, Rancho La Brea. **A.** Ventral aspect. **B.** Anterior aspect. Bar = 1 mm.

condyles and cotyles are of moderate size. The enlarged neural canal is slightly higher than wide.

DISCUSSION. This species has not previously been reported from the Pleistocene of California.

Arizona elegans prefers open areas with chaparral, sagebrush, or grassy vegetation or barren deserts. Its present range includes Los Angeles County (Stebbins, 1985).

Genus *Lampropeltis* Fitzinger, 1843

Lampropeltis getulus (Linnaeus, 1766)

(Fig. 13)

REFERRED MATERIAL. Maxilla: 51925 (IL fragment); MTV: 14948, 19994, 20151, 28575, 51938, 51960, 52069 (2), 52080 [3 (2 fused)], 52114 (2); PTV: 40284 (3), 51938, 52107, 52126.

COMPARISONS. Maxillae of *Lampropeltis* are short, robust, generally contain 13–15 alveoli (n = 9), and lack diastemata. The palatine process is long, narrow, directed posteriorly, and located about one-third the maxillary length back from the anterior end. Anteriorly, the maxilla is high and narrow.

Pituophis and *Arizona* have longer, thinner maxillae, with palatine processes located more posteriorly. *Pituophis* usually has 17 maxillary alveoli. *Masticophis* and *Coluber* also have longer maxillae, with wider palatine processes that are directed medially. *Masticophis* has 17–19 maxillary alveoli. The anterior portion of the maxilla in *Rhinocheilus, Lampropeltis triangulum* (Lacepede, 1788), *L. pyromelana* (Cope, 1866), and *L. zonata* (Lockington, 1876) is more depressed than in *L. getulus.*

Lampropeltis getulus vertebrae (Fig. 13) have been discussed by Auffenberg (1963), Holman (1965), Van Devender and Mead (1978), Meylan (1982), and Mead *et al.* (1984). Their MTV are moderately short and broad. The neural arch is moderately depressed, with laminae that are flat to slightly convex laterally. The zygapophyses are moderately to strongly produced laterally. The neural spine is of medium height and generally has an angular overhang posteriorly. In large specimens, the neural spine may be thickened dorsally. Cotyles and condyles are of moderate size. Accessory processes are long, very thick, and blunt distally. This species is peculiar in that the dorsoventral diameter of the accessory processes may abruptly increase distally in mature specimens (Fig. 13B). The hemal keel is usually strongly produced ventrally, thin, and spatulate to gladiate. Subcentral ridges are strongly developed and are accentuated by the deep subcentral lymphatic fossae that are present throughout the column. Notches are often present between the cotyle and parapophyses throughout the MTV and PTV. In large specimens, lateral processes from the ventrolateral lip of the cotyle may nearly contact the ventral edge of the parapophysis, causing the notch to approximate a foramen.

PTV of *Lampropeltis* are not nearly so well differentiated from MTV as in most species. They are more elongate, with more depressed neural arches. Subcentral lymphatic fossae are somewhat deeper, and paracotylar notches are large and well developed, causing emargination of the ventrolateral lip of the cotyle.

Vertebrae of *Lampropeltis getulus* may be distinguished from those of *Pituophis* as described above. *Arizona* and *Elaphe* are readily distinguished from *Lampropeltis getulus* by their shorter vertebrae that lack subcentral lymphatic fossae on the MTV. In *Lampropeltis* PTV, the centra are slightly more elongate, the neural arches more depressed, the zygapophyses more divergent, and the accessory processes longer and larger in diameter than in either *Elaphe* or *Arizona.* Vertebrae of *Rhinocheilus lecontei* are similar to those of *Lampropeltis getulus* but are distinguished by being shorter and having wider hemal keels, weaker subcentral lymphatic fossae, smaller zygapophyses, and shorter neural spines.

Vertebrae of other *Lampropeltis* species have weaker hemal keels and subcentral lymphatic fossae. They also lack thickened neural spines and accessory processes. Furthermore, vertebrae of *L. triangulum* and related forms are more elongate and depressed.

ALLOCATED MATERIAL. IATV: 52185; IMTV: 27777, 52057, 52080, 52185, 52200.

COMPARISONS. Anterior ATV of *Lampropeltis getulus* have moderately depressed neural arches that have laterally convex laminae. The posterior neural arch notch is shallow and obtuse. Zygapophyses are not divergent. Accessory processes are short, thick, and blunt. Cotyles and condyles are very small. Hypapophyses are long, ventrally directed, and squared distally. Subcentral lymphatic fossae are present, but shallow; anterior lymphatic notches are negligible.

In immature vertebrae, the neural canal is high and the cotyle is slightly depressed. The zygosphene is convex dorsally. The hemal keel is relatively broad, low, and rounded in transverse outline, its lateral borders sloping and indistinct. Subcentral ridges are moderately distinct. Subcentral lymphatic fossae are present anteriorly in the region of the subcentral foramen but are not as distinct as in adults. Anterior lymphatic notches are poorly developed.

DISCUSSION. Brattstrom (1953b, 1958) reported *Lampropeltis getulus* from Rancho La Brea. Other reports from California include McKittrick (Brattstrom, 1953a), Newport Beach Mesa (Hudson and Brattstrom, 1977), and Redtail Peaks and Tunnel Ridge (Van Devender and Mead, 1978).

Lampropeltis getulus is a very wide ranging species throughout the southern half of the United States. It occupies most terrestrial habitats within its range (Wright and Wright, 1957). It is found in Los Angeles County today (Stebbins, 1985).

Genus *Rhinocheilus* Baird and Girard, 1853

Rhinocheilus lecontei Baird and Girard, 1853

REFERRED MATERIAL. MTV: 52115 (3).

COMPARISONS. Vertebrae of this monotypic genus have been described by Hill (1971), Van Devender and Mead (1978), and Mead *et al.* (1984). *Rhinocheilus* vertebrae are short to moderately elongate. Their neural arches are moderately depressed, but have strongly convex laminae. Zygapophyses are rather small and only moderately produced laterally. The zygosphene is flat dorsally, and crenate anteriorly. The neural spine is of medium height, thickened dorsally, and has strong anterior and posterior overhangs. Accessory processes are long, thick, and blunt and may be thicker distally than proximally as in *Lampropeltis getulus.* The hemal keel is strong and spatulate and has well defined lateral edges. Subcentral lymphatic fossae are present throughout the column but are not as strong as in *L. getulus.*

PTV of *Rhinocheilus* are of approximately the same relative length as MTV. Zygapophyses are less divergent in the PTV, and the cotyle and condyle are smaller. However, accessory processes are relatively larger. The hemal keel is produced ventrally.

This species most closely resembles *Lampropeltis getulus,* but may be distinguished from it as described under that account. *Hypsiglena* vertebrae are smaller and more depressed and have relatively larger and more laterally produced zygapophyses.

ALLOCATED MATERIAL. ATV: 52191.

COMPARISONS. ATV of *Rhinocheilus* have slightly more vaulted neural arches than MTV with extremely convex laminae. The posterior neural arch notch is moderately deep and slightly obtuse. The zygosphene is crenate but may be slightly convex dorsally. Zygapophyses are small and not divergent. The neural spine is slightly higher than in MTV, its anterior border is vertical, and its posterior border retains a strong overhang. Accessory processes are short, laterally directed, and blunt. The hypapophysis is long, ventrally directed, and rounded distally.

DISCUSSION. *Rhinocheilus lecontei* was reported from Tunnel Ridge in California (Van Devender and Mead, 1978). Stebbins (1985) lists deserts, prairies, and brushland as habitats for this nocturnal species. It is known from the Los Angeles area today (Stebbins, 1985).

Subfamily NATRICINAE Bonaparte, 1840

Genus *Thamnophis* Fitzinger, 1843

Thamnophis couchii species complex (after Rossman and Stewart, 1987)

REFERRED MATERIAL. MTV: 15038, 15974, 16046, 17242, 46925, 51944 (3), 51952 (3), 52072, 52083, 52101 (13), 52106, 52129, 52131, 52133; PTV: 18859, 23075, 23133, 30100, 51944, 52095, 52101, 52166.

COMPARISONS. The MTV of members of the *Thamnophis couchii* complex are moderately elongate to short. The neural arch is moderately vaulted, and its laminae are slightly convex. Zygapophyses are produced laterally. Epizygapophyseal spines are moderately developed to absent. Neural spines are medium in height but short, with moderate anterior and strong to moderate posterior overhangs. Accessory processes are typically medium in length and acute distally. Hypapophyses are short, bladelike, and obtusely pointed posteroventrally, and the anteroventral edge is often strongly angular. Subcentral ridges are moderate to strong. The lymphatic notch is often present throughout the column. Ventrolateral processes are often present on the lip of the cotyle.

Great variability and a large degree of overlap in features makes specific identification of *Thamnophis* vertebrae difficult. Holman (1962) used characters of the neural spine to identify certain species groups within the genus. Members of the *Thamnophis couchii* group and *Thamnophis sirtalis* (Linnaeus, 1758), which live in the Los Angeles area today, have neural spines that are somewhat longer than high and usually lack strong anterior overhangs, although the anterior border may be slightly inclined forward. Anterior overhangs are strongly developed in the western species *T. elegans* (Baird and Girard, 1853), *T. eques* (Reuss, 1843), and *T. marcianus* (Baird and Girard, 1853). *Thamnophis cyrtopsis* (Kennicott, 1861) has a much lower, longer neural spine.

The members of the *Thamnophis couchii* group display a wider range of vertebral morphology than any other species group of *Thamnophis* examined. Most of the referred specimens have the weak or absent anterior overhangs of the *T. couchii* group and *T. sirtalis.*

Most of the specimens of the *T. couchii* group available for comparison were relatively large individuals (e.g., *T. gigas* Fitch, 1940). These were easily distinguished from *T. sirtalis* on the basis of the shorter centra and more laterally produced zygapophyses of the former. However, the smallest individuals tend to converge in shape because the elongate character of the centrum of *T. sirtalis* is less distinct in young individuals, becoming more pronounced with age. Much of the fossil material represents snakes that are smaller to much smaller than most of the comparative specimens of the *T. couchii* group available and falls within the range of shape overlap. The bulk of the fossil material appears to represent a single population of relatively small individuals that are, on the whole, closer to the *T. couchii* group than to *T. sirtalis.* Yet, some specimens were much larger than the rest and clearly represent *T. sirtalis.* A conservative approach was adopted in assigning these specimens. Most fell near the range of shape overlap and were assigned only to genus (*Thamnophis* sp., below). Others matched the extreme condition seen in the *T. couchii* group and were clearly unlike any *T. sirtalis* specimens observed. These were assigned to the *T. couchii* group. Intracolumnar and ontogenetic variation are approximately as described under *Thamnophis* sp.

DISCUSSION. Until recently, the members of the *T. couchii* group were considered to be subspecies of a single variable species, *T. couchii* (Fitch, 1984). Rossman and Stewart (1987), on the basis of detailed morphological studies and the biochemical evidence of Lawson and Dessauer (1979), have accorded four of these subspecies full species status: *T. couchii, T. hammondii* (Kennicott, 1860), *T. gigas* Fitch, 1940, and *T. atratus* (Kennicott, 1860) (with three subspecies). Although members of this group share certain vertebral characters, a more detailed morphometric analysis of larger samples will be required to determine whether these species can be reliably separated from each other on the basis of isolated vertebrae. Clearly, a form allied to the semiaquatic *T. couchii* had differentiated from the more terrestrial *T. elegans* and *T. sirtalis* groups by the time period of the Pit 91 deposit.

No member of the *Thamnophis couchii* group has previously been reported from the fossil record. Most species of the *T. couchii* group are semiaquatic, living near marshes and streams and feeding principally on fish and anuran larvae (Fitch, 1984). In this regard, their ecology resembles that of many members of the genus *Nerodia. Thamnophis hammondii* is found in the Los Angeles area today (Stebbins, 1954, 1985).

Thamnophis sirtalis (Linnaeus, 1758)

REFERRED MATERIAL. MTV: 18048, 20485, 51943, 52128, 52174 (3).

COMPARISONS. *Thamnophis sirtalis* MTV are moderately to very elongate. The neural arch is vaulted and its laminae are convex. Zygapophyses are moderately produced laterally. Epizygapophyseal spines are typically well developed. The neural spine is of medium height with strong posterior overhangs and weaker anterior overhangs. Accessory processes are medium to long, thick, and blunt. Hypapophyses are short, blade-like, and directed strongly caudad. The anteroventral surface is strongly sinuous. Subcentral ridges are very prominent. Notches between the parapophyses and the ventrolateral lip of the cotyle are well developed throughout the column. Small processes often project from the ventrolateral lip of the cotyle.

DISCUSSION. The fossil material is indistinguishable from the comparative material examined. *Thamnophis sirtalis* has not previously been reported from the Pleistocene of the Southwest. This widespread species is usually found near aquatic or mesic environments, ranging into fields and woodlands. Dixon (1967) reported only two records of this species historically in Los Angeles County, which is near the southernmost extent of its present range in California (Stebbins, 1985).

Thamnophis sp.

REFERRED MATERIAL. Maxillae: 41286 (L, fragment), 52169 (L, fragment), 47727 (R), 51936 (R), 51959 (R); palatine: 41212 (L); pterygoid: 17455 (R, pathologic); dentaries: 51947 (R, distal fragment), 52171 (R); compound bone: 52084 (R); MTV: 10074, 12542, 12783, 13475, 13799, 14154, 14629, 14980, 14997, 15233, 15453, 15475, 15600, 15662, 15680, 15760, 15771, 15807 (fragment), 15810, 15872, 15946, 15984, 16002, 16058, 16080, 16087, 16104, 16113, 16124, 16132 (fragment), 16152 (2), 16153, 16301, 16367, 16437, 17246, 17318, 17453, 17476, 17638, 17702, 18115, 18175, 18299, 18331, 18345, 18798, 18993, 19067, 19142, 19682, 20893, 20989, 21373, 21701, 22193, 22492, 23927, 24465, 24579 (3), 16910 (2), 27293, 27430, 27637, 28251, 30561, 30856, 31119, 31273 (3), 32475, 32885, 33049, 33766, 35991, 36618, 36882, 37296, 38000, 39671, 43420 (2) (articulated), 43707 (2), 44056 (2), 44684, 44766, 44804, 45761, 46175, 46205, 46326, 47041, 48093, 49132 (fragment), 49557, 50706, 51060, 51381, 51434, 51563, 51903 (2), 51949 (6), 51953 (18), 52053, 52055, 52061 (10), 52066 (2), 52068 (2), 52073 (19), 52079 (2), 52085 [23 (2 fused)], 52087, 52089, 52091, 52097, 52099, 52102 (96), 52105 (3), 52109 (10), 52112 (8), 52118 (2), 52125 (7), 52130, 52135 (8), 52137, 52139, 52141, 52146, 52147, 52218 (217); PTV: 14154, 15461, 16152, 16521, 16966 (3), 17363, 17722, 18228, 20419, 21311, 22095, 22598, 23665, 23863, 25487, 26007 (2), 26024 (2), 26823, 27090, 27352, 28240, 30922, 32114, 32720, 32885, 33259, 35897, 41625 (2), 43707, 45535, 45654, 46043, 48191, 51205, 51460, 51903, 51930, 51949 (2), 51953 (7), 52053, 52054, 52061 (2), 52066 (2), 52073 (3), 52075, 52085 (9), 52087, 52094, 52102 (35), 52104 (3), 52109 (4), 52112 (7), 52117, 52121, 52130, 52135 (4), 52142, 52146, 52157, 52161, 52199 (6), 52205, 52207, 52218 (68).

COMPARISONS. Dentigerous bones of *Thamnophis* usually have more alveoli per unit length than similar bones of colubrines (a notable exception is *Drymobius margaritiferus*). *Thamnophis* maxillae have medium-sized ectopterygoid and palatine processes and 21–25 alveoli. Anteriorly, the shaft of the bone curves strongly mediad. The last two to three maxillary teeth are distinctly enlarged and compressed. *Thamnophis* maxillae lack diastemata.

Maxillae of *Drymobius margaritiferus* also have high tooth counts, and the last two to three teeth are also enlarged and compressed. However, these two genera differ in the shapes of their teeth and ectopterygoid processes. Teeth of *Thamnophis* are strongly recurved near the base, and the distal portion is straight or may even bend back ventrad near the tip, giving the tooth a slightly sinuous appearance. In addition, anterior maxillary teeth are as large as or larger than all but the posterior enlarged teeth. Teeth of *D. margaritiferus,* however, are smoothly recurved throughout and steadily decrease in size anteriorly. Finally, the caudal border of the ectopterygoid process of *Thamnophis* is approximately perpendicular to the shaft of the maxilla, whereas in *D. margaritiferus* this border is sloped strongly rostrad. *Nerodia* has maxillary tooth counts similar to those of *Thamnophis,* but *Nerodia* may usually be distinguished by its longer palatine and ectopterygoid processes that are not directed as sharply ventrad. Also, the ectopterygoid process of *Nerodia* is usually narrower and is roughly squared distally, whereas in *Thamnophis* this process is longer anteriorly, with a medial border that slopes toward the maxillary shaft.

The palatine of *Thamnophis* is elongate and has 14–16 alveoli. The choanal process is relatively broad and strongly recurved. The maxillary process is long, narrow, and rounded in cross section. The pterygoid process is usually strongly forked.

Lampropeltis and *Rhinocheilus* palatines have fewer teeth than those of *Thamnophis. Arizona, Coluber, Masticophis,* and *Pituophis* have choanal processes that are recurved only weakly or not at all. The maxillary process is shorter in *Arizona* and *Masticophis* and flatter in *Coluber.* The palatine of *Drymobius margaritiferus* has more teeth (19) and lacks a forked pterygoid process. *Nerodia,* with similar alveolar counts, has a more curved choanal process that slopes toward the shaft. The choanal process is broader in *Thamnophis,* occupying four to four and one-half alveolar spaces, whereas in most *Nerodia* it occupies only three. Also, the maxillary process is larger and more posteriorly placed in *Nerodia.*

Pterygoids of *Thamnophis* have 20–34 alveoli (n = 35, 10 species). The alveoli extend nearly to the posterior end of the bone. The quadrate process is relatively short. The palatine process has a distinctive ventrolateral notch distally for the reception of the forked posterior end of the palatine.

Lampropeltis, Masticophis, Nerodia, Rhinocheilus, and *Salvadora* have longer, narrower quadrate processes. The pterygoid of *Coluber* is more constricted posterior to its ectopterygoid articulation. *Drymobius margaritiferus* does not have a distal notch on its palatine process.

The dentary of *Thamnophis* has 27–30 alveoli. Meckel's groove usually closes opposite the sixth alveolus. *Thamnophis* dentaries are distinguishable from those of most colubrines by the higher alveolar counts. *Drymobius margaritiferus,* with similar alveolar counts, may usually be distinguished by the fact that the distal end of its dentary is more strongly curved medially. Furthermore, the lateral notch for the compound bone is narrower in *D. margaritiferus.* Tooth shapes differ as described for the maxilla. In *Thamnophis,* the distal portion of the dentary narrows abruptly in the vicinity of the anterior end of Meckel's groove, whereas in *Nerodia* the dentary tapers smoothly throughout.

In *Thamnophis,* the prearticular crest of the compound bone is more elevated than the surangular crest and is relatively strongly arched. The supraangular foramen is located far rostrally, and the *M. adductor posterior: pars profundus* inserts on a pronounced ridge on the medial surface of the prearticular crest. This ridge runs from immediately below the quadrate condyle rostrodorsally to the anterior edge of the prearticular crest. The ridge of insertion for the *M. adductor mandibulae externus superficialis* is poorly developed or absent.

The compound of *Pituophis* differs as described for that genus. In *Coluber, Masticophis,* and *Rhinocheilus,* the surangular and prearticular crests are roughly equal in height. *Lampropeltis getulus* has a narrower mandibular fossa than does *Thamnophis. Salvadora* has a distinctly shorter compound bone with a relatively higher surangular crest than does *Thamnophis. Arizona* has relatively shorter mandibular fossae and retroarticular processes than does *Thamnophis.* In *Drymobius margaritiferus* the compound differs from that of *Thamnophis* in that the supraangular foramen is not located as far rostrally, the mandibular fossa is shorter, and the ridge of insertion of the *M. adductor posterior: pars* *profundus* is less pronounced, running more abruptly dorsad to intersect the middle of the prearticular crest. *Nerodia* has a stronger, more arched prearticular crest and a well developed ridge of insertion for the *M. adductor mandibulae externus superficialis.*

Vertebrae of *Thamnophis* have been described by Auffenberg (1963). Identification of various natricine genera has been discussed by Auffenberg (1963), Brattstrom (1967), Holman (1962, 1977a), and Meylan (1982). MTV of this speciose genus are variable but present some distinguishable patterns. MTV are generally elongate with strong subcentral ridges. Neural arches are moderately vaulted to moderately depressed with convex to nearly flat laminae. Epizygapophyseal spines are generally well developed. Zygapophyses are moderately to strongly divergent. The zygosphene is generally narrow, flat, or nearly flat dorsally, and its anterior edge is flat to crenate. The neural spine is of medium to low height but is usually characterized by distinctive anterior and posterior overhangs. Accessory processes are of variable length but are generally thick and blunt distally. The hypapophysis is short, strongly sigmoid ventrally, and caudally directed.

In the PTV, the hypapophysis is much shorter and more blunt than in the MTV. The notch between parapophysis and cotyle is large, and subcentral lymphatic fossae are weakly to strongly developed.

Seminatrix, Storeria, Tropidoclonion, and *Virginia* have elongate MTV, but have low to obsolete neural spines (Auffenberg, 1963). *Nerodia* and related genera usually have shorter vertebrae with higher, shorter neural spines.

ALLOCATED MATERIAL. ATV: 17862, 20906, 21888, 24621, 49349, 52067, 52073, 52075 (2), 52079, 52085, 52087 (2), 52102 (6), 52109, 52112, 52117, 52135, 52138, 52160, 52182, 52199, 52205, 52218 (11); PCV: 16124, 24009, 26007, 30561, 50343, 52087, 52102 (2), 52109, 52155, 52218 (14); IATV: 14968, 51930 (2), 52209; IMTV: 14477, 14997, 15036, 16089, 16362, 25300, 40889, 43116, 51953, 52061 (4), 52066 (4), 52067 (3), 52075 (3), 52078, 52085 (8), 52087, 52094, 52102 (8), 52104 (5), 52109 (5), 52112 (2), 52125 (2), 52148, 52156, 52199, 52205, 52218 (21); IPTV: 29827, 50918, 51717, 52066, 52073 (2), 52075 (2), 52085 (4), 52087, 52109 (3), 52135, 52199; H: 30922, 52104, 52137, 52182 (3), 52199 (3).

COMPARISONS. The neural arch of the ATV is highly vaulted and has convex laminae. The neural canal is higher than wide. Epizygapophyseal spines are usually reduced. The neural spine is about as tall as in the MTV but is much shorter (anteroposteriorly). Accessory processes are very short, thick, and blunt. Hypapophyses are often slightly longer and may be slightly more to much more ventrally directed. They may be sharp to nearly squared ventrally.

The precloacal vertebrae of *Thamnophis* have small cotyles and condyles. Their hypapophyses are short and thickened ventrally.

Vertebrae of immature *Thamnophis* may be somewhat shorter to much shorter than those of adults. Vertebrae of neonates tend to be quite similar in relative proportions among species. Most specific vertebral differentiation apparently occurs during postnatal ontogenesis. The condition of the neural arch in neonates is little different from that seen in adults except that the posterior notch is generally wider and more obtuse. Zygapophyses of neonatal *Thamnophis* are less divergent than those of adults. Neural spines are comparable in height but slightly to much shorter anteroposteriorly. Accessory processes are generally shorter and acutely pointed distally. Hypapophyses of neonates tend to be more spine-like, have simple anterior edges, are sharply pointed, and are directed strongly caudad.

DISCUSSION. *Thamnophis* is the only natricine genus presently found in the extreme southwestern United States (Stebbins, 1985). The referred remains are either too fragmentary to assign to species or fall within the range of overlap for *T. sirtalis* and the *T. couchii* group.

It is worthwhile to underscore here highly convergent morphologies of the dentigerous elements of *Thamnophis* and *Drymobius margaritiferus.* This convergence may reflect dietary similarities. Close comparisons of skull elements of these two genera and of the vertebrae of *Drymobius* with racers should be made when considering any ophidian paleofauna from the southwestern states or Central America. No other species of *Drymobius* were available for comparison.

Family VIPERIDAE Bonaparte, 1840

Subfamily CROTALINAE Gray, 1825

Genus *Crotalus* Linnaeus, 1758

Crotalus viridis (Rafinesque, 1818)

REFERRED MATERIAL. Dentary: 52170; MTV: 14729 (2), 14974, 14975, 15014 (fragment), 17798, 17997, 18049, 20167, 22603, 27648, 29963, 29964, 30992 (fragment), 34702, 37476, 42121, 47848, 48486, 51127, 51906, 51942, 51963, 51967, 51968, 52119 [2 (1 fragmentary)], 52213 [3 (1 fragmentary)]; PTV: 10031, 14970, 15996, 22776, 43061, 49556 (fragment).

COMPARISONS. The dentary of *Crotalus* is easily distinguished from those of most other North American snakes. It is very deep and narrow with a gently curved distal tip. Its depth does not taper anteriorly until the third alveolus and then only slightly. Meckel's groove is usually open lingually to the distal tip, but in a few cases it is closed at the tip or is closed to a suture just posterior to the tip, only to reopen at the tip. A foramen is present on the lingual side distally.

Most colubrid species have dentaries that are not as deep or taper gradually from the posterior to rostral end. Meckel's groove is variable but is never entirely open lingually to the tip. No other crotaline genus observed possesses a distal foramen on the lingual side.

The single fossil dentary falls within the range of variability of recent *Crotalus viridis* but should be considered a tentative assignment at the species level because of overlap of characters among species.

Crotalus vertebrae may be identified by characters given by Auffenberg (1963), Brattstrom (1964), and Holman (1965). *Crotalus* MTV are short to very short and broad. The neural arches are moderately to strongly depressed, with flat laminae. The neural canal is moderately depressed and, in anterior aspect, is usually wider ventrally than dorsally. Zygapophyses vary from moderately to extremely divergent. In large forms, the prezygapophyses may become elongate and subrectangular with the long axis laterally directed. Prezygapophyseal buttresses are very high. Cotyles and condyles are large. Neural spines vary from high to low, anterior overhangs are generally absent, and posterior overhangs may be present. Accessory processes are very short and generally acute or blunt. Subcentral ridges may vary from moderate to poorly developed. The hypapophysis is long, thick laterally, posteroventrally directed, and often sharply pointed distally.

Neural arches of *Crotalus* PTV may be slightly more depressed than those of MTV. Zygosphenes are crenulate anteriorly. Hypapophyses are shorter and more posteriorly directed. Subcentral lymphatic fossae tend to be weak or absent throughout most of the column. However, in the posterior portion of the PTV, fossae may be apparent ventrally between the parapophyses and the cotyle, creating a slight notch in anterior view and faint emargination of the ventrolateral edge of the cotyle.

Agkistrodon has larger fossae lateral to the cotyle than does *Crotalus.* These fossae usually have a single large foramen in *Agkistrodon,* whereas in *Crotalus* the foramina are smaller and may be multiple (Holman, 1963, 1965). *Sistrurus* has relatively longer centra and may have a small spine on the zygosphene anterior to the neural spine (Holman, 1965).

These vertebrae are assigned to *Crotalus viridis* on the basis of the shape of their centra, which are relatively longer than in most other *Crotalus* species, and their relatively low neural spines. MTV of *C. atrox* Baird and Girard, 1853, *C. molossus* Baird and Girard, 1853, and *C. ruber* Cope, 1892 have shorter centra and higher neural spines. The centra of MTV in *C. mitchelli* (Cope, 1861) are somewhat shorter, and their neural spines are lower. *Crotalus scutulatus* (Kennicott, 1861) has higher neural spines. *Crotalus cerastes* Hallowell, 1854 MTV differ in that they have wide, dorsally convex zygosphenes.

ALLOCATED MATERIAL. ATV: 31086, 41014, 51955, 52119; IMTV: 52110, 52134 (2), 52201, 52213 (2); H: 41327.

COMPARISONS. ATV in *Crotalus* have about the same relative length as MTV. Neural arches of ATV are slightly more vaulted with slightly convex laminae. Zygapophyses are much less divergent than those of the MTV. Accessory processes are extremely short and sharply pointed. Hypapophyses of ATV are extremely long, thinner than in MTV, and ventrally directed.

Vertebrae of immature *Crotalus* are only slightly shortened relative to those of adults. Zygapophyses are less divergent, and their facets tend to be rounded. Accessory processes are short but thin and pointed. Cotyles and condyles of immatures tend to be flattened dorsally and slightly drawn out ventrally imparting a subtriangular shape.

DISCUSSION. This species is known from a wide variety of habitats, including coastal sand dunes, wooded regions, near water courses, and prairies, but is not known from desert regions. *Crotalus viridis* occurs in the Los Angeles area today (Stebbins, 1985).

Crotalus viridis was reported from Rancho La Brea by Brattstrom (1953b, 1958). Other Rancholabrean records of this species from California include the McKittrick Asphalt deposit, Hawver Cave (Brattstrom, 1953a), Mescal Cave (Brattstrom, 1958), and Costeau Pit and Newport Beach Mesa (Hudson and Brattstrom, 1977).

CONCLUSIONS

Eight modern snake taxa are added to the known herpetofauna from Rancho La Brea, increasing the number of recognized snake species from four to 12. Newly reported taxa are *Diadophis punctatus, Hypsiglena torquata, Tantilla* sp., *Arizona elegans, Masticophis lateralis, Rhinocheilus lecontei, Thamnophis couchii* species group, and *T. sirtalis.* Of these, *M. lateralis* and the *T. couchii* group have not previously been reported as fossils.

FAUNAL COMPOSITION AND LOCAL PALEOENVIRONMENT

The composition of the Pit 91 snake fauna suggests that the local paleoenvironment probably included a stream and associated riparian woodland. Other habitats in the vicinity may have included chaparral, sage scrub, and/or patches of open grassland. These reconstructions are based on the relative abundance of fossil taxa (Table 1) and the habitat preferences of the living species (Table 2). The reconstructions are corroborated by geological and paleobotanical evidence (Woodard and Marcus, 1973; Warter, 1976; Shaw and Quinn, 1986).

The relative abundance of a taxon is represented by the percentage of the total number of identified specimens (NISP) for that taxon in the assemblage (Table 1). NISP is used because of difficulties inherent in determining the preferable minimum number of individuals (MNI) in snake assemblages

Table 1. Numbers of identified specimens (NISP) of snake species from Pit 91. Taxon names are abbreviated with first two letters of genus and first letter of species name.

Skeletal elements*	Snake taxa†													
	Ar.e	Co.c	Co.–Ma.	Di.p	Hy.t	La.g	Ma.l	Pi.m	Rh.l	Ta.sp	Th.c	Th.s	Th.sp	Cr.v
VT	5	56	58	66	30	25	10	145	4	10	39	7	936	50
MX	0	1	0	1	0	1	0	3	0	0	0	0	5	0
DN	0	0	0	0	0	0	0	0	0	0	0	0	2	1
CP	0	1	0	1	0	0	0	1	0	0	0	0	1	0
PT	0	0	0	0	0	0	0	1	0	0	0	0	1	0
PL	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Total NISP	5	58	58	68	30	26	10	150	4	10	39	7	946	51
Percent NISP	0.3	3.8	3.8	4.5	2.1	1.8	0.7	9.9	0.3	0.7	2.7	0.5	64.0	3.4

* VT = vertebrae, MX = maxilla, DN = dentary, CP = compound bone, PT = pterygoid, PL = palatine.

† *Arizona elegans, Coluber constrictor, Coluber–Masticophis, Diadophis punctatus, Hypsiglena torquata, Lampropeltis getulus, Masticophis lateralis, Pituophis melanoleucus, Rhinocheilus lecontei, Tantilla* sp., *Thamnophis couchii* species group, *Thamnophis sirtalis, Thamnophis* sp., *Crotalus viridis.*

(Meylan, 1982). Abundance of skeletal elements in fossil assemblages depends on two major factors: (1) the species' densities in the local environment and (2) the proximity of the populations to the depositional environment (Shotwell, 1955). A third factor, the number of elements per individual, may be important because the number of body segments is variable even among lower-level taxa.

The abundance of each taxon in conjunction with its presently preferred habitats (Table 2) gives a crude indication of paleohabitat and its proximity to the site. Moreover, skull and juvenile elements are thought to represent a population near the site of deposition because of their fragile nature and greater probability of destruction if subjected to transport.

The genus *Thamnophis,* which accounts for more than 67% of the identifiable assemblage (Table 1), suggests that there may have been an aquatic habitat near the site. Most members of the *T. couchii* group are semiaquatic and feed on amphibian larvae and fish. The presence of the *T. couchii* group suggests that there was a permanent or semipermanent body of water. *Thamnophis sirtalis* suggests mesic areas. *Diadophis punctatus* inhabits relatively moist fields and woodlands (Table 2). Stream and overbank deposits in stratigraphic section (Shaw and Quinn, 1986) confirm the inference that the site was located at or near a stream with associated riparian woodland.

Four other species are well represented (Table 1) in the Pit 91 assemblage: *Pituophis melanoleucus, Crotalus viridis, Coluber constrictor,* and *Lampropeltis getulus.* These may be found today in a wide variety of habitats, but are most characteristic of chaparral and grassland associations in the western United States. The remaining species, accounting for only about 2% of the NISP (Table 1), are characteristic of semiarid or arid habitats, ranging from desert through chaparral and prairies. Their low abundance suggests either low population sizes in the immediate vicinity or that an occasional specimen found its way into the deposit from neighboring habitats. Some of these remains are abraded, which could indicate allochthonous origins, such as via stream transport. Also, a riparian woodland would provide ideal roosting and nesting sites for raptors that might forage in nearby open country.

The paleoenvironment in the region of Pit 91 appears to have consisted of two habitat components: (1) a moist riparian area near the site of deposition, inferred from the abundance of *Thamnophis* remains and the presence of stream deposits, and (2) a distal semiarid habitat, perhaps similar to modern chaparral or coastal sage associations, inferred from the presence of small numbers of *Arizona elegans, Masticophis lateralis,* and *Rhinocheilus lecontei.* Warter (1976) gives a detailed account of the flora of Pit 91. Her interpretations generally agree with those presented here.

It is noteworthy that the semiaquatic and mesic habitat snakes contributed the highest percentage of NISP and the lowest diversity (i.e., the *T. couchii* group, *T. sirtalis,* and *Diadophis punctatus*). Remains identified to only generic level (*Thamnophis* sp.) probably represent one or both of the above forms. Conversely, the species that prefer semiarid habitats are more diverse. This suggests that the riparian habitat was somewhat isolated within a more extensive semiarid region, a condition similar to the historic environment of the Los Angeles region. The presence of a permanent water source indicates a slightly moister climate, as suggested by Brattstrom (1953b).

EXTINCTIONS AND HABITAT REQUIREMENTS OF REPTILES AND AMPHIBIANS

Very few extinctions appear to have occurred among North American reptile or amphibian species at the

Table 2. **Habitat preferences of the Pit 91 snakes, based on the relative abundance of modern species in that habitat. Species names are abbreviated with the first two letters of the genus and the first letter of the species name.**

	Snake species†											
Habitats*	Th.c	Th.s	Di.p	Pi.m	La.g	Cr.v	Co.c	Hy.t	T.sp	Ar.e	Rh.l	Ma.l
FW	H‡	I	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne
RW	I	H	H	I	I	I	I	L	L	I	L	L
F	Ne	L	I	I	I	I	L	Ne	Ne	L	Ne	L
G	Ne	L	I	H	H	H	H	I	I	H	H	I
C	Ne	L	I	H	H	H	I	H	H	H	H	H
X	Ne	Ne	Ne	I	I	L	L	H	H	H	H	I

* FW = freshwater semiaquatic, RW = riparian woodland, F = forest, G = grassland, C = chaparral, X = xeric.

† *Thamnophis couchii, Thamnophis sirtalis, Diadophis punctatus, Pituophis melanoleucus, Lampropeltis getulus, Crotalus viridis, Coluber constrictor, Hypsiglena torquata, Tantilla* sp., *Arizona elegans, Rhinocheilus lecontei, Masticophis lateralis.*

‡ H = highest abundance, I = intermediate, L = lowest abundance, Ne = not expected.

end of the Pleistocene, in marked contrast to the many extinctions that occurred among large birds (Welty, 1975) and large mammals (Kurten and Anderson, 1980) at that time. About 14% of the avian species (Howard, 1962) and 39% of the mammalian species from Rancho La Brea are extinct (Stock, 1956; Akersten *et al.*, 1979). Nearly all of the extinct mammals were larger than a hare. The extinct birds were mainly large raptors and carrion eating forms. Megafaunal extinctions can be accounted for by the overkill hypothesis of Martin (1967, 1984). However, the actual impact of paleoindian hunters is not known with certainty, and the hypothesis competes with many other ecological and climatic models. One thing is certain, terminal Pleistocene events had very different effects on large mammals, small mammals, and reptiles. Eagerness to embrace the overkill hypothesis should not be allowed to obscure other factors that may have influenced the composition of the modern fauna.

Guilday (1967) argues convincingly that large mammals will disappear first during periods of rapidly changing climate in which critical habitats are reduced to small refugia or extirpated. Extinction of large scavenging birds that depended on the mammalian megafauna would naturally follow. Small mammals throughout the United States are known to have experienced substantial range fluctuations and to have occurred in faunal assemblages that are considered ecologically incompatible by modern standards (Fay, 1988). Thus, although few small mammal species went extinct at the end of the Pleistocene, they were obviously affected by the climatic changes that occurred but to a lesser extent than the megafauna (Martin, 1967, 1984).

If fluctuating resource levels and habitat size contributed to the alteration of the endothermic fauna seen in the terminal Pleistocene, the low resource requirements of small ectotherms suggests that they will be the last species to be affected by these forces. Pough (1983) and Regal (1983) characterize amphibians and reptiles, and lizards, respectively, as components of low energy-flux systems. Many reptiles and amphibians specialize in low productivity habitats, such as deserts, that are considered suboptimal or harsh for endothermic species. Furthermore, metabolic rates of ectothermic species are usually modulated by changing weather conditions such that annual periods of inhospitable weather can be readily accommodated, as during aestivation. Thus, trends toward increasing aridity (Van Devender and Spaulding, 1979) and seasonality (Graham and Lundelius, 1984; Guthrie, 1984) during late Pleistocene and early Holocene times probably favored many reptiles by increasing the areas that they could exploit more effectively than could endothermic competitors. In addition, low resource requirements per individual may allow ectotherms to maintain viable populations in small refugia with insufficient area (hence resources) to support viable populations of similar-sized endotherms, let alone megafauna.

If this hypothesis is true, then there may be a basic dichotomy between endothermic and ectothermic faunas in the rate of change in their species compositions. Faunal turnover would be much more rapid among endotherms, whereas ectotherms would have greater species longevities. If extant species of mammals and reptiles are followed backward through time via literature records on fossil occurrences, it is readily observed that the origins of extant mammal species are much nearer the present than are the origins of extant reptile species. In fact, most mammal species that are represented in the fossil record appear to span shorter time intervals than do reptile species (LaDuke, 1987).

Thus, it is probably no coincidence that when terrestrial mammals and reptiles are considered together, the amount of biological disruption experienced by each species (i.e., extinction, morphological change, and range modification) at the end of the Pleistocene appears to be correlated with the absolute quantity of resource requirements of individuals of that species.

Giant tortoises (*Geochelone*) are not ecologically comparable to other North American reptiles because of their large size and herbivorous habits. They regularly require large masses of vegetation for maintenance and growth. Thus, their resource requirements may be more comparable to those of a medium-sized endotherm. Hibbard (1960) suggested that these tortoises went extinct in North America as a direct result of physical rather than biotic influences (i.e., low winter temperatures coupled with the inability to hibernate). It is also known that paleoindians preyed on at least one giant tortoise (Clausen et al., 1979).

Fay (1984, 1986, 1988) suggests an alternative to the above model. Amphibians and reptiles may be capable of acclimating to climatic change more readily than mammals. This would also produce the pattern above but does not exclude the resource hypothesis. The two phenomena acting in concert would accentuate the pattern of increased span of species life. These various hypotheses are representative of a field of study rife with opportunities for further research.

Alternatively, the pattern of more gradual change exhibited by ectotherms could have been produced by an inability of paleontologists to discern species with the precision that is often achieved with mammals. Paleoherpetologists must often use elements that are less reliable than the morphologically labile mammalian teeth in making identifications. Thus, we might expect amphibians and reptiles to have a greater apparent species longevity. Carefully controlled quantitative studies of biometric variability in living and fossil reptiles may help to resolve these issues.

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JANET HAIG AND PATSY A. MCLAUGHLIN

TWO NEW HERMIT CRABS OF THE GENUS *PAGURUS* (*PROVENZANOI* GROUP) (CRUSTACEA, ANOMURA, PAGURIDAE) FROM THE EASTERN PACIFIC, WITH NOTES ON THEIR ECOLOGY

ALAN W. HARVEY AND PATSY A. MCLAUGHLIN

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THE IDENTITY OF *PAGURUS LEPIDUS* (BOUVIER) (DECAPODA, ANOMURA, PAGURIDAE) AND DESCRIPTION OF A NEW EASTERN PACIFIC INSULAR SPECIES

JANET HAIG[1] AND PATSY A. MCLAUGHLIN[2]

ABSTRACT. The name *Pagurus lepidus* (Bouvier) has been assigned to several small closely allied hermit crab species in the Eastern Pacific. *Pagurus lepidus* is a member of the *provenzanoi* group of *Pagurus,* an informal group of the genus that has both Western Atlantic and Eastern Pacific representatives. Because species from the Pacific have not received the systematic attention afforded their Atlantic relatives, several species of the group from the Gulf of California, Mexico, western Central America, and Eastern Pacific atolls and archipelagos have been commonly referred to only as the *Pagurus lepidus* species complex.

Pagurus lepidus, herein redescribed and illustrated, is a geographically variable species, whose range is now documented from the Gulf of California, Mexico, to Peru. Certain specimens previously assigned questionably to *P. lepidus* are also described and illustrated as a new insular species, *P. nesiotes,* distributed from Clipperton Island to the Galapagos Archipelago.

INTRODUCTION

Pagurus lepidus (Bouvier) is one of the few named pagurids occurring in the shallow waters of the Gulf of California, Mexico, and as a result this name has been applied, at one time or another, to virtually all of the region's small hermit crabs with striped walking legs. Although it was Bouvier (1898) that first described *Pagurus lepidus* (as *Eupagurus*) from a collection made in the Gulf of California, the first documented capture of this species is from the Bay of Panama by J.G.H. Kinberg, zoologist aboard the Royal Swedish frigate "Eugenie", under the command of C.A. Virgin, during her circumnavigation of the world from 1851 to 1853. It remained, cataloged only as *Eupagurus* sp., in the collections of the Naturhistoriska Riksmuseet, Stockholm, until its recent rediscovery.

Some years ago one of us (JH) began to notice distinct, albeit subtle, differences in the color patterns among the Gulf of California pagurids. Subsequent examinations revealed certain morphological differences as well. One character in particular, the lateral marginal plate of the telson, was found to differ among specimens. For example, in certain specimens the lateral margin was simply a weakly calcified or chitinous plate (Fig. 1A). In others this plate was terminated anteriorly by a prominent spine (Fig. 1B). In still others, this plate was composed of distinct individual spinules (Fig. 1C) or spines (Fig. 1D). These differences were found to correlate with some of the observed differences in color patterns.

Bouvier's description of *P. lepidus* was based on two specimens collected at "Baie de la Paz, Basse Californie", Mexico, and whereas his description was relatively detailed, it dealt with general characters and color patterns that have since proved to be analogous among several species. *Pagurus lepidus* is a moderately common intertidal to shallow subtidal species in the Gulf of California; however, it is not alone in exhibiting a preference for this habitat. Several additional, but undescribed, taxa have been confounded with this species (e.g., Haig *et al.,* 1970; Ball and Haig, 1974; Snyder-Conn, 1980). We have now had an opportunity to examine the syntypes of *Pagurus lepidus* and have found that only two of the subsequently published reports of this species (i.e., Glassell, 1937; Forest and de

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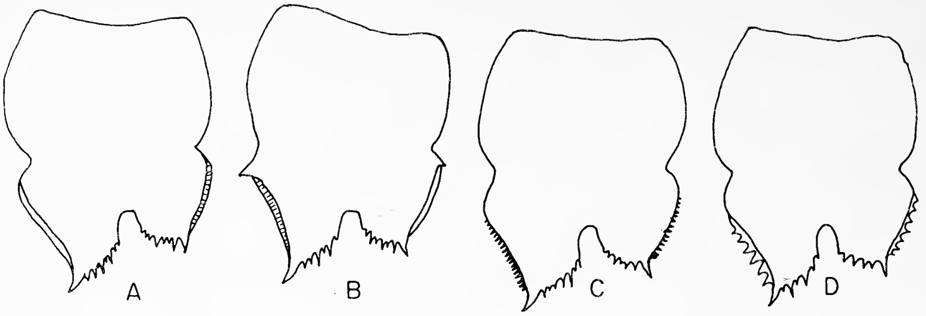

Figure 1. Diagrammatic telson types: **A,** simple entire or weakly marked lateral marginal plates on posterior lobes; **B,** entire or weakly marked lateral marginal plates of posterior lobes delineated by anterior spine(s); **C,** lateral marginal plates of posterior lobes divided into individual spinules; **D,** lateral marginal plates divided into prominent spines.

Saint Laurent, 1968) referred exclusively to this taxon. Specimens included in these other reports, as well as supplemental collections, represent new species that will be described in forthcoming publications.

Not only does *P. lepidus* exhibit the sexual dimorphism common to other members of the *provenzanoi* group of *Pagurus* (see McLaughlin, 1975), it has been found to also exhibit morphological variations correlated to its geographic distribution. Consequently, only a few characters and specific differences in color patterns can be used to separate *P. lepidus* from the other sympatric species of the subtropical and tropical Eastern Pacific. From the material available we have found that intraspecific variation in *P. lepidus* considerably exceeds that of most Western Atlantic species of the group as described by Lemaitre *et al.* (1982).

Chace (1962) reported ?*Pagurus lepidus* from Clipperton Island, noting that his specimens agreed in most characters with Bouvier's (1898) description but differed in the shape of the ocular acicles. We have reexamined the Clipperton Island specimens, and although clearly belonging to the *provenzanoi* group, they are distinct from all of the Gulf of California species of the *lepidus* complex and are herein described as *Pagurus nesiotes* new species.

MATERIALS

Materials for this study have come from the Crustacea collections formerly of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), American Museum of Natural History (AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution (USNM), Natural History Museum of Los Angeles County (LACM), Naturhistoriska Riksmuseet, Stockholm (NHRM), Smithsonian Oceanographic Sorting Center (SOSC), and from individual collectors. Specimens will be returned to their repositories of origin and/or deposited in these museums and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

SYSTEMATICS

Pagurus lepidus (Bouvier, 1898)

Figures 2A–G, 3A–G

Eupagurus lepidus Bouvier, 1898:381.

Pagurus lepidus: Glassell, 1937:256; Chace, 1962:623 by implication (in part, see discussion); Forest and de Saint Laurent, 1968:116; Haig *et al.*, 1970:19 (in part, see discussion); Ball and Haig, 1974:102 (in part, see discussion); Snyder-Conn, 1980:283 (in part, see discussion).

Pagurus(?) *lepidus:* Moran, 1984:76, fig. 5.

?*Pagurus lepidus:* Von Prahl, 1986:96 (see discussion).

Not ?*Pagurus lepidus:* Chace, 1962:623, fig. 2 (= *Pagurus nesiotes,* new species).

LECTOTYPE (herein selected). ♂ (SL 2.1 mm), MNHN, Paris, Pg 246, 1898. **Type locality.** Baie de la Paz, Basse Californie [Baja California Sur], Mexico.

PARALECTOTYPE. ♂ (SL = 2.2 mm), MNHN, Paris, Pg 246, 1898.

OTHER MATERIAL EXAMINED. Gulf of California, Sonora, Mexico: Puerto Peñasco, 1 ♂ (SL = 1.1 mm), November 23–26, 1955, collector E.P. Chace, USNM 99802; Puerto Peñasco, 1 ♂ (SL = 2.4 mm), intertidal, July 17, 1967, collector P. Pickens, AHF 2791-01 (LACM 67-241.1); Norse Beach, 3 ♂, 1 ovigerous ♀ (SL = 1.7–2.6 mm), Choya Bay Survey station 66033, shore, August 15, 1966, collectors T. & B. Burch, AHF 2789-01 (LACM 66-354.1); Norse Beach, 3 ♂, 2 ♀ (SL = 1.2–2.4 mm), shore, December 2, 1967, collector A. Havens, AHF 2790-01 (LACM 67-198.2); Coquina Reef, 1 ♂, 4 ovigerous ♀ (SL = 2.0–2.8 mm), lower intertidal, June 1973, collectors A. Kuris, M. Brody, E. Snyder, AHF 2792-01 (LACM 73-215.1); Station Beach, 3 ♂, 1 ♀, 2 ovigerous ♀ (SL = 2.0–2.4 mm), intertidal, July 27, 1988, collector A. Harvey, NHRM, RMNH D 38112; Station Beach, 9 ovigerous ♀ (SL = 1.4–2.1 mm), intertidal, December 1988, collector A. Harvey, USNM 244080; Turner's Island south of Tiburon Island, 3 ♂ (SL = 1.7–2.0 mm), "Velero III" station 1042-40, shore, January 24, 1940, AHF 2787-01 (LACM 40-14.5). Bahía La Paz, Baja California Sur, Mexico,

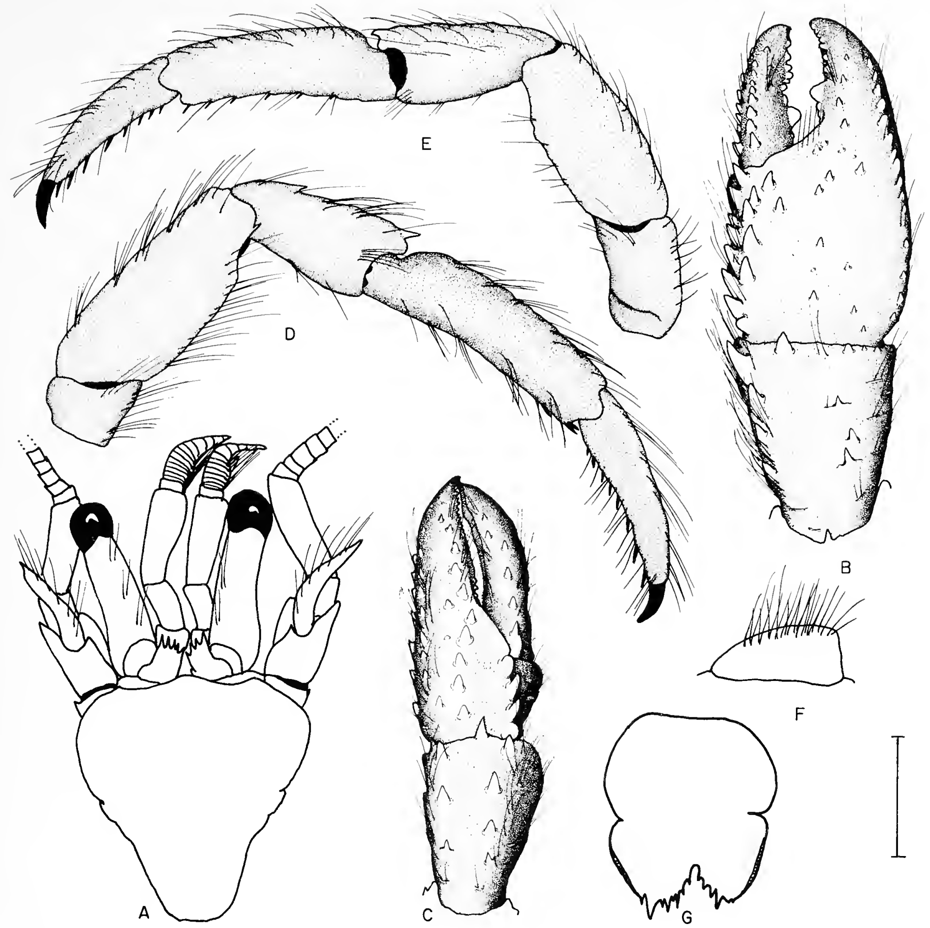

Figure 2. *Pagurus lepidus* (Bouvier) lectotype [MNHN Pg 24, Baja California Sur, Mexico]: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** right 2nd pereopod (lateral view); **E,** left 3rd pereopod (lateral view); **F,** anterior lobe of sternite of 3rd pereopods; **G,** telson. Scale = 1 mm (A–E) and 0.5 mm (F, G).

26°50′45″N, 111°54′20″W, 3 ♂, 2 ovigerous ♀ (SL = 1.4–2.0 mm), Templeton Crocker Expedition "Zaca" station 144 D-1, 2 m, April 15, 1936, AMNH 12574. South Bay, Isla Cedros, W. Baja California Sur, Mexico, 1 ♀ (SL = 2.1 mm), "Velero III" station 287-34, 20–30 m, March 10, 1934, AHF 2786-01 (LACM 34-161.3). Punta Pequeña, Bahía de San Juanico, W. Baja California Sur, Mexico, 2 ♂, 1 ♀ (SL = 1.6–2.7 mm), "Magbay" Expedition, 3.5 m, February 8, 1964, collectors T. Hopkins, T. Scanland, AHF 2788-01 (LACM 64-176.1). Outside Bahía Magdalena, W. Baja California Sur, Mexico, 1 ♂ (SL = 2.2 mm), "Magbay" Expedition, 20 m, February 1, 1964, collectors T. Hopkins, T. Scanland, AHF 2795-01 (LACM 64-177.1). Bahía Tenacatita, Jalisco, Mexico, 19°17′N, 104°50′W, 1 ♂ (SL = 1.7 mm), "Te Vega" Expedition station 18-22, 1.5–3.5 m, May 27, 1968, collector P. Smith, AHF 2629-03 (LACM 68-372.1). Mizata, Depto. La Libertad, El Salvador, 2 ♂ (SL = 1.5, 1.7 mm), shore, December 6, 1978, collector D. Moran, AHF 1623-01 (LACM 78-212.1). Gulf of Panama, 1 ♂ (SL = 1.5 mm), "Eugenie" Expedition, 1852, NHRM 7177. Panama Bay, Panama, 1 ♂, 1 ♀, 1 ovigerous ♀ (SL = 1.2–1.3 mm), December 12, 1981, collector T. Spight, AHF 2793-01 (LACM 81-129.1). Punta Paitilla, Panama, 8°58.1′N, 79°31′W, 1 ovigerous ♀ (SL = 1.5 mm), "Te Vega" Expedition station 18-14b, 2 m, May 6, 1968, collector E. Ball, AHF 2616-05 (LACM 68-373.1). Atacames Reef, Ecuador, 1 ♀ (SL = 1.2 mm), "Te Vega" Expedition station 18-8, 8 m, April 23, 1968, collectors M. Youngbluth, P. Smith, AHF 2607-03 (LACM 68-377.1). Manta, Ecuador, 0°56′S, 80°43′W, 1 ♂ (SL = 1.7 mm), "Te Vega" Expedition station 18-5, 6.3 m, April 19, 1968, collectors E. Ball, P. Smith, AHF 2605-06 (LACM 68-374.1). Punta Mandinga, Salinas, Ecuador, 2°11′S, 80°43′W, 2 ♂, 2 ovigerous ♀ (SL = 0.8–1.4 mm), "Te Vega" Expedition station 18-4, intertidal, April 16, 1968, collector E. Ball, AHF 2604-03 (LACM 68-376.1). Talara, Peru, 4°34′S, 81°07′W, 4 ♂, 4 ovigerous ♀ (SL = 1.3–1.8 mm), "Te Vega" Expedition station 18-2, 5 m, April 9, 1968, collector E. Ball, AHF 2602-02 (LACM 68-375.1).

DIAGNOSIS. Shield longer than broad. Ocular acicles multispinose. Antennal flagellum with 1–3 short setae each article and scattered longer setae. Carpus of right cheliped with 4 or 5 spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm horizontal, margin with row of protuberances or spines. Dactyli of ambulatory legs

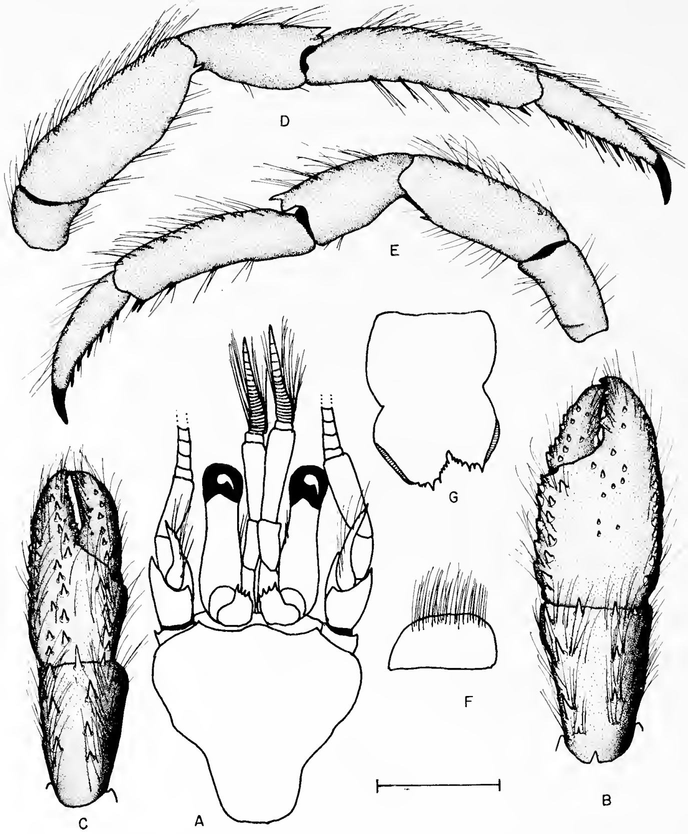

Figure 3. *Pagurus lepidus* (Bouvier) [NHRM 7177, Bay of Panama]: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** right 2nd pereopod (lateral view); **E,** left 3rd pereopod (lateral view); **F,** anterior lobe of sternite of 3rd pereopods; **G,** telson. Scale = 1 mm (A–E) and 0.5 mm (F, G).

each with 5–9 corneous spines on ventral margin; carpi each with spine at dorsodistal margin and P_2 also with dorsal surface usually slightly spinulose or with 1 small spine proximally. Posterior lobes of telson with terminal margins oblique, lateral margins with narrow, undifferentiated plate and without delimiting spine anteriorly. In life, chelipeds with distal four-fifths of fingers greenish-white or white; meri with pinkish-white band distally. Ambulatory legs with greenish-brown longitudinal stripes.

REDESCRIPTION. Shield longer than broad, anterior margin between rostrum and lateral projections concave, posterior margin roundly truncate. Rostrum obsolete, unarmed; lateral projections unarmed or with minute terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles one-half to four-fifths length of shield, broadened basally and with corneae slightly dilated, with longitudinal row of tufts of setae on dorsomesial face. Ocular acicles somewhat subquadrate, with 3–6 terminal marginal spines; separated basally by approximately one-half basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by one-fourth to one-half length of ultimate segment. Ultimate segment with scattered setae dorsally and ventrally. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral face.

Antennal peduncles slightly overreaching corneae. Fifth and 4th segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins occasionally with accessory small spine and with long or moderately long setae; dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally, particularly apparent in small individuals, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 1–3 short setae or bristles on every article and frequently also with scattered longer setae (1–2 articles in length).

Right cheliped with dactylus equal to or as much as one-half again as long as palm. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus varying from 1 strong calcareous tooth in proximal half and small calcareous teeth distally to 1–3 small calcareous teeth proximally and row of corneous teeth distally, terminating in corneous tip. Cutting edge of fixed finger with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth interspersed with small calcareous teeth in distal half or only with alternating calcareous and corneous teeth, terminating in small calcareous or corneous claw. Dactylus overlapped by fixed finger. Dorsomesial margin of dactylus with row of small acute spines and long setae, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long stiff setae, ventral surface with tufts of long stiff setae. Palm one-half to two-thirds length of carpus; dorsomesial margin with irregularly double row of spines, strongest proximally, dorsal surface with numerous tufts of long stiff setae and varying in armature from scattered spinules or small spines and median inverted V-shaped row of stronger spines to only few scattered spinules, dorsolateral margin with low protuberances proximally becoming row of small spines on fixed finger or row of spines increasing in size on fixed finger. Fixed finger often with irregular row of small spines. Carpus slightly shorter to slightly longer than merus; dorsomesial margin with row of 4 or 5 rather widely spaced spines, 1 or 2 spines on or near distal margin, dorsal surface unarmed or slightly spinulose and with tufts of long setae, dorsolateral margin unarmed or with row of spines, distolateral margin sometimes with small spine and ventrolateral distal angle usually with acute spine, lateral and mesial faces with scattered setae. Merus subtriangular; dorsal margin with few tufts of setae and often small spine on distal margin, ventromesial and ventrolateral margins unarmed or with 1 small spine on ventromesial margin and short row of small spines on ventrolateral margin in distal half. Ischium unarmed.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Cutting edge of dactylus with row of corneous teeth, terminating in corneous claw; dorsal surface with row of stiff setae near cutting edge, midline with row of spines and frequently 2nd row of longer setae, dorsomesial margin with low protuberances or row of small spines; mesial margin and ventral surface also with tufts of long setae. Palm one-half to two-thirds length of carpus; midline armed with irregular double row of spines, extending onto the fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with row of tufts of long setae and usually row of small spines in ventral half and 2nd row of protuberances or spines and tufts of long setae marginally, dorsomesial face horizontal with margin marked by row of protuberances or moderate to strong spines and tufts of setae, mesial face with low protuberances and tufts of setae. Carpus usually equaling merus in length; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae. Merus triangular; dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with row of spines, usually only on proximal half in large males, ventral surface with long setae laterally. Ischium with acute spine at ventrolateral distal angle and often also with row of small spines on ventromesial margin.

Second and 3rd pereopods with dactyli and propodi varying in length and width; 3rd right usually longest and most slender, 3rd left shortest and broadest. Dactyli slightly less than half to almost equaling length of propodi, approximately one-third to one-fifth as broad (proximally) as long, terminating in strong curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 5–9 corneous spines and long stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long stiff setae, ventral surfaces each with pair of corneous spines at distal margin and 1 additional spine in distal third (2nd) or 1st, 2nd, or 1st and 2nd paired spines followed by row of widely spaced corneous spines proximally (3rd). Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low protuberances, 2nd usually slightly spinulose and/or with small spine developed proximally, also with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins; ventral margins with low protuberances and tufts of long setae or with small spine on ventrolateral margin distally (2nd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular, unarmed. Fourth pereopods with small preungual process at base of claw; propodal rasp with 5–8 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long dense setae.

Exopod of left uropod with row of 6–10 thick setae on inner margin. Telson with terminal margins oblique, each armed with row of spines, 1 or 2 usually stronger and sometimes corneous-tipped; lateral margins delimited by narrow plate, no anterior spine.

COLOR. Northern Populations in Life. Antennal flagellum with 2 transparent articles proximally followed by greenish-brown articles interrupted every 3 articles by 1 white or transparent article. Shield transparent centrally with mottled green flecked with yellow marginally and posteriorly. Ocular peduncles mottled greenish-brown on white with flecks of pink distally and dorsal patch of pink proximally, corneae crimson; acicles with reddish-brown flecks on greenish-white background, distal margin without flecks. Antennular peduncles with ultimate and penultimate segments greenish-white with red flecks, basal segment greenish-white in distal half and pink in proximal half. Chelipeds greenish-brown or olive with white spines often tinged with dark red-brown basally on palms and carpi, distal four-fifths of fingers white or greenish-white, meri with distal pinkish-white band and remainder mottled greenish or olive flecked with reddish-brown. Ambulatory legs with dactyli greenish-white distally and greenish-brown with short darker greenish-brown longitudinal stripes proximally; propodi with pink patch on lateral face near distal margin and pink band proximally, greenish-brown longitudinal stripes on greenish or grayish-white background centrally; carpi with light pink distally and dark greenish-brown longitudinal stripes on greenish or grayish-white background in proximal two-thirds; meri pink proximally and distally with dark greenish-brown longitudinal stripes on light green or gray background centrally (PAMcL, unpublished data).

Southern Population in Life. Antennal flagellum usually with 3 olive drab articles interrupted by 1 white article. Shield mottled olive drab and white. Ocular peduncles mottled white and olive drab, corneae red. Antennular peduncles with white patch dorsally and green bands proximally on ultimate segment and dark green band distally on penultimate segment. Chelipeds with white dactyli, and fixed fingers, palms, carpi, and meri mottled olive drab and white. Ambulatory legs with distal halves of dactyli white, proximal halves with short brown stripes; propodi with longitudinal brown stripes on pale background, with yellow spots between stripes; carpi and meri with dark brown longitudinal stripes on pale background (E.E. Ball, field notes).

In Preservative. Palms and carpi of chelipeds red-orange, fingers white. Stripes of ambulatory legs reddish-orange. All color fading with time to straw yellow.

DISTRIBUTION. West Pacific coastal Baja California, Baja California Sur, and Gulf of California, Mexico to Peru; intertidal to 20 m.

AFFINITIES. As previously indicated, *Pagurus lepidus* is the name that has been applied to at least six small hermit species occurring in the shallow waters of the Eastern Pacific. All of these species are similar in morphology and color patterns. Distinctions among the species can only be made by careful structural examination or comparisons of colors in living animals. These structural characters include the multispinose condition of the ocular acicles, as opposed to the simple, single-spined condition; the presence of short setae on the articles of the antennal flagellum rather than long (more than three articles in length), randomly placed or serially paired setae; and the horizontal as opposed to sloping dorsomesial face of the left chela. Although *P. lepidus* exhibits considerable variations over its geographic range, it can be distinguished from the majority of similarly striped species by the absence of an anterior spine on the lateral margin of the posterior telsonal margin plates and by the almost horizontal dorsomesial surface of the left chela. The setation of the antennal flagellum, consisting of short and scattered moderately long (one to two articles in length) in *P. lepidus* is diagnostic only when compared with species having truely long and/or serially paired setae.

VARIATIONS. There are distinct differences between the specimens of *P. lepidus* collected in the Gulf of California and the outer coast of the Baja California Peninsula and those from Central and South America. If specimens from the extremes of the range are examined, these differences appear significant enough to suggest that two distinct taxa may be involved. However, despite the relative paucity of material from the central portion of the range (southern Mexico and northern Central America), we have observed enough character clines to convince us that we are dealing with one highly variable species.

The Puerto Peñasco, Sonora, Mexico, region was the source of more than half of the specimens examined. A characteristic of *P. lepidus* from this region is a difference in the length–width ratios of the dactyli of the left and right 3rd pereopods, regardless of overall body size. Proximally the 3rd left dactylus is one-third to one-fourth as broad as long, whereas the 3rd right is usually only one-fourth to one-fifth as broad as long. At this apparent northern end of its range, *P. lepidus* reaches a large overall size (shield length in excess of 2.5 mm), and with increasing size additional morphological changes in the ambulatory legs usually occur that have not often been observed in the Central and South American population. This is particularly apparent in the length relationships of the dactyli to their respective propodi. In small individuals (shield lengths less than 1.7 mm) within this northern population, the dactyli, especially the 3rd left, usually are from three-fourths to nine-tenths the length of the propodi; both segments are visually quite short. With increasing size, the dactyli become more slender and the propodi elongate. In specimens with shield lengths greater than 2.0 mm, the length of the dactylus varies from two-thirds to sometimes less than one-half the length of the propodus. Concurrent with changes in dactylar length and width are changes in the armature of the ventral margins. Small specimens commonly have six or seven corneous spines on the ventral margins of the dactylus. With increasing size, the number of spines increases to seven to nine or occasionally 10. Generally the armature of the right chela consists of scattered moderately strong spines on the dorsal surface of the palm, with an inverted V of stronger spines medianly. However, with increasing size, the strength of the chela armature is reduced, becoming virtually obsolete in very large specimens. Frequently the ischium of the left cheliped is armed with a row of small spines.

None of the specimens collected in the southern half of the range of *P. lepidus* had a shield length in excess of 2.0 mm, and this may be the reason that no marked changes in length–width ratios in the dactyli of the right and left 3rd pereopods were observed. The length relationships between propodi and dactyli, however, were different in this smaller southern population. Generally the dactyli were two-thirds to three-fourths as long as the propodi. Similarly, the number of spines on the ventral margins of the dactyli varied from five to six. Few specimens exhibited strong spination on the dorsal surface of the right chela, and no spines were observed on the ventral margin of the ischium of the left chela. In the color descriptions reported for the two populations, slight variations also could be detected.

However, there are exceptions. For example, the only notable difference between the lectotype (Fig. 2A–G) and the Panamanian specimen collected by the "Eugenie" (Fig. 3A–G) is the number of dactylar spines on the ventral margins of the 2nd and 3rd pereopods. Among the northern populations a few specimens of comparable size to those found farther south, including one specimen from Puerto Peñasco, had proportionally longer dactyli and only five spines on the ventral margins. Similarly, one of the southern specimens had an appreciably more slender 3rd right dactylus with seven spines on the ventral margin. Geographically correlated differences were apparent among the 58 specimens we critically examined, but there was a sufficient number of intermediate conditions to suggest a clinal variation from north to south.

DISCUSSION. Bouvier's (1898) description included many of the general characteristics of most species assignable to the "*Pagurus lepidus*" complex, e.g., obtusely rounded rostrum, multispinose ocular acicles, spinulose chelipeds, striped ambulatory legs. Bouvier was not aware of the number of distinct taxa in the region that could be described by these same characters.

Glassell (1937) did not provide a description of his specimens other than certain characters cited in his key to distinguish this taxon from other *Pagurus* species collected by the Templeton Crocker Expedition. None of these characters will separate *P. lepidus* from the other Eastern Pacific species of the complex. Although Glassell did describe color patterns remaining in his preserved material, these patterns fit at least three species of the complex. We have been able to reexamine these specimens now housed in the collection of the American Museum of Natural History and can confirm their identity as *P. lepidus.*

In his questioned referral of the Clipperton Island specimens to *P. lepidus,* Chace (1962) used for comparison a lot of specimens in the national collections that had previously been identified as *P. lepidus.* We have reexamined this lot from Puerto Peñasco, Mexico (USNM 99802), and found that only one of the eight specimens actually is *P. lepidus.* The remaining seven specimens represent an undescribed species (Harvey and McLaughlin, 1990). Chace (1962) recognized that his Clipperton Island specimens possessed ocular acicles with a single terminal spine, whereas the ocular acicles of Bouvier's (1898) *P. lepidus* and the Puerto Peñasco specimens had multispinose acicles. Although he was unwilling to designate a new species on the basis of one lot of comparative material, he suspected that the Clipperton Island specimens might, in fact, represent a distinct taxon. We have now been able to confirm that suspicion.

Haig *et al.* (1970) and Ball and Haig (1974) recognized that several species were probably confounded under the name *P. lepidus.* However, as they did not have access to Bouvier's (1898) material at that time, they were unable to accurately distinguish among these taxa. We have reexamined the materials included in both of these reports and have found that one lot of specimens from Punta Pequeña, Bahía de San Juanico, Baja California Sur, Mexico (Haig *et al.,* 1970), and specimens from Mexico, Ecuador, and Peru (Ball and Haig, 1974) do represent *P. lepidus.*

Snyder-Conn (1980) gave a generalized description of *P. lepidus* but repeated Haig's opinion that this species had been confounded with several others represented in the Gulf of California fauna. Although one specimen that she collected has proved to be *P. lepidus,* it is probable that she included other local taxa in her report.

Moran (1984) provided notes and illustrations of the hermit crabs he identified as *Pagurus* (?) *lepidus.* However, he remarked that his identification was doubtful because this was one of several closely related species of the genus that were in need of revision. We have been able to examine two of his five specimens. These, at least, do represent *P. lepidus.*

Pagurus lepidus was among the decapods listed by Von Prahl (1986) as inhabitating a coral rubble community in Utria Sound, Colombia. *Pagurus lepidus* is known from this type of habitat, and the locality is within its distributional range. However, Von Prahl's report can only questionably be included in the synonymy of *P. lepidus* as other *provenzanoi* group species have similar habitats and ranges. Von Prahl was unfortunately killed in a plane crash in 1989, thus his material has not been available for verification.

More recently five other references to "*Pagurus lepidus*" have come to our attention, i.e., Westervelt (1967), Romero (1982), Rodriguez de la Cruz (1987), Romero and Carvacho (1988), and Villalobos Hiriart *et al.* (1989). None have been cited in the synonymy of this species as it is impossible to know which, or how many, of the species heretofore confounded under the name *P. lepidus* may be represented by these reports.

Pagurus nesiotes new species

Figures 4A–G, 5A–F

?*Pagurus lepidus:* Chace, 1962:623, fig. 2. Not *Pagurus lepidus* (Bouvier).

Pagurus sp.: Birkeland *et al.,* 1975:67.

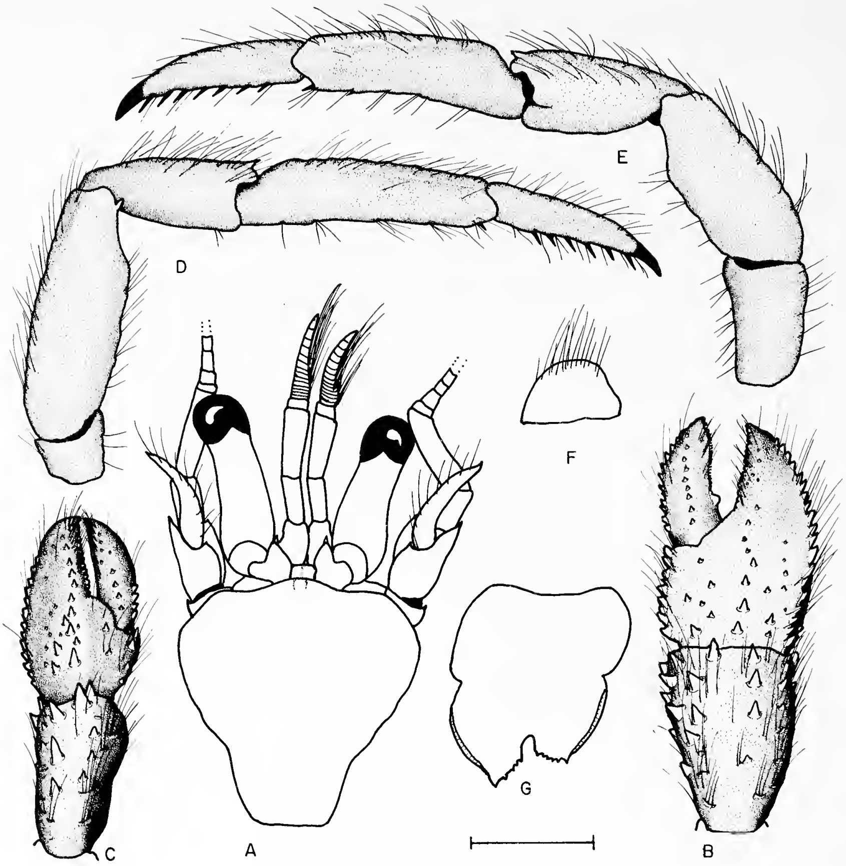

Figure 4. *Pagurus nesiotes* new species, paratype [USNM 22194, Clipperton Island]: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** right 2nd pereopod (lateral view); **E,** left 3rd pereopod (lateral view); **F,** anterior lobe of sternite of 3rd pereopods; **G,** telson. Scale = 1 mm (A–E) and 0.5 mm (F, G).

HOLOTYPE. Ovigerous ♀ (SL = 2.0 mm). **Type locality.** Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 110975.

PARATYPES. 1 ♂, 1 ovigerous ♀ (SL = 1.8, 1.4 mm). Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 221940. Malpelo Island, Colombia, 3 ♂ (SL = 1.6–1.8 mm), subtidal, February 29–March 3, 1972, collector C. Birkeland, AHF 728 (LACM 72-345.1). Galapagos Islands: Charles Island, 1 ♀ (SL = 1.5 mm), "Eugenie" Expedition, 15–22 m, May 15–17, 1852, NHRM 7167; Post Office Bay, Charles Island, 1 ♂ (SL = 1.3 mm), "Velero III" station 167-34, 30 m, January 19, 1934, AHF 3424 (LACM 34-40.4); Post Office Bay, Charles Island, 3 ♂ (SL = 1.2–1.6 mm), "Velero III" station 193-34, 15–18 m, January 27, 1934, AHF 3426 (LACM 34-67.4); off James Bay, James Island, 1 ♂ (SL = 1.4 mm), "Velero III" station 182-34, 60 m, January 24, 1934, AHF 3425 (LACM 34-56.2); west side Academy Bay, Santa Cruz Island, 3 ♂, 1 ♀, 1 ovigerous ♀ (SL = 1.3–2.4 mm), 3–8.5 m, August 25–27, 1976, collector P. Abrams, formerly AHF 762, now divided between MNHN, RMNH D 38105; 00°54′11″S, 90°18′15″W, 12 ♀, 3 ovigerous ♀, 5 juveniles (SL = 0.6–2.2 mm), "Anton Bruun" station 16/66112, 8–10 m, May 19, 1966, collector S. Earle, SOSC; south end of Darwin (Culpepper) Island, 2 ♂, 2 ♀ (SL = 1.2–2.2 mm), approximately 11 m, May 13, 1984, LACM 84-29.4; south side of Darwin (Culpepper) Island, 2 ♂ (SL = 1.3, 2.3 mm), 9–13 m, May 13, 1984, LACM 84-29.5; northwest side of Pinta (Abingdon) Island, 1 ♂, 1 ovigerous ♀ (SL = 1.8, 2.0 mm), 10–13 m, May 17, 1984, LACM 84-37.1; off Punta Espejo, east end Marchena (Bindloe) Island, 1 ovigerous ♀ (SL = 1.9 mm), 12 m, May 11, 1984, LACM 84-26.1.

DIAGNOSIS. Shield as long or longer than broad. Ocular acicles terminating in single spine. Antennal flagellum naked or with 1–4 very short setae every 1–4 articles. Carpus of right cheliped with irregular double row of spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm strongly sloping, margin usually spinulose or spinose. Dactyli of ambulatory legs with 6–10 corneous spines on ventral margins; carpi each usually with spine at dorsodistal margin. Posterior lobes of telson with terminal margins oblique to rounded, lateral margins with narrow plate undifferentiated or with individual denticles clearly distinguishable, no delimiting spine anteriorly. In preservative, chelipeds with finger tips white, carpal and meral segment solidly

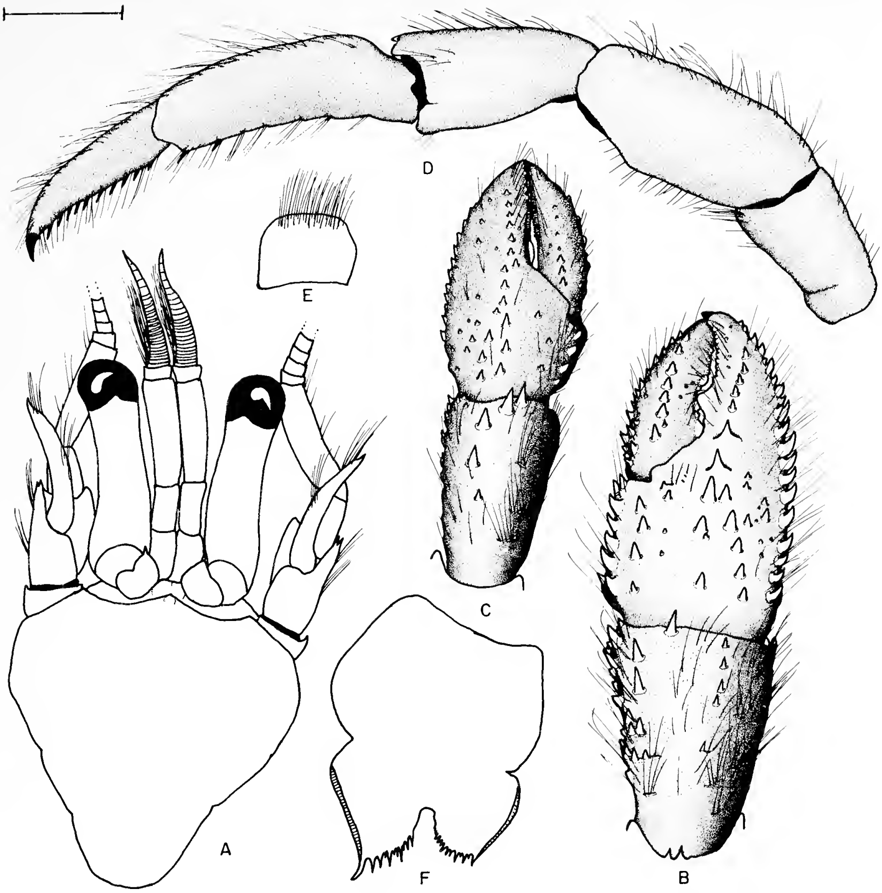

Figure 5. *Pagurus nesiotes* new species, paratype [formerly AHF 762; now RMNH D 38105; Galapagos Islands]: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** left 3rd pereopod (lateral view); **E,** anterior lobe of sternite of 3rd pereopods; **F,** telson. Scale = 1 mm (A–E) and 0.5 mm (F).

colored. Ambulatory legs each with longitudinal stripes and additional broad distal band on merus.

DESCRIPTION. Shield equal to or longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum obsolete or obtusely triangular, sometimes weakly produced; lateral projections broadly rounded or obtusely triangular, unarmed. Dorsal surface of shield with scattered setae.

Ocular peduncles one-half to four-fifths shield length, broad basally, and usually tapering to very slightly dilated corneae. Ocular acicles subtriangular to subovate, terminating in 1 marginal or submarginal spine, rarely with 2nd spine in close proximity; separated basally by two-thirds basal to slightly more than basal width of 1 acicle; interocular lobes weakly developed.

Antennular peduncles equaling or exceeding ocular peduncles by up to one-half length of ultimate segment. Ultimate segment with few setae on dorsal surface. Penultimate segment with few scattered setae. Basal segment with 1 acute spine on dorsolateral margin.

Antennal peduncles overreaching corneae by less than one-fourth to more than one-third length of ultimate segment. Fifth and 4th segments with few tufts of setae. Third segment with acute spine at ventrodistal margin, partially obscured by tuft of setae. Second segment with dorsolateral distal angle produced, terminating in 1 or 2 spines, lateral margin sometimes with small spine distally and with long setae; dorsomesial distal angle unarmed or with small spine, mesial face with scattered setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in usually acute spine, mesial margin with moderately long setae. Antennal flagellum naked or with 1–4 very short setae every 1–4 articles.

Right cheliped with dactylus one-fourth to one-half again as long as palm. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of very small calcareous teeth distally, terminating in small corneous claw. Cutting edge of fixed finger with 1 very prominent broad tooth proximally and small calcareous teeth distally, terminating in corneous tip. Dactylus equaling or exceeding length of propodus by approximately one-fourth own length with single or double row of small acute spines on dorsomesial margin proximally but sloping ventrally to tip, dorsal surface somewhat elevated in midline and armed with row of strong spines and long setae, mesial and ventral surfaces with scattered long setae. Palm equaling or two-thirds the length of carpus; dorsomesial margin with irregular row of acute strong spines and often 2nd adjacent row, dorsal surface with scattered small spines, 2 rows of strong spines occasionally forming inverted V in midline and extending onto fixed finger as row of smaller spines, dorsolateral margin with row of moderately weak to strong spines, decreasing in size on fixed finger, surfaces with scattered long setae. Carpus equaling or slightly longer than merus; dorsomesial margin with double, sometimes irregular, row of spines, 1 or 2 spines on or near distal margin, dorsal surface with row of smaller spines laterad of midline, tending to become obsolete in large individuals, dorsolateral margin not delimited or with row of small spines, lateral face with tufts of long setae, laterodistal margin often with 1 or 2 spines dorsally, ventrolateral margin usually with 1 or 2 spines distally, mesial face with scattered setae. Merus subtriangular; dorsal margin with tufts of setae, distal margin with 1 or 2 spines, ventromesial and ventrolateral margins each with row of spines, strongest laterally. Ischium unarmed or with row of small spines or low tubercles on ventromesial margin.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus one and one-fourth to twice length of palm; cutting edge with row of corneous teeth, terminating in corneous claw. Cutting edge of fixed finger with small calcareous teeth that may be replaced distally with corneous teeth. Dorsal surface of dactylus with row of small spines in proximal half near cutting edge and row of spines or spinulose tubercles on dorsomesial margin, surfaces with scattered long setae. Palm one-third to one-half length of carpus; dorsal surface with midline elevated and armed with irregular double row of strong spines, extending onto fixed finger as single row, dorsomesial face strongly sloping ventrally, armed with irregular row of very small spines or spinules in ventral half and single or double row of spines marginally, dorsomesial face strongly sloping, surface and margin each sometimes with row of moderate to strong spines or only with few small spinules, all surfaces with scattered long setae. Carpus equaling or slightly shorter than merus; dorsolateral margin with row of strong spines and tufts of long setae, dorsomesial margin with few spines or more frequently with few spinulose tubercles, distal margin usually with strong spine, lateral face sometimes spinulose, laterodistal margin usually with 2 or 3 spines, ventrolateral margin with row of strong acute spines, mesial face with scattered setae and occasionally 1 or 2 small spinules or tubercles on ventromesial margin distally. Merus triangular; dorsal margin with tufts of setae, ventromesial margin with 2 to several spines, ventrolateral margin with row of acute spines and long setae. Ischium with acute spine at ventrolateral distal angle and usually with row of small spines on ventromesial margin.

Second and 3rd pereopods similar. Dactyli one-half to two-thirds length of propodi (shortest on left 3rd and generally shorter in larger individuals), one-third to one-sixth as broad proximally as long, terminating in strong curved corneous claws, dorsal, mesial, and lateral faces all with scattered moderate to long setae, ventral margins each with row of 6–10 corneous spines and few short to moderately long setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long setae; ventral surfaces each with corneous spine at distal margin (2nd) and often 1 or 2 additional spines in distal third or occasionally row of spinules (3rd). Carpi one-half to three-fourths length of meri; dorsodistal margins each usually with 1 small spine, occasionally lacking on left 3rd, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri each with low protuberances on dorsal and ventral surfaces, lateral face of 2nd with strong acute spine at ventrodistal angle and sometimes with 1 or 2 spines on ventral margin (left). Ischia with few setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods varying from subrectangular to subsemiovate, unarmed. Fourth pereopods apparently without preungual process at base of claw; propodal rasp of 4 or 5 rows of corneous scales; dorsal margins of segments with long setae.

Exopod of left uropod with row of 3–6 thick setae and frequently 1 or 2 thinner setae on inner margin. Telson with posterior lobes subtriangular; terminal margins oblique or rounded, each armed with row of spines, largest at external angle; lateral margin with narrow plate delimited, sometimes with individual denticles clearly developed; no anterior spine.

COLOR (in formalin for 2 months). Shield and ocular acicles pale orange. Antennular peduncles purple, penultimate segment with distal orange ring; flagellum orange. Antennal peduncles orange, distal segment with longitudinal red stripe; acicle orange with white tip. Ocular peduncles pale with random purple blotches. Chelipeds orange with purple tubercles; chelae paler, with white fingers; meral and carpal segments red. Meri of 2nd and 3rd pereopods purple with broad distal orange band; carpi purple with little orange distally; proximal halves of propodi purple, distal halves white with patch of orange distally; dactyli white with purple proximally. All areas appearing purple overlaid with narrow longitudinal stripes. Fourth and 5th pereopods pale orange (JH, unpublished data, lab notes).

DISTRIBUTION. Clipperton Island, Malpelo Island, and Galapagos Archipelago; subtidal to 60 m.

ETYMOLOGY. The specific name is from the Greek *nesiotes,* an island dweller; a noun in apposition.

AFFINITIES. Of species within the *P. lepidus* complex, *P. nesiotes* appears most closely related to *Pagurus villosus* Nicolet, 1849, with which it shares the less common character, simple ocular acicles. *Pagurus nesiotes* can immediately be distinguished from *P. villosus* by the setation of the antennal flagella. In the former species one to four short setae are present on every one to four articles. In the latter species a pair of long setae is present on each article, at least in the proximal half. *Pagurus nesiotes* is distinguishable from *P. lepidus* not only by its simpler ocular acicles but by the marked slope of the dorsomesial face of its left chela.

DISCUSSION. As previously indicated, Chace (1962) believed that his Clipperton Island specimens agreed in most general respects with Bouvier's (1898) description of *P. lepidus* and with specimens from Puerto Peñasco, Sonora, Mexico, previously identified as *P. lepidus.* However, he noted one striking difference, i.e., the lack of multispinose ocular acicles, which were described for *P. lepidus* and which were present in the Mexican specimens. Although Chace (1962) felt that it was quite possible this character might prove to be of specific importance, he was reluctant to assign a new specific name to the Clipperton Island material until more information was available from other localities.

We have been able to examine the specimen discussed in Birkeland *et al.* (1976) and cited in that report only as *Pagurus* sp. It too is *P. nesiotes.* As far as is presently known, this is truly an insular species.

ACKNOWLEDGMENTS

We are indebted to Harold Feinberg, American Museum of Natural History, Jacques Forest, Muséum National d'Histoire Naturelle, Paris, Raymond Manning, National Museum of Natural History, Smithsonian Institution, and Rafael Lemaitre, Smithsonian Oceanographic Sorting Center, for making their specimens of *P. lepidus* and *P. nesiotes* available to us. One of us (PAMcL) also thanks the Swedish National Science Research Council and Drs. Å. Franzen and Å. Andersson of the Invertebrate Section of the Naturhistoriska Rijksmuseet, Stockholm, for providing the opportunity to work with the Museum's pagurid collections. We acknowledge, with thanks, the several collectors who have deposited their collections with the Allan Hancock Foundation or provided material for this study: P. Abrams, E. Ball, T. and B. Burch, D. Moran, A. Harvey, A. Havens, T. Hopkins, A. Kuris, P. Pickens, T. Scanland, J. Stames, and T. Spight.

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TWO NEW HERMIT CRABS OF THE GENUS *PAGURUS* (*PROVENZANOI* GROUP) (CRUSTACEA, ANOMURA, PAGURIDAE) FROM THE EASTERN PACIFIC, WITH NOTES ON THEIR ECOLOGY

ALAN W. HARVEY AND PATSY A. MCLAUGHLIN[1]

ABSTRACT. During ecological studies of the shallow-water hermit crab fauna of the northwestern Gulf of California, Mexico, two new species of the *provenzanoi* group of *Pagurus* were recognized. Additional material has shown that one of these species, *P. vetaultae* n. sp., has been found as far south as Panama, whereas the second, *P. arenisaxatilis* n. sp., appears not only to be endemic to the northern Gulf of California, Mexico, but to be one of the most abundant hermit crabs in the region. It is the only species in the northern Gulf that commonly inhabits both rocky and sandy shores. Despite the broader distribution of *P. vetaultae* through shallow subtidal regions of Mexico and Central America, this species appears to be restricted to coarse gravel substrates. Both species are described and illustrated.

INTRODUCTION

Following the description of *Pagurus lepidus* (Bouvier, 1898) virtually all small intertidal pagurids from the Gulf of California, Mexico, and/or the west coast of Baja California, Mexico, were routinely assigned to this taxon or to a complex of species confounded under this name (e.g., Glassell, 1937; Haig *et al.*, 1970; Ball and Haig, 1974; McLaughlin, 1975; Snyder-Conn, 1980). Haig and McLaughlin (1990) recently reexamined the syntypes of Bouvier's (1898) species and provided a detailed redescription and illustrations of this taxon. For the first time it is now possible to accurately report on some of the other taxa in this species complex.

Field and laboratory studies by one of us (AWH) on the intertidal hermit crabs of the northern Gulf of California included three species previously assigned to the *Pagurus lepidus* complex. One has proved to be *P. lepidus* s.s.; the other two are new species described herein, together with brief summaries of their ecology. One of these species, *P. vetaultae* n. sp., was first found in the Bay of Panama by Carl Bovallius during a trip to the Pacific coast of Central America in 1882–83 but was never described. The other, although quite abundant on a variety of substrates in the intertidal region, appears restricted in its distribution to the Gulf of California.

As with Atlantic species of the *provenzanoi* group (see McLaughlin, 1975; Lemaitre *et al.*, 1982), Pacific representatives are morphologically difficult to distinguish from one another. One extensively used diagnostic character is the dorsomesial surface of the left chela. It is described either as horizontal (Fig. 1A) or sloping (Fig. 1B, C) and usually is not influenced by animal size. However in *P. vetaultae* n. sp., the slope of the dorsomesial face varies from slight to substantial. The armament of this surface may be so strong that it gives the slightly sloping surface the visual impression of being horizontal.

MATERIALS

Materials for this study have come from the Crustacea collections formerly of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), National Museum of Natural History, Smithsonian Institution (USNM), Naturhistoriska Riksmuseet, Stockholm (NHRM), and from individual collectors. Specimens will be re-

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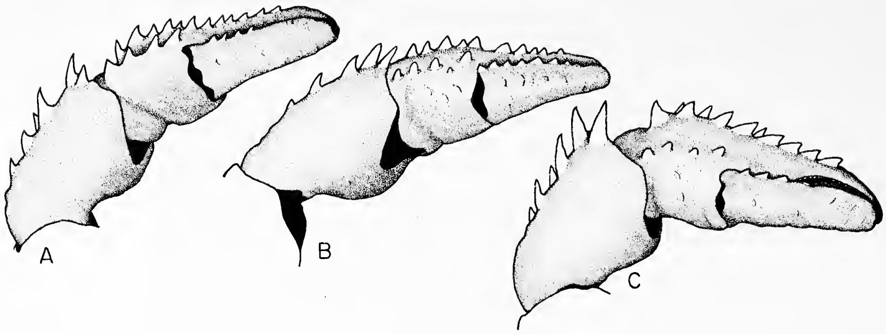

Figure 1. Lateral views of carpi and chelae of left chelipeds (setae omitted) depicting angulation of dorsomesial surface of chelae: **A,** *Pagurus lepidus* (Bouvier) with horizontal surface; **B,** *Pagurus vetaultae* n. sp. with weakly sloping surface; **C,** *Pagurus vetaultae* n. sp. with strongly sloping surface.

turned to their repositories of origin and/or deposited in these and the following museums: Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Natural History Museum of Los Angeles County (LACM), Museum National d'Histoire Naturelle (MNHN). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

DESCRIPTIONS

Pagurus arenisaxatilis new species

Figure 2A–H

Pagurus lepidus: Chace, 1962:623, in part (by implication) (see remarks).

HOLOTYPE. Ovigerous ♀ (SL = 2.1 mm), USNM 243896. **Type locality.** Between Pelican Point and Choya Bay, Sonora, Mexico, February 3, 1988, collector A. Harvey.

PARATYPES. Baja California, Mexico: San Felipe Bay, 6 ♂, 2 ♀, 1 ovigerous ♀ (SL = 1.2, 2.4 mm), intertidal, January 1, 1976, collectors R. Brusca, B. Wallerstein, AHF 7615 (LACM 76-595.1); San Felipe Bay, 1 ♂ (SL = 1.9 mm), "Velero III" station 1071-40, 5 m, February 2, 1940, AHF 4015 (LACM 40-43.1); off Diggs Point, San Felipe Bay, 1 ♂, 1 ovigerous ♀ (SL = 1.5, 1.7 mm), 30 m, June 3, 1934, collector S. Glassell, USNM; off Willard Point, Bahia San Luis Gonzaga, 1 ♂ (SL = 2.1 mm), "Velero III" station 716-37, 3.5–5.5 m, March 23, 1937, AHF 3711 (LACM 37-119.6). Sonora, Mexico: Adair Bay, 1 ♂ (SL = 2.2 mm), Choya Bay Survey station 67041, 6 m, March 18, 1967, collectors Burch and Kawchak, AHF 675 (LACM 67-242.1); same locality, 1 ♂ (SL = 2.5 mm), Choya Bay Survey station 67042, 10 m, March 18, 1967, collectors Burch and Kawchak, AHF 678 (LACM 67-242.1); same locality, 4 ♂, 2 ♀ (SL = 0.9–2.1 mm), Choya Bay Survey station 70106, shore, July 18, 1970, collectors Burch and Seivings, AHF 709, 7010 (LACM 70-283.1); Pelican Point, 2 ♂ (SL = 1.8, 2.3 mm), Choya Bay Survey station 68045, shore, April 13, 1968, collectors Burch and Avery, AHF 6819 (LACM 68-384.1); between Pelican Point and Choya Bay, 6 ovigerous ♀ (SL = 1.5–2.1 mm), intertidal, February 3, 1988, collector A. Harvey, NHRM, RMNH; same locality, 4 ovigerous ♀ (SL = 1.7–2.7 mm), intertidal, January 19, 1988, collector A. Harvey, LACM 88-291.1; same locality, 5 ♂, 3 ♀, 1 ovigerous ♀ (SL = 0.9–2.6 mm), intertidal, July 26, 1988, collector A. Harvey, USNM; same locality, 2 ovigerous ♀ (SL = 1.7, 1.8 mm), intertidal, February 22, 1989, collector A. Harvey, MNHN; off Choya, 1 ♂ (SL = 2.0 mm), Choya Bay Survey station 67164, 17.5 m, November 4, 1967, collectors Burch, Hanson, and Skoglund, AHF 679 (LACM 67-243.1); sandy beach, Choya, 4 ♂, 1 ovigerous ♀ (SL = 1.7–2.1 mm), Choya Bay Survey station 66033, shore, August 15, 1966, collectors T. and B. Burch, AHF 6612 (LACM 66-355.1); same locality, 1 ♂ (SL = 1.7 mm), Choya Bay Survey station 66046, shore, October 14, 1966, collectors Burch, Avery, and Scott, AHF 6613 (LACM 66-356.1); Choya Bay, 16 mile reef, 1 ♀ (SL = 1.3 mm), station GA-72, March 1968, collectors G. and M. Avery, AHF 6818 (LACM 68-385.1); Puerto Peñasco, 1 ♂, 1 ♀, 5 juveniles (SL = 0.8–1.4 mm), November 23–26, 1955, collector E.P. Chace, USNM 211423; same locality, 2 ♂, 3 ♀, 2 ovigerous ♀ (SL = 2.0–2.9 mm), 1967, collector A. Havens, RMNH; same locality, 1 ♂, 3 ♀, 1 ovigerous ♀ (SL = 2.0–2.9 mm), intertidal, December 3, 1967, collector A. Havens (NHRM Cat. No. 4175); same locality, 1 ♂ (SL = 2.1 mm), Choya Bay Survey station 69030, shore, February 15, 1969, collectors Burch, Hanson, Bennett, and Schroder, AHF 6913 (LACM 69-229.1); off Rocky Point, 2 ♂ (SL = 1.8, 1.9 mm), "Velero III" station 1072-40, 20 m, February 2, 1940, AHF 4016 (LACM 40-44.6); inside Georges Island (just south of Bahia San Jorge), 1 ♂ (SL = 1.5 mm), "Velero III" station 1075-40, 21–23 m, February 3, 1940, AHF 4017 (LACM 40-47.1); south of Isla Tiburon, 1 ♂ (SL = 1.8 mm), "Velero III" station 731-37, 122.5 m, March 28, 1937, AHF 3712 (LACM 37-134); south side Isla Tiburon, 1 ♂ (SL = 3.2 mm), "Curray-Orca" Cruise station 194, 13 m, March 27, 1960, collector R.H. Parker, AHF 6055 (LACM 60-181.1).

DIAGNOSIS. Shield slightly longer than broad. Ocular peduncles one-half to two-thirds shield length. Articles of antennal flagella with irregularly alternated long and short setae. Carpus of right cheliped with irregular double row of spines on dorsomesial margin and 1 or 2 additional spines near distal margin. Left cheliped with dorsomesial face of palm strongly sloping; ischium with ventromesial margin unarmed or with few spinules.

Dactyli of ambulatory legs each with 8–13 corneous spines on ventral margin. Anterior lobe of sternite of 3rd pereopods subsemicircular. Posterior lobes of telson with simple to spinous lateral margins, without delimiting spine anteriorly. In life, chelipeds with distal halves of dactyli and fixed fingers white, palms and carpi tan to olive.

DESCRIPTION. Shield (Fig. 2A) slightly longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping; posterior margin subtruncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, with very small terminal spinule. Dorsal surface of shield with scattered tufts of setae (not illustrated).

Ocular peduncles (Fig. 2A) one-half to two-thirds shield length, broad basally and moderately stout, corneae slightly dilated. Ocular acicles subrectangular, multispinose (2–5 marginal or submarginal spines), separated basally by slightly more than one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles (Fig. 2A) overreaching ocular peduncles by one-half to two-thirds length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered on dorsal and ventral margins (setae not shown). Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral face.

Antennal peduncles (Fig. 2A) overreaching corneae by approximately one-half length of ultimate segment. Fifth and 4th segments with few tufts of setae. Third segment with small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins with long or moderately long setae and occasionally small accessory spinule; dorsomesial distal angle with small spine, mesial face with long setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum usually with 2 or 3 moderately long (2–3 articles length) and usually 2–4 short setae or bristles per article, at least in proximal half.

Mouthparts typical for species of the *provenzanoi* group as described by McLaughlin (1975) and Lemaitre *et al.* (1982).

Right cheliped (Fig. 2B) with dactylus approximately as long as palm, slightly overlapped by fixed finger. Cutting edge of dactylus with 1 or 2 strong and several small calcareous teeth in proximal half and row of small corneous teeth in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half and small calcareous teeth interspersed with corneous teeth distally, terminating in corneous tip. Dorsomesial margin of dactylus with row of small acute spines, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long stiff setae, dorsomesial margin with tufts of long stiff setae, ventral surface with few scattered setae. Palm slightly shorter than carpus; dorsomesial margin with irregular double row of spines and dense tufts of setae, dorsal surface with irregular rows of spines and tufts of long setae proximally and usually scattered small spines on fixed finger, dorsolateral margin with row of spines extending to tip of fixed finger and with tufts of long setae. Carpus approximately as long as merus; dorsomesial margin with irregular double row of spines, 1 or 2 spines on or near distal margin, dorsal surface with row of small spines laterad of midline and 2nd row near weakly delimited dorsolateral margin, ventrolateral margin with 1 or 2 small spines distally, dorsal surface with numerous long setae, lateral and mesial faces with scattered setae. Merus subtriangular; dorsal margin with few tufts of setae, distal margin with 1 small spine, ventromesial margin unarmed, ventrolateral margin with short row of small spines. Ischium unarmed.

Left cheliped (Fig. 2C) with dactylus and fixed finger somewhat spoon-shaped. Dactylus one-third to one-half times longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal midline and dorsomesial margin each with row of spines in proximal half, dorsal surface also with row of stiff setae near cutting edge and second row of longer setae in midline, mesial margin and ventral surface also with tufts of long setae. Palm one-half to two-thirds length of carpus; elevated in midline and armed with irregular double row of spines, extending nearly to tip of fixed finger, dorsolateral face strongly sloping ventrally, with row of small spines or spinules in ventral half and second row of protuberances or spines and tufts of long setae marginally, dorsomesial face strongly sloping, with few scattered spines or low protuberances and tufts of setae, dorsomesial margin not delimited. Carpus slightly shorter than merus; dorsomesial margin with row of numerous small spines, dorsolateral margin with row of few widely spaced strong spines, and both with tufts of long setae, distal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, laterodistal and ventrolateral margins each with acute spine. Merus subtriangular; dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with short row of spines only on proximal half and with tufts of setae. Ischium unarmed or with few spinules on ventromesial margin.

Second and 3rd pereopods (Fig. 3D, E) similar. Dactyli one-half to two-thirds length of propodi, slightly less to slightly more than one-fifth as broad as long, terminating in strong curved corneous claw; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 8–13 corneous spines and long setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long setae, ventral surfaces each with single or pair of corneous spines at distal margin and 1 or 2 ad-

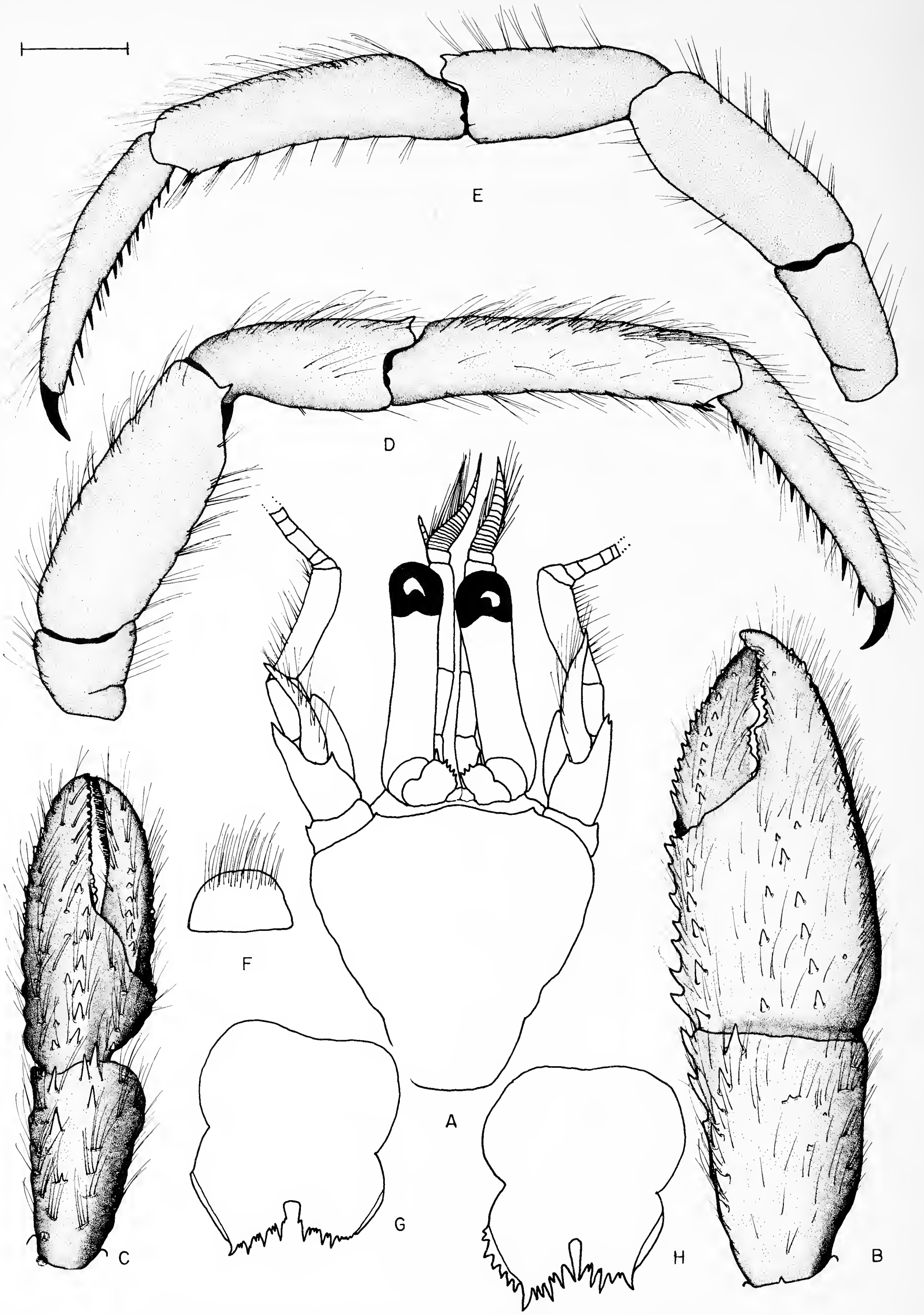

Figure 2. *Pagurus arenisaxatilis* new species, paratype USNM 243893: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** right 2nd pereopod (lateral view); **E,** left 3rd pereopod (lateral view); **F,** anterior lobe of sternite of 3rd pereopods; **G,** telson with simple lateral margins of posterior lobes. Paratype RMNH: **H,** telson with spinous lateral margin on right posterior lobe. Scale = 1 mm (A–E) or 0.5 mm (F–H).

ditional spines in distal third. Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low, occasionally spinose, protuberances and tufts of long setae, mesial and lateral faces and ventral surfaces with scattered setae. Meri with tufts of long setae on dorsal and ventral margins, ventrolateral margins each with acute spine distally and frequently also 1–3 spines on ventral margin (2nd) or unarmed (3rd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods (Fig. 2F) subsemicircular, unarmed. Fourth pereopods with small preungual process at base of claw; propodal rasp with 3–5 rows of corneous scales, dorsal margins of dactyli, propodi, carpi, and meri (distally) with long dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson (Fig. 2G, H) with posterior lobes subtriangular to subquadrate, terminal margins usually oblique, each armed with 3 or 4 strong spines, interspersed with smaller spines, lateral margins with narrow plate simple (Fig. 2G), or less frequently with row of spines (Fig. 2H); no anterior spine on lateral plate.

COLOR (in life). Antennal flagellum olive drab to brown with white in patterns of 2 dark–1 white, 3 dark–1 white, 4 dark–1 white, progressing distally. Shield with tan to brown splotches. Ocular peduncles, antennules, and antennae mottled or spotted with tan to olive. Right cheliped with distal half of dactylus and tip of fixed finger white, palm, carpus, and merus tan to olive. Left cheliped with tips of dactylus and fixed finger white, palm tan to olive with spines often white-tipped; carpus tan to olive; merus tan to olive with white band distally on mesial and lateral faces and dorsally separated from distal margin by dark patch. Ambulatory dactyli with 3 short olive to tan stripes proximally on white background; propodi with median band consisting of short tan to olive stripes; carpi with longitudinal tan to olive stripes on white background covering most of segment; meri with central band composed of tan to olive stripes (PAMcL, lab notes).

DISTRIBUTION. At present known only from the northern Gulf of California, Mexico, intertidal to 30 m.

ETYMOLOGY. The specific name is derived from the Latin *arena,* sand, and *saxatilis,* dwelling among stones, reflecting the mixed habitat of this species.

AFFINITIES. *Pagurus arenisaxatilis* is similar in general morphology to the other *Pagurus lepidus* complex species occurring in the Gulf of California. Like these other species, in life it is characterized by longitudinal stripes on the ambulatory legs. However, the irregular long and short setae on the articles of the antennal flagellum immediately distinguish this species from the others. In the absence of the antennal flagella, *P. arenisaxatilis* is best distinguished by a combination of characters, i.e., sloping dorsomesial face of left chela, long pereopodal dactyli with 8–13 ventral spines, and no delimiting spine on the anterior margin of the lateral telson plates. This species exhibits considerable variation in the development of the lateral plates of the posterior lobes of the telson. Although no anterior telsonal spine has been observed in any of the specimens examined, the plate may be undifferentiated, composed of partially to completely fused denticles (Fig. 2G) or differentiated into distinct small teeth (Fig. 2H). In the development of the multifid ocular acicles, this species also exhibits differences from the other Gulf species. The acicle tends to be ovate in shape with a single large spine usually prominent medially, and with one to four smaller spines developed mesiad of it. In most other species the multifid acicles are subrectangular in shape and consist of three to five equally strong spines.

REMARKS. One lot of specimens in the national collections from Puerto Peñasco, Mexico, identified as *P. lepidus* was used by Chace (1962) for comparison with specimens from Clipperton Island. Haig and McLaughlin (1990) reexamined this lot (USNM 99802) and found that only one of the eight specimens was referrable to *P. lepidus.* The remainder are identifible as *P. arenisaxatilis.*

ECOLOGY. *Pagurus arenisaxatilis* is one of the most abundant hermit crabs in the northern Gulf of California. Of the intertidal pagurid hermit crabs in the area, it has the broadest vertical range, extending from the upper midintertidal to the shallow subtidal, and is the only species commonly found on both rocky and sandy shores.

This small species uses a variety of shells, usually less than 20 mm in length, such as *Morula ferruginosa* (Reeve), *Anachis coronata* (Sowerby), *A. varia* (Sowerby), small specimens of *Cerithium stercusmuscarum* (Valenciennes), and *Olivella dama* (Wood). Local patterns of shell use may vary widely, however, depending on which shell species are locally common and perhaps also on the presence of other hermit crab species. Shells used by *P. arenisaxatilis* tend to be in poor condition; in a sample of 118 specimens collected during the winter of 1985, 74% of shells used were damaged, and 89% were at least partially encrusted by coralline algae. Other common encrustors included several bryozan species (36.4%) and spirorbid (29.7%) and serpulid (15.2%) polychaetes. Several non-encrusting epibionts are also commonly associated with *P. arenisaxitilis*-occupied shells. Most notably, the polychaete *Polydora* sp. (33.1%) is typically found in the apex of the shell, the slipper limpet *Crepidula* (20.3%), believed to be a new species, is found just inside the shell aperture, and a gammarid amphipod (seasonally variable, sometimes near 100%) is found deep inside the shell. Like most hermit crabs in the northern Gulf, *P. arenisaxitilis* is relatively free of the external parasites that infect hermit crabs in other regions. An abdominal bopyrid isopod, *Stegophryxus* n. sp. (J. Markham, personal communication), is rare (<1%); a single specimen, subsequently lost, carried an unidentified rhizocephalan.

Pagurus vetaultae new species

Figures 1B, C; 3A–H

HOLOTYPE. ♂ (SL = 2.1 mm), USNM 243894. **Type locality.** Venecia Cove (near San Carlos and Guaymas, Sonora, Mexico), March 20, 1989, collector S. Vetault.

PARATYPES. Venecia Cove, Sonora, Mexico, 1 ♂, 2 ovigerous ♀ (SL = 1.7–1.8 mm), March 20, 1989, 3–7 m, collector S. Vetault, USNM 243895. Hymalaya Bay, Sonora, Mexico, 1 ♀ (SL = 1.4 mm), −1 m, November 24–26, 1988, collectors S. Vetault and A. Harvey, AHF 882 (LACM 88-292.1). Northeast of Bahia Santa Elena, Costa Rica, 1 ♂ (SL = 2.0 mm), "Searcher" station 384, 18 m, February 13, 1972, AHF 729 (LACM 72-8.1). Las Perlas, Pedro Gonzalez, Gulf of Panama, 5 ♂, 2 ♀ (SL = 1.3–2.3 mm), April 22–25, 1882, collector C. Bovallius, NHRM 7175, 7180.

OTHER MATERIAL. 8 ♂ (SL = 1.1–1.8 mm), "Searcher" station 471, north side Isla del Cano, Costa Rica, 9 m, March 14, 1972, AHF 2794-01 (LACM 72-63.1).

DIAGNOSIS. Shield as long or slightly longer than broad. Ocular peduncles three-fourths to four-fifths shield length. Articles of antennal flagella with very short setae. Carpus of right cheliped with 3 or 4 widely spaced spines on dorsomesial margin, distal margin with 2 or 3 strong spines. Left cheliped with dorsomesial surface of palm slightly to strongly sloping; ischium with acute spine at ventrolateral distal angle. Dactyli of ambulatory legs each with 6–9 corneous spines on ventral margin, dactylus of left 3rd pereopod four-fifths to nine-tenths length of propodus. Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular. Posterior lobes of telson with lateral margins simple but delimited by spine anteriorly, at least on 1 side. In life, chelipeds each with 2 or 3 broad dark brown stripes on palms, dactyli and fixed fingers each with 1 stripe dorsally on cream base color; carpi with 2 dark brown stripes dorsally.

DESCRIPTION. Shield (Fig. 3A) as long as to slightly longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin truncate. Lateral projections broadly rounded, unarmed, overreaching obsolete unarmed rostrum. Dorsal surface of shield with scattered setae (not shown in illustration).

Ocular peduncles (Fig. 3A) three-fourths to four-fifths shield length, moderately slender, with corneae only slightly dilated. Ocular acicles subrectangular, multispinose (3–5 marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles (Fig. 3A) overreach ocular peduncles by one-third to one-half length of ultimate segment. Ultimate and penultimate segments with few scattered setae (not shown in illustration). Basal segment with 1 acute spine on lateral face.

Antennal peduncles (Fig. 3A) overreaching corneae by one-fourth to one-third length of ultimate segment. Fifth and 4th segments with scattered setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral margin with accessory spine and few long setae; dorsomesial distal angle unarmed or with small spinule, mesial face with long setae (not illustrated). First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum reaching to or beyond tip of right cheliped, with 2 or 3 very short (<1 article length) setae every article.

Mouthparts typical for *provenzanoi* group species (cf. Lemaitre *et al.*, 1982).

Right cheliped (Fig. 3B) with dactylus approximately as long as palm, overlapped by fixed finger. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 or 2 strong and few smaller calcareous teeth in proximal half and row of small corneous teeth in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1–4 strong calcareous teeth in proximal half, smaller calcareous teeth interspersed with small corneous teeth in distal half, terminating in corneous tip. Dorsomesial margin of dactylus with row of small acute spines, dorsal surface slightly elevated in midline and also armed with row of more widely spaced spines and tufts of long setae, dorsomesial margin and ventral surface with tufts of long stiff setae. Palm slightly shorter than carpus; dorsomesial margin with irregular double row of spines, strongest proximally, dorsal surface with two widely separated rows of spines and long setae and numerous tufts of long stiff setae, few additional spines distally and on fixed finger, dorsolateral margin with low protuberances or small spines proximally increasing in size distally and on fixed finger. Carpus slightly shorter than or equal to length of merus; dorsomesial margin with row of 3 or 4 spines, dorsodistal margin with 1–3 acute spines, dorsal surface with row of small spines or tubercles laterad of midline and also numerous tufts of long setae, dorsolateral margin not delimited, distolateral margin with 0–3 small spines, lateral and mesial faces with scattered setae, ventrolateral distal angle with acute spine. Merus subtriangular; dorsal margin with few tufts of setae, dorsodistal margin with 1 spine, ventromesial margin unarmed or with row of low protuberances or spinules, sometimes 1 small spine distally, ventrolateral margin with 1–3 acute spines in distal half. Ischium unarmed or with small spine at ventrolateral distal angle.

Left cheliped (Figs. 1B, C; 3C, D) with dactylus and fixed finger somewhat spoon-shaped, with prominent hiatus. Dactylus longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of spines in midline and row of spines or protuberances on dorsomesial margin, all surfaces with tufts of long setae. Palm one-half to two-thirds length of carpus; dorsal surface slightly elevated in midline, and armed

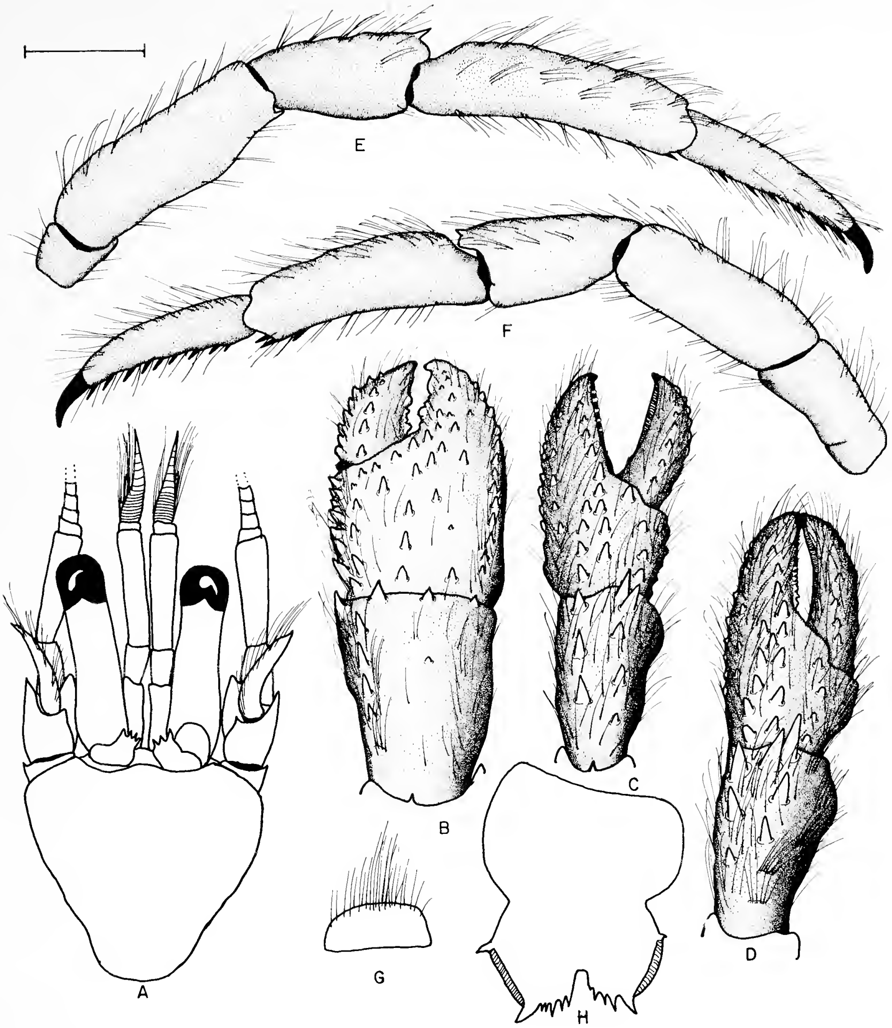

Figure 3. *Pagurus vetaultae* new species, paratype USNM 243895: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped; **D,** chela and carpus of left cheliped (dorsal view, Bay of Panama paratype NHRM 7175); **E,** right 2nd pereopod (lateral view); **F,** left 3rd pereopod (lateral view); **G,** anterior lobe of sternite of 3rd pereopods; **H,** telson. Scale = 1 mm (A–F) or 0.5 mm (G, H).

with double row of spines, extending onto the fixed finger as single or double row, dorsolateral face strongly sloping ventrally with row of small spines in ventral half and second row of spines marginally, dorsomesial face weakly to strongly sloping with few low protuberances or scattered spinules, dorsomesial margin indicated by row of small to moderately strong spines, all surfaces with numerous tufts of long stiff setae. Carpus shorter than merus; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, mesial and lateral faces each with short transverse ridges and long setae, laterodistal margin with acute spine dorsally and 2nd spine at ventral angle. Merus triangular; dorsal margin with tufts of setae and acute spine at distal margin, ventromesial and ventrolateral margins each with row of spines and tufts of long setae. Ischium with acute spine at ventrolateral distal angle.

Second and 3rd pereopods (Fig. 3E, F) generally similar. Dactyli one-half to three-fourths length of propodi (2nd and 3rd right), or four-fifths to nine-tenths length of propodus (left 3rd); terminating in strong curved corneous claws, dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–9 corneous spines and long stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long stiff setae, ventral surfaces each with 1 corneous spine at distal margin and usually 1 additional spine in distal third (2nd) or pair of spines at distal margin and 1 additional spine in distal quarter (3rd). Carpi slightly less than to approximately equaling length of meri;

dorsodistal margins each with 1 spine, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins, ventral margins with small spine on ventrolateral margin distally (2nd) or with low protuberances and tufts of long setae (3rd). Ischia with row of long setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods (Fig. 3G) subrectangular to subsemicircular, slightly skewed, unarmed. Fourth pereopods with very small preungual process at base of claw; propodal rasp of 5 or 6 rows of corneous scales, dorsal and ventral margins of segments with long setae.

Exopod of left uropod with several thick setae on inner margin. Telson (Fig. 3H) with subrectangular posterior lobes; terminal margins oblique, each armed with row of spines, outermost strongest; lateral margins with narrow plate delimited anteriorly by small to moderately large spine at least on one side.

COLOR (in life). Carapace base color cream, with areas of light orange brown, sometimes with bluish tinge centrally, and darker brown patch on each side laterally. Ocular peduncles generally opaque with narrow white ring at base of corneae, reddish flecks and darker patch proximally and distally; corneae black with flecks of pink. Antennular peduncles transparent or with brownish tinge, each segment with proximal and subdistal white chromatophore and median black ring. Antennal peduncles transparent with longitudinal reddish-brown stripe dorsally and ventrally on 5th segment, 4th segment with white chromatophore distally and dark brown mesial and lateral patches; acicle light blue-gray with white chromatophores and brown bands; flagellum with 3 reddish-brown articles separated by 1 transparent article with white chromatophore. Chelae of chelipeds with 2 broad or 3 more narrow dark brown stripes proximally on palm and 1 stripe each on dactylus and fixed finger, otherwise cream-colored; carpi with 2 dark brown stripes dorsally, dark brown or black mesially and with dark and light stripe laterally; meri dark brown with cream-colored dorsal stripe and distal band. Dactyli of ambulatory legs cream-colored distally with 3 short dark brown stripes over bluish-gray base color proximally; propodi and carpi each with broad dark stripes, meri with dark dorsal stripe and lateral patch (PAMcL, lab notes; AWH, field notes).

ETYMOLOGY. This species (pronounced "ve-tō′-ā") is named for its collector, Sarah Vetault.

DISTRIBUTION. San Carlos–Guaymas area of the Gulf of California, Mexico, to Bay of Panama, 1–7 m.

AFFINITIES. *Pagurus vetaultae* morphologically is most closely allied with *P. redondoensis* Wicksten from southern California. In both species the dorsomesial margin of the left chela slopes; however, it may only be weakly sloping and be so strongly armed with spines as to give the visual impression of a level surface. Both species also have a similar number of corneous spines on the ventral margins of the dactyli of the 2nd and 3rd pereopods and similar armature of the dorsomesial margin of the carpus of the right cheliped. However, the two species may be easily separated by the length of the antennal flagella and the setation of the flagellar articles. We have reexamined the holotype of *P. redondoensis* (AHF 783) and several of Wicksten's nonparatypic specimens and found the flagella usually shorter than the right cheliped. Wicksten (1982) described the articles of the antennal flagella as having "1 or 2 short (1 or 2 articles in length) setae on each side." However, in addition to these short setae, one or two considerably longer setae also are present on at least every second article in the proximal half of the flagellum. Only very short (<1 article in length) setae are present on the flagellum of *P. vetaultae* over its entire length. In the absence of the antennal flagella, which Wicksten notes can be easily broken, the length ratios of the dactylus and propodus of the 3rd pereopod usually provide a reliable diagnostic character for separating the two taxa. In *P. vetaultae* the dactylus is nearly (four-fifths to nine-tenths) as long as the propodus. In *P. redondoensis* the dactylus is usually only two-thirds to three-fourths the length of the propodus, although this is not true of the holotype. In life *P. vetaultae* is easily distinguished by its distinctive coloration.

DISCUSSION. Although only the materials specified are paratypes, we have examined additional, but damaged, specimens from Costa Rica, whose disarticulated appendages clearly are referrable to *P. vetaultae.*

ECOLOGY. This species was found at low densities in the shallow subtidal in the central Gulf of California primarily on coarse gravel substrates, in contrast to the sympatric *P. lepidus* and *P. galapagensis* (Boone), which prefer rocky substrates with dense patches of *Sargassum* (*P. lepidus* similarly favors *Sargassum* beds in the northern Gulf intertidal, where it co-occurs on rocky shores with the far more numerous *P. arenisaxatilis*). *Pagurus vetaultae* collected in Hymalaya Bay used *Morula ferruginosa* and *Anachis coronata* shells, which tended to be heavily encrusted with coralline algae but otherwise lacked the significant epibiont populations or physical damage that characterize the shells used by *P. galapagensis* and the more northern *P. arenisaxatilis.* One of the Costa Rican specimens was parasitized by an abdominal bopyrid isopod. The single female specimen was damaged and could only be identified as *Stegophpryxus* (n.?) sp. (J. Markham, personal communication).

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Janet Haig made materials in the Allan Hancock Foundation available for study and reviewed the manuscript. Dr. Å. Franzén, Swedish Natural History Museum, made the Bovallius material available.

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GOMPHOTARIA PUGNAX, A NEW GENUS AND SPECIES OF LATE MIOCENE DUSIGNATHINE OTARIID PINNIPED (MAMMALIA: CARNIVORA) FROM CALIFORNIA

LAWRENCE G. BARNES AND RODNEY E. RASCHKE

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GOMPHOTARIA PUGNAX, A NEW GENUS AND SPECIES OF LATE MIOCENE DUSIGNATHINE OTARIID PINNIPED (MAMMALIA: CARNIVORA) FROM CALIFORNIA

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ABSTRACT. The nearly complete skeleton of *Gomphotaria pugnax*, a new genus and species of giant fossil pinniped, has been discovered in the latest Miocene (*ca.* 5 to 8.5 million years) marine Capistrano Formation in southern California, U.S.A. This remarkable pinniped is assignable to the otariid subfamily Dusignathinae and is convergent with true walruses of the subfamily Odobeninae by possessing large upper canine tusks but is unlike odobenines in other cranial and postcranial osteological features. Both upper and lower canines are enlarged, procumbent, and worn anteriorly, indicating that the animal may have probed the substrate in search of benthic invertebrates for food. Extreme breakage and subsequent wear of the large, single-rooted cheek teeth indicate that at least some, if not all of the food species (e.g., mollusks) probably had hard shells. Absence of a highly vaulted palate, present in walruses, indicates that *G. pugnax* did not suck bivalve inner tissues from the shells using the tongue-piston method employed by walruses. Although *G. pugnax* is distinguishable from type and referred specimens of all previously described odobenines and dusignathines, the continuing problem of disparate materials continues to plague interpretation of the group, and there are as yet unresolved problems of synonymies among previously described taxa.

INTRODUCTION

This is a preliminary report of a new genus and species of giant fossil pinniped from the Capistrano Formation in Orange County, southern California (see also Barnes and Raschke, 1989). The fossil was excavated from the latest Miocene (5 to 8.5 million years (Ma)) part of the siltstone facies of the Capistrano Formation. This formation is part of a thick sequence of Miocene and Pliocene marine sedimentary rocks in the southeastern part of the Los Angeles Basin that has produced important and abundant fossil marine vertebrates. The fossil was discovered in the hilly area of San Clemente, near the Pacific Ocean, in 1980, by paleontologists who were salvaging fossils during construction-related grading.

In recent years, our knowledge of the evolutionary history of sea lions, fur seals, and walruses in the family Otariidae (*sensu lato*) has increased greatly. The fossil record has had a major impact on interpretations of otariid phylogeny as is evidenced in reviews by Mitchell (1968, 1975), Repenning (1975, 1976), Repenning and Tedford (1977), Tedford (1976), Barnes (1979, 1987, 1989), Barnes, Domning, and Ray (1985), and Wozencraft (1989a, b). These authors have proposed several schemes of classification for the sea lions, fur seals, walruses, and their extinct relatives. As a result, the classification of the group is currently controversial (see Barnes, 1987; Barnes, Domning, and Ray 1985: 36, 38, table 1), and Wyss (1987) and Berta, Ray, and Wyss (1989) have even argued that walruses are closely related to the phocid seals.

We classify the new taxon described here in the extinct otariid subfamily Dusignathinae of Mitchell, 1968. Prior to the present study, the subfamily Dusignathinae was monotypic, *Dusignathus santacruzensis* Kellogg, 1927, being the only included species. The holotype of *D. santacruzensis* is from the latest Miocene part of the Purisima Formation near Santa Cruz in central California, and that formation is broadly correlative in age with the Capistrano Formation of southern California (Repenning and Tedford, 1977:4, 43–44; Barnes, 1976: 331, table 5, 1985:18).

Kellogg (1927) had considered *D. santacruzensis* to be a sea lion, although he recognized that it had characters of both sea lions and walruses. When Mitchell (1968:1894–1895) diagnosed the subfamily Dusignathinae, he listed characters that showed the taxon to be intermediate between sea lions and walruses, and it occupied this intermediate position in his phylogeny (Mitchell, 1968:fig. 16). Mitchell later suggested (1975:18) a somewhat different relationship when he indicated that he considered

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Dusignathus Kellogg, 1927, to be more closely related to the Desmatophocinae than to the Otariinae. Repenning and Tedford (1977), however, considered *Dusignathus* to be a member of the subfamily Imagotariinae Mitchell, 1968 (Imagotariinae being a senior synonym of Dusignathinae on the basis of page priority) and classified it within the family Odobenidae (walruses).

The importance of the new fossil described here is that it records, for the first time in a dusignathine, definitely associated cranial and forelimb bones, elements of critical importance in pinniped systematics. This information will be pivotal to the description and understanding of other taxa represented by disparate and less complete parts. Therefore, description of the taxon now is timely and will facilitate research on other taxa and specimens. The new taxon also documents previously unknown diversity in the Dusignathinae. We describe the cranium, dentaries, and some forelimb bones because they serve to differentiate the new taxon from all previously described large otariid pinnipeds of similar age. We intend to prepare a subsequent paper illustrating and describing in detail cranial variability and postcranial osteology of the new taxon based on the holotype and other specimens; however, that work is beyond the scope of this study.

METHODS AND MATERIALS

The classification used in this study is derived from those of Mitchell (1968) and Barnes (1979, 1989) in which Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusignathinae, and Odobeninae are recognized as separate subfamilies within the family Otariidae, *sensu lato.* The subfamily Dusignathinae is recognized here based on characters listed by Mitchell (1968: 1894–1895) and on additional characters. We restrict our characterization and comparisons of *D. santacruzensis* to its holotype because referral of postcranial bones to the species is tenuous. Geochronologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979) following the revised radiometric time scale of Dalrymple (1979).

Cranial measurements in Table 1 that were defined by Sivertsen (1954:18–20) are identified by his numbers in brackets. Other measurements are as defined by Barnes (1972:fig. 1, 1979:4–5). The anatomical terminology, including dental nomenclature, used here is adapted from that of Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Mitchell and Tedford (1973), Barnes (1972, 1979, 1989), and Repenning and Tedford (1977). The bones shown in the illustrations were coated with a sublimate of ammonium chloride to make their features more visible.

Acronyms used for institutions are:

LACM—Natural History Museum of Los Angeles County, Los Angeles, California.
UCMP—University of California Museum of Paleontology, Berkeley, California.
USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Otariidae Gill, 1866
Subfamily Dusignathinae Mitchell, 1968

TYPE GENUS. *Dusignathus* Kellogg, 1927.

INCLUDED GENERA. *Dusignathus* Kellogg, 1927; and *Gomphotaria,* new genus.

Gomphotaria, new genus

DIAGNOSIS OF GENUS. A genus of Dusignathinae differing from *Dusignathus* by having cranium with high sagittal crest, rostrum laterally expanded distally to accommodate tusks, postglenoid process of squamosal relatively larger, mastoid–paroccipital crest more compressed anteroposteriorly and expanded dorsoventrally, relatively larger horizontal shelf projecting laterally over external acoustic meatus, external aperture of stylomastoid foramen directed anterolaterally rather than ventrolaterally; by having dentary relatively shallower dorsoventrally and relatively thicker transversely, with more recumbent coronoid process, more prominent laterally projecting angle of dentary, relatively larger and more rugose symphyseal surface, pterygoid process tabular and directed medially rather than posteromedially, and lesser degree of angular divergence from mandibular symphysis at midline (indicating longer and narrower skull); and by having upper and lower canines much larger, developed as tusks, more procumbent, and having fluted roots covered with thick cementum and exposed outside of alveoli, cheek teeth with crowns more bulbous, and upper and lower P1 more shallowly rooted.

TYPE AND ONLY INCLUDED SPECIES. *Gomphotaria pugnax,* new species, latest Miocene, California.

ETYMOLOGY. Derived from Greek; *gomphos,* for peg, nail, or bolt; in reference to the simple, round-rooted, peglike cheek teeth of this pinniped; plus *otaria,* a root derived from the generic name of the South American sea lion, the type genus of the family Otariidae, in reference to the otariid affinities of this taxon.

Gomphotaria pugnax, new species

Figures 1, 2, 3a

DIAGNOSIS OF SPECIES. The genus is presently monotypic and the generic diagnosis serves for the species.

HOLOTYPE. LACM 121508, virtually complete skeleton, including cranium, left and right dentaries, collected 21 August 1980 by L.G. Barnes, Edward D. Mitchell, Marilyn M. Morgan, Rodney E. Raschke, and Mark A. Roeder.

TYPE LOCALITY. LACM 4631, San Clemente, Orange County, California. The holotype was excavated approximately 70 m north of Highway 101 at 10 to 12 m depth in a hill in the SW¼, SW¼, Sec. 28, T. 8 S., R. 7 W., San Clemente, California topographic quadrangle, USGS, 1968, 1:24,000 scale, at approximately 33°26′26″ north latitude, and 117°37′20″ west longitude.

FORMATION AND AGE. Siltstone facies of the upper part of the Capistrano Formation, latest Miocene, *ca.* 5 to 8.5 Ma, correlative with most of the Hemphillian North American Land Mammal Age.

The Capistrano Formation, a laterally extensive marine sedimentary rock unit in southern Orange County, includes strata of latest Miocene and early Pliocene age, consists mostly of silty shales interbedded with diatomites and sandstones, and rests conformably on the Middle and Late Miocene marine Monterey Formation (Edgington, 1974). This formation was deposited in the extreme southeastern part of the structural and depositional basin known as the Los Angeles Basin. The siltstone facies of the Capistrano Formation, described by Woodford (1925) for exposures in the San Juan Capistrano area of Orange County, consists of olive brown to gray (when weathered) and dark brown to black (when fresh), sandy siltstone, with interbedded sandstones and diatomaceous shales. There are localized occurrences of breccia at the base of this formation. The siltstone member is the deepwater, offshore (distal) facies of the Capistrano Formation, and is laterally equivalent to, and interfingers with, the nearshore (proximal) facies of the Capistrano Formation, known as the Oso Sand Member (Vedder, 1972), which has yielded horses, rabbits, and other fossils of Hemphillian age. Although the published vertebrate paleontological record of the Capistrano Formation appears to be meager (Barnes, 1976; Barnes, Raschke, and Brown, 1984, 1987), many fossils have been recovered from the rock unit and await description. The age of the rock unit has been determined partly on the basis of its stratigraphic and structural relationships with other rock units of known age and partly on the basis of published and unpublished fossils. The Capistrano Formation is broadly correlative with the lower part of the Almejas Formation on Isla Cedros, Baja California, and with the Purisima Formation near Santa Cruz in central California (Repenning and Tedford, 1977:4, 43–44; Barnes, 1976: 331, table 5, 1984, 1985:18).

ETYMOLOGY. Derived from Latin; *pugnax*, for combative or contentious; in reference to the probable appearance in life of this giant, adult, male individual with procumbent anterior teeth, large extremely worn cheek teeth, and a high forehead.

DESCRIPTION AND COMPARISONS. Cranium. The cranium (Fig. 1, Table 1) is massive, with large procumbent canines, stout zygomatic arches, relatively small orbits (for a pinniped), a relatively small braincase, a thick nuchal crest, and a high sagittal crest. Apparently the cranium was originally completely preserved, but when it was exposed by earth-moving machinery, much of the ventral surface was scraped away. Because of this, the left side and posterior part of the palate, the left zygomatic arch, and most of the basicranium are missing. Remaining parts of the cranium are preserved in excellent condition.

Table 1. Measurements (in mm) of the holotype cranium of *Gomphotaria pugnax*, new genus and species, LACM 121508. See Methods and Materials for methods of measurements. Parentheses around a measurement indicate that it was estimated by doubling a half width.

Length as preserved (rostral tip to dorsal margin of foramen magnum)	466.0
Length of tooth row, C to M^1	177.0
Width of rostrum across canines (12)	(164)
Width of rostrum across base of I^3	(65)
Width of palate across alveoli of P^4	(114)
Width across antorbital processes (5)	139.5
Width across greatest intertemporal constriction	45.0
Width of braincase at anterior edge of glenoid fossa (8)	(100)
Zygomatic width (17)	(280)
Auditory width (19)	(230)
Mastoid width (20)	(250)
Greatest width of anterior nares	50.9
Greatest height of anterior nares	56.2
Width of zygomatic root of maxilla (14)	38.5
Transverse diameter of infraorbital foramen	27.6
Anteroposterior diameter right I^3 alveolus	33.3
Anteroposterior diameter right canine alveolus	68.8
Anteroposterior diameter right P^1 alveolus	21.2
Anteroposterior diameter right P^2 alveolus	20.6
Anteroposterior diameter right P^3 alveolus	19.8
Anteroposterior diameter right P^4 alveolus	16.5
Anteroposterior diameter right M^1 alveolus	20.3

The individual represented by the holotype was an old adult male (Group I of Sivertsen (1954)) on the basis of the following observations: (1) of the nine cranial sutures that Sivertsen considered useful for age determination, eight are closed and fused, six are obliterated, only the anterior part of the interfrontal suture and the posterior part of the premaxillary–maxillary suture are still visible, and the basioccipito–basisphenoid suture is presumed to have been fused and obliterated; (2) the cranium yields a suture age of at least 34 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the old range for the adult age class; (3) as in Recent adult male otariines and many fossil otariids, a sagittal crest is present; (4) the canines are fully erupted and heavily worn; (5) bones throughout the skeleton have extreme development of crests, rugosities, processes, and other secondary age and male sex characters; and (6) a bac-

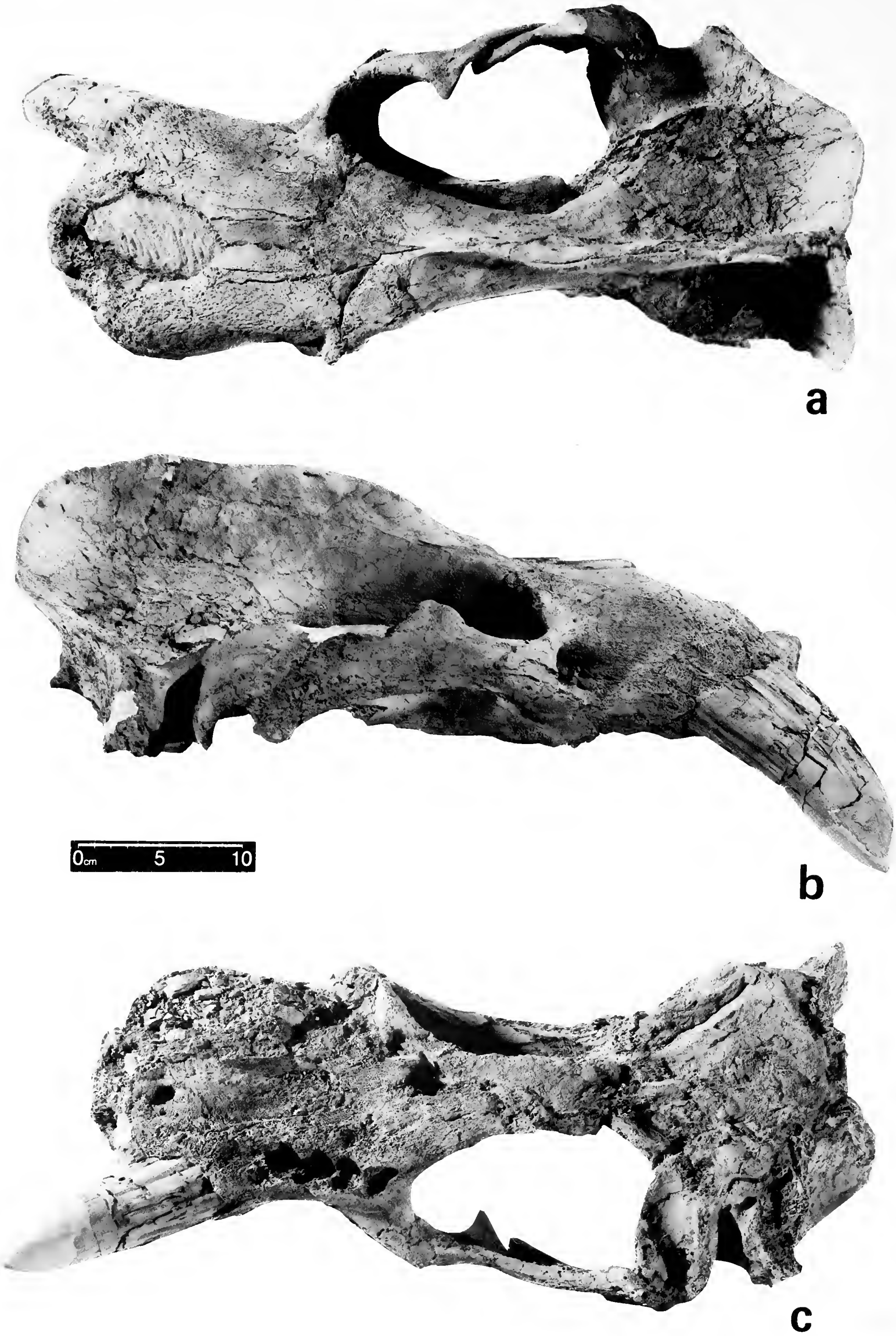

Figure 1. *Gomphotaria pugnax,* new genus and species, holotype cranium, LACM 121508, from LACM locality 4631; **a,** dorsal view; **b,** right lateral view; **c,** ventral view.

ulum is present. We have given the basioccipito–basisphenoid suture a score of 4 in Table 2, indicating our belief that it was closed and obliterated, even though it is not preserved on the specimen. This suture is one of the first to fuse during ontogeny, and it definitely fuses prior to fusion of the basisphenoid–presphenoid suture, and this latter suture is fused in the holotype. The exceptionally high sagittal crest is rivaled only by that of Recent California sea lions (*Zalophus californianus* (Lesson, 1828)) in which the crest is a diagnostic male secondary sex character (Orr et al., 1970). Males of most fossil and living otariids have at least some development of a crest, but sagittal crests are absent in odobenine walruses.

The rostrum is large and expands distally (Fig. 1a) around the roots of the large upper canines. The anterior narial opening is shaped as an elongated oval and is bordered by rounded margins of the premaxillae. Immediately anterior to the narial opening, the premaxillae protrude to form a prominent, slightly up-turned tuberosity. Such a tuberosity is primitively present in various otariid pinnipeds, especially members of the Otariinae and Imagotariinae. There is no prominent prenarial shelf as in species of *Allodesmus* (Mitchell, 1966; Barnes, 1972). The convex cheek region of the maxilla around the canine root is very rugose and perforated by many small foramina. Most parts of the sutures between the premaxillae and maxillae are obliterated by fusion. An exception to this is the part of the suture that is adjacent to the nasal bones. The ascending (posterior) process of each maxilla extends posteriorly for approximately one-half of the length of the nasals (Fig. 1a). The nasal bones are elongated and, as in Allodesminae, taper posteriorly to form wedges between the anterior processes of the frontals. Rather than having transversely flat anterior terminations as in most Otariidae, the anterior ends of the nasals of *G. pugnax* are oblique, with retracted medial margins, so that they are separated to form a small gap between them anteriorly.

The anterior processes of the frontals are prominent and, unlike the condition in other known kinds of otariid pinnipeds, are elevated and lap anteriorly over the posterior ends of the nasals and maxillae. Each frontal process is confluent with a prominent antorbital process. Immediately posterior to the nasals, the frontals are cleft medially by a shallow sulcus marking the interfrontal suture. The frontals are elevated and join with the parietals over the intertemporal region and the braincase to form a highly elevated and arched sagittal crest (derived character). This crest is irregular and relatively rugose, indicating prominent temporal muscle attachments, and has a fine median groove marking the course of the obliterated interparietal suture. Over the intertemporal region, the sagittal crest tapers ventrolaterally to the orbital margin, however, posteriorly its vertical sides descend abruptly to the surface of the braincase. Posteriorly the sagittal crest is confluent with the right and left parts of the nuchal crest, that flare posteriorly over and beyond the occipital shield and curve anterolaterally to join the dorsal surface of the mastoid processes. Small scattered foramina pierce the irregular surface of the braincase.

The occipital shield is high and broad. A prominent, median, vertical crest on the supraoccipital extends from immediately dorsal to the foramen magnum to the nuchal crest. A convex area lies dorsolateral to each condyle and extends outward to the nuchal crest. The exoccipitals flare broadly and are somewhat concave posterior to the mastoid processes. There is no indication of a large, posteroventrally projecting paroccipital process, such as occurs primitively in enaliarctine, desmatophocine, and allodesmine otariids (Barnes, 1979, 1989).

Table 2. Degree of closure of sutures of holotype cranium of *Gomphotaria pugnax*, new genus and species, LACM 121508. Suture nomenclature, numbers, and methods follow Sivertsen (1954).

Suture number	Suture name	Degree of closure
I.	Occipito-parietal	4
II.	Squamoso-parietal	4
III.	Interparietal	4
IV.	Interfrontal	3
V.	Coronal	4
VI.	Basioccipito-basisphenoid	4?
VII.	Maxillary	4
VIII.	Basisphenoid-presphenoid	4
IX.	Premaxillary-maxillary	3
Total (suture age)		34

The orbit (Fig. 1b) is small compared to most fossil and Recent pinnipeds, being approximately 68 mm in diameter. In anterior view, the aperture of the large infraorbital foramen is roughly triangular. The dorsal branch of the jugal is centered above it (primitive condition), being neither retracted toward the orbit as in Allodesminae (see Barnes, 1972), nor flared out anteriorly over the infraorbital foramen as in Otariinae. The ventral branch of the jugal ascends from the level of the cheek tooth row, and does not depart from the snout at the level of the cheek tooth alveoli as in Allodesminae. The zygomatic part of the jugal is upturned into a small, thick postorbital process, which has a rather sharp, crestlike posterior margin. Ventral to the orbit, the jugal is thick, and is exceptionally deep where it curves posteroventrally ventral to the zygomatic process of the squamosal and slightly underhangs the anterolateral corner of the glenoid fossa (Fig. 1b, c).

A broad, anteroposteriorly elongate squamosal fossa separates the zygomatic process of the squamosal from the lateral wall of the braincase. This fossa is continuous laterally with a very prominent shelf that projects laterally dorsal to the external acoustic meatus. This shelf extends between the zygomatic process of the squamosal and the vertically expanded, rectangularly shaped, combined mastoid and paroccipital process. The zygomatic process of the squamosal flares anterolaterally and arches anterodorsally, becoming abruptly very slender in its anterior part dorsal to the jugal.

The right bony orbital wall is virtually complete, although the bone surface has many small cracks.

There appears to have been a moderate-sized, somewhat bilobed orbital vacuity approximately in the middle of the orbital wall. The lacrimal foramen has been lost (derived character). Directly posterior to the orbital aperture of the infraorbital foramen is a small sphenopalatine foramen. Within the posterior part of the orbit, the opposing orbital walls are closely appressed, somewhat as in derived species of Otariinae, and not widely separated as in the Recent walrus (*Odobenus rosmarus* (Linnaeus, 1758)). Because of this, the optic foramina of *G. pugnax* are relatively close together. They are located lower on the cranium than in typical Otariinae, but more dorsally than in *O. rosmarus*. The relatively small orbital fissure is ventrolateral to the optic foramen, separated from it by a strut of bone, and located immediately dorsal to the strut of the pterygoid that forms the lateral margin of the palate.

The palate (Fig. 1c) is elongated and its entire surface is perforated by numerous tiny foramina. Relatively small, paired, incisive foramina are present at the anterior end. The cheek tooth rows diverge slightly posteriorly, and between them the median part of the palate is slightly vaulted (derived character). This vaulting is different from that in *O. rosmarus*, because the vaulted portion is narrow and anteroposteriorly elongated, and easily half of the apparent vaulting results from the addition of rugose bony tissue along the lingual side of the cheek tooth alveoli. Between the P^3's are a pair of prominent palatine foramina, in the same location as in species of Enaliarctinae (see Barnes, 1979, 1989), and these foramina are likewise continuous with anteriorly directed sulci (primitive character). These sulci demarcate the medial edge of the abovementioned areas of rugose bone medial to the cheek tooth alveoli. Unlike the homologous palatine foramina in enaliarctinces, which are directed anteriorly, these are nearly vertically oriented (derived character). The infraorbital plate of the maxilla has a thick, rounded border extending posteriorly to the pterygoid region, and there is only a vestigial pterygoid process near the maxilla–palatine suture.

There are no alveoli for I^{1-2}, teeth that are primitively present in most species of otariids, and in *G. pugnax* the place that such teeth occupy in other pinnipeds is merely a rugose pad of bone (derived character). The two very large I^3's were present; the alveolus for left I^3 is crushed, but the uncrushed, procumbent, right one is oval in cross section and measures approximately 22.5 mm transversely by 33.3 mm anteroposteriorly. The canine, developed into a tusk, is also very procumbent and very large. Although the apex of the crown of the right canine was badly broken by earth-moving machinery, enough remains to show that it suffered extreme abrasion during life. There is no trace of any enamel remaining on it. The root is deeply fluted by alternating longitudinal grooves and ridges, and has thick deposits of cementum. To the point of breakage, the right canine of the holotype extends 135 mm from the alveolus and we estimate that in life it extended more than 150 mm from the alveolus. At the alveolar margin, the canine root measures 69.5 mm anteroposteriorly by 49 mm transversely. The crown of the canine tapers and curves slightly ventrally and medially.

The row of five cheek tooth alveoli on either side of the palate is oblique to the sagittal plane in the mouth, extending from the posteromedial side of the canine to the lateral side of the palate near the base of the zygomatic arch. The maxilla extends ventrally along the labial border of the alveolar row, with pointed projections separating the alveoli. The alveoli are for five cheek teeth identified as P^{1-4} and M^1. They are slightly procumbent and crowded, so that interalveolar septa are thin or absent. The middle tooth, P^3, is deeply rooted, with an alveolus approximately 33 mm deep. The alveoli of the more anterior and posterior teeth are less deep. The alveoli of P^{1-4} are circular, whereas that for M^1 is bilobed. The alveolus for P^1 is very shallow (*ca.* 10 mm). In fact, owing to its proximity to the root of the canine tusk, it could not have been much deeper. The alveolus for P^2 is approximately 30 mm deep, and that of the P^4 is approximately 22 mm deep. The shallow, bilobed alveolus for M^1 indicates that the root of that tooth had a vestige of the double-rooted condition (primitive).

Because of the extensive damage to the basicranium (Fig. 1c), only part of the right squamosal and ear region can be described. The glenoid fossa is broad with rounded edges and with a ventrally deflected anterolateral corner. The external acoustic meatus is anteroposteriorly compressed between the postglenoid and mastoid processes (derived condition), and a space of only approximately 15 mm separates the two processes. The entrance to the external acoustic meatus is therefore narrow and high, in contrast with the situation in *Imagotaria downsi* Mitchell, 1968, for example, in which the entrance to the meatus is broad and low, even though the inframeatal lip is wrinkled from anteroposterior compression. The dorsal surface of the external acoustic meatus of *G. pugnax* is perforated by several small holes, not usually present in otariids, and these may be the result of some pathology. The inframeatal lip bears a small foramen 2.5 mm in diameter. The aperture of the stylomastoid foramen is large and, as in *I. downsi* and *Pontolis magnus* (True, 1905a), is directed anterolaterally toward the inframeatal lip.

The tympanic bulla is mostly broken away to reveal a natural internal cast of siltstone. We left this matrix cast intact because it is our only indication of the former size and shape of the bulla. The entire bulla was positioned posteromedial to the glenoid fossa, in the primitive carnivoran and otariid condition. The matrix cast indicates that the tympanic cavity was large and nearly spherical, with a somewhat flattened medial side. Its size indicates that the ventral surface of the bulla descended to a point ventral to the postglenoid and mastoid pro-

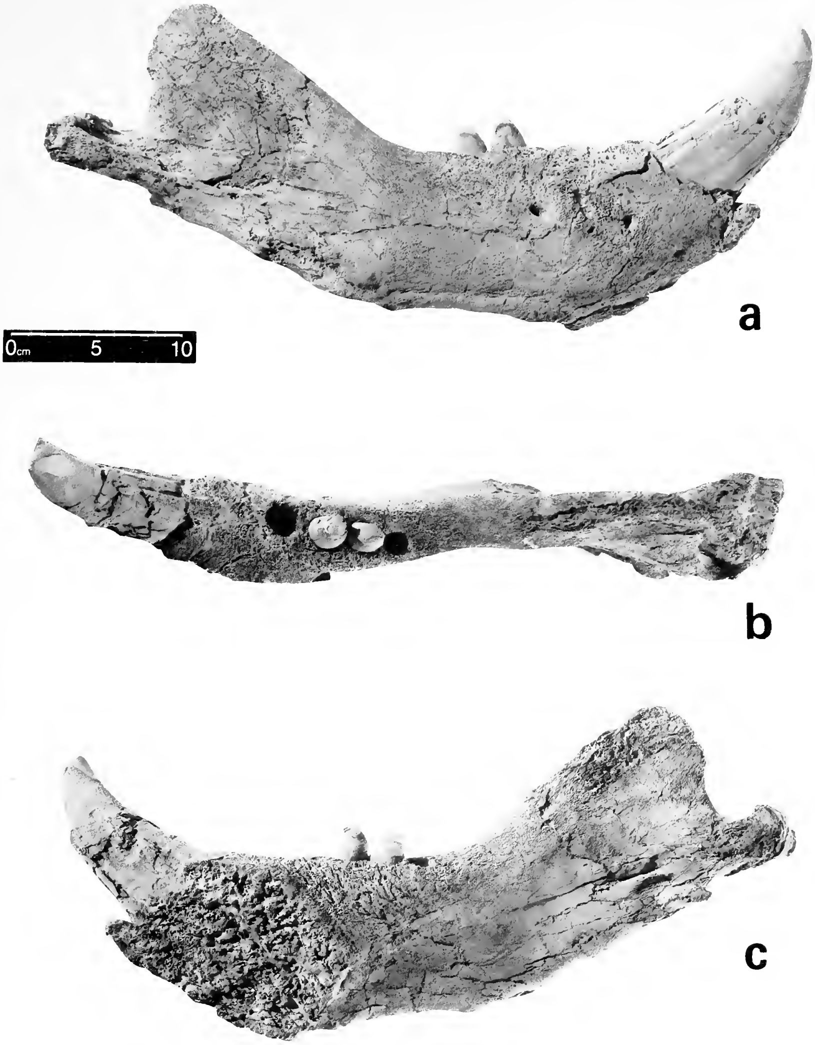

Figure 2. *Gomphotaria pugnax,* new genus and species, holotype right dentary, LACM 121508, from LACM locality 4631; **a,** lateral view; **b,** occlusal view; **c,** medial view.

cesses. This condition is unlike that of the imagotariine *P. magnus,* in which the bulla is flat and does not project ventral to the surrounding processes.

Dentary. The holotype of *G. pugnax* includes a complete right dentary and an incomplete left dentary (Fig. 2, Table 3). The horizontal ramus is deep dorsoventrally, like that of *Dusignathus santacruzensis,* but is much thicker transversely, with its thickest portion at the anterior end. The bone surface is very rugose and pitted. A sulcus along the ventrolateral margin of the ramus extends from the posterior margin of the symphysis to just anterior to the angle (Fig. 2a). On the lateral surface of each dentary are four mental foramina; two large, centrally located foramina, and a smaller both anteriorly and posteriorly. Unlike the condition in *D. santacruzensis,* there is no genial tuberosity in *G. pugnax.* The mandibular symphysis (Fig. 2c) is more oval than rhomboidal in shape, unfused, and very rugose. A large fossa is present just posterior to the ventral edge of the symphysis. The dorsal margins of both dentaries have rugose, pitted exostoses along the tooth rows. The coronoid process ascends gradually from the alveolar row and is low and rounded. The masseteric fossa is deep and elongated (Fig. 2a), unlike that of *D. santacruzensis,* in which the fossa is deep but somewhat square. The condyle is large with a laterally directed shelflike strut. A large, medially directed pterygoid process is present.

There are no alveoli for lower incisors, nor space for them, between the two enlarged canines. The lower canines are large, procumbent tusks, smaller

Table 3. Measurements (in mm) of dentaries of *Gomphotaria pugnax,* new genus and species, holotype, LACM 121508. — indicates a measurement was not possible.

	Right	Left
Total length	410.0	378.0
Length alveolar row, C-M_1	182.0	170.0
Length of symphysis	140.5	142.0
Breadth of symphysis	92.5	86.0
Depth of ramus at P_3	100.0	91.0
Anteroposterior diameter alveolus C	59.4	—
Anteroposterior diameter alveolus P_1	—	19.3
Anteroposterior diameter alveolus P_2	21.8	20.2
Anteroposterior diameter alveolus P_3	21.9	21.8
Anteroposterior diameter alveolus P_4	21.6	23.2
Anteroposterior diameter alveolus M_1	15.8	—

than the upper tusks, oval in cross section, with prominent fluting below the crown. The apex of the right canine is intact and is heavily worn. Two patches of thin, smooth enamel remain; one laterally and one posteromedially. A large oblique wear surface on the posterolateral side is from occlusion with the upper canine. A wear surface on the medial side undoubtedly results from occlusion with the large I^3. The anterior face of the crown also shows extreme wear, caused not by occlusion with any other tooth but by external abrasion.

The lower postcanine dentition consists of P_{1-4} and M_1. The lower cheek tooth row is oriented slightly obliquely to the axis of the horizontal ramus. Opposite to the situation with the upper row, it extends from the posterolabial side of the canine to the lingual side of the dentary posteriorly (Fig. 2b). On each dentary of the holotype, one tooth was lost by accident or pathology and its alveolus had become filled with a secondary bony growth. On the right dentary, the P_1 had been lost and, on the left, it was the M_1. Unlike the procumbent upper cheek teeth, the lower cheek tooth alveoli are vertically oriented, and the posterior ones even slope slightly posteriorly. All of the alveoli (and roots) of the lower cheek teeth are nearly round. The largest and most deeply rooted, as with the uppers, are in the middle of the row, with the P_1 and M_1 being the smallest. The cheek teeth are crowded, progressively closer posteriorly, so that there is virtually no interalveolar septum between the P_4 and M_1.

There is a large (15 mm) diastema between the posterior margin of the canine alveolus and P_1. The left P_1 alveolus is approximately 11 mm deep. The P_2 alveoli are 24 and 28 mm deep. The left P_3 alveolus is 37.5 mm deep, and the right tooth is in place in the dentary. The root of the right P_3 has thick cementum and a longitudinal groove on the labial side (Fig. 2a), a vestige of an earlier, more primitive, two-rooted condition. The crown of this tooth is almost entirely worn off, but enough remains to indicate that it was circular in cross section and had smooth, thin enamel.

The left P_4 alveolus is approximately 28 mm deep, and the right P_4 is also in place in the dentary. This tooth resembles the P_3, and also has a faint longitudinal labial sulcus on its root (Fig. 2a). The crown is similarly worn off, but sufficient parts of it remain to show that there is a relatively prominent, smoothly rounded lingual cingulum. The right alveolus for M_1 is approximately 20 mm deep and indicates that the root of this tooth was circular in cross section.

Forelimb. Association of the right forelimb with the holotype is critical because the bones serve to differentiate this species from at least two other walrus-like fossil taxa that are not known by crania or mandibles (see comparisons in Discussion). The humerus of the holotype is fused pathologically at the elbow joint with the radius and ulna (Fig. 3a). This fusion is of unknown cause, but is an arthrosis in the general sense. Exostoses at the joint are massive; however, the diagnostic characters of the bones are clearly visible.

The humerus is relatively elongated, with an elongated, anteriorly directed deltoid crest. As in species of Otariinae and *Allodesmus,* the deltoid crest has a nearly straight anterior border, and curves rather abruptly to the shaft of the bone distally. The head of the humerus is relatively large, and the greater tuberosity extends proximally beyond it. As in walruses in general and in *Valenictus imperialensis* Mitchell, 1961, the deltoid tuberosity is on the lateral side of the deltoid crest.

The radius is relatively short and stout, although less so than the radius belonging to the forelimb of an unidentified walrus-like pinniped that was reported by Mitchell (1962) from the Purisima Formation at Santa Cruz. This specimen (LACM 3011) has limb bones that are more massive than any pinniped yet described, with the possible exception of the aberrant walrus-like *V. imperialensis.* The forelimb from Santa Cruz was identified as a possible new genus and species of odobenid by Mitchell (1962) and was tentatively assigned to *D. santacruzensis* by him (Mitchell, 1975:19) and by Repenning and Tedford (1977). Lacking associated

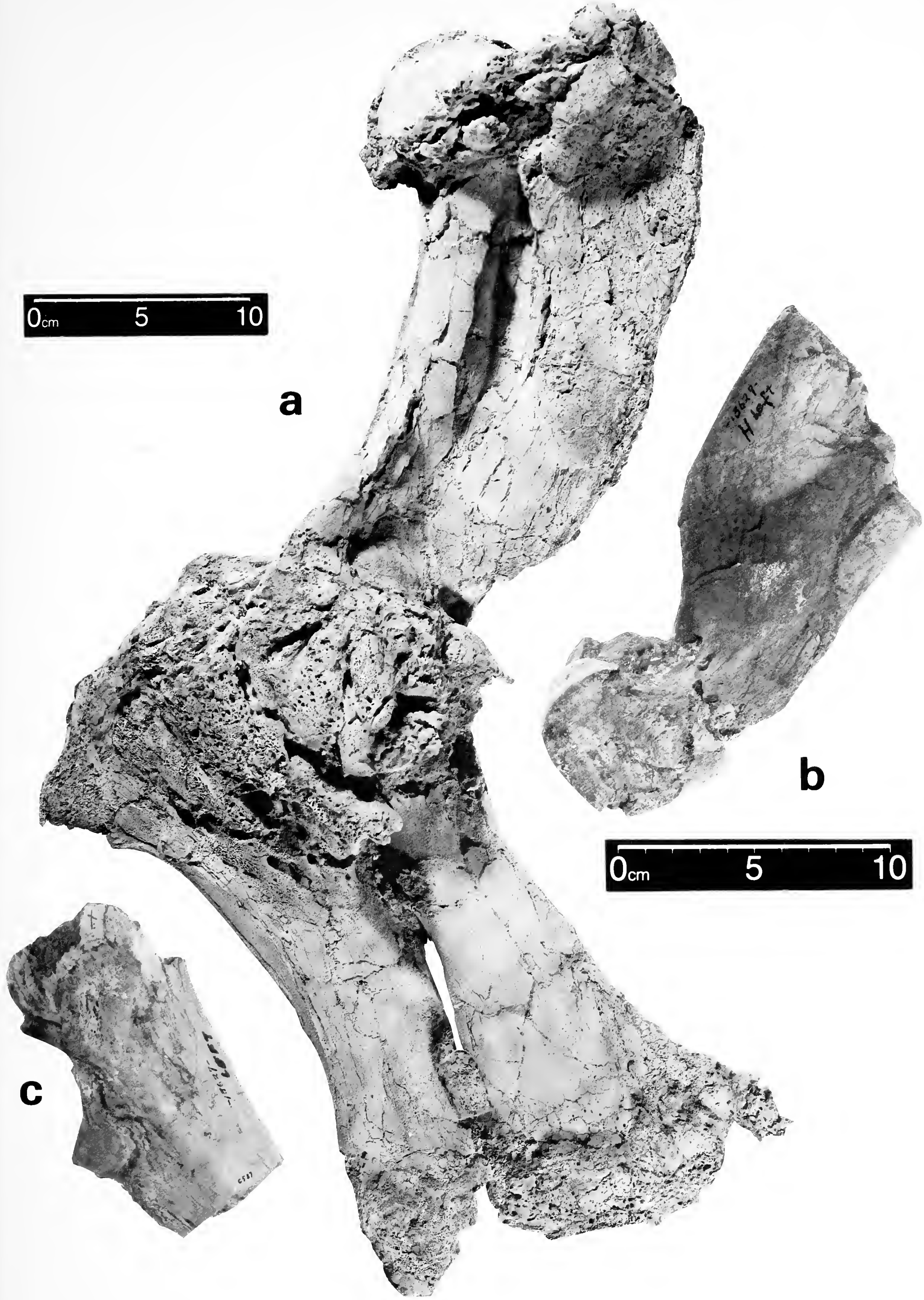

Figure 3. Forelimb bones of fossil pinnipeds; **a,** *Gomphotaria pugnax,* new genus and species, holotype, right humerus, radius, and ulna, pathologically fused at the elbow joint, LACM 121508, from LACM locality 4631, lateral view; **b** and c, *Pliopedia pacifica* Kellogg, 1921, holotype, USNM 13627; **b,** distal end of left humerus, lateral view; **c,** proximal part of left ulna, lateral view; to different scales—scale bar for **a** at upper left and scale bar for **b** and **c** at lower right.

cranial material, and in light of the variety of walrus-like pinnipeds now known to have existed in latest Miocene time, identification of these bones remains tenuous. The shaft of the radius of *G. pugnax* is nearly circular at midlength. Distally the radius expands anteriorly, and on its lateral surface it bears two deep ligamental grooves as is typical of Imagotariinae and Odobeninae (see Repenning and Tedford, 1977).

The ulna of *G. pugnax* is also stout, but it is more slender than the ulna that was found associated with the radius (LACM 3011) from Santa Cruz cited above. The olecranon process of the ulna is large, broad, and flares posteriorly. Its shape is very unlike the narrower and more knoblike olecranon processes on ulnae of typical fossil and Recent odobenine walruses and of the ulna (LACM 3011) from Santa Cruz. The closest similarities to *G. pugnax* among described fossil pinniped ulnae are those that have been assigned to Imagotariinae (e.g., Repenning and Tedford, 1977:pl. 13, figs. 1, 2).

DISCUSSION

PALEOBIOLOGY

The dentition of *G. pugnax* is very unusual for a pinniped, both in its composition and in its apparent use during life. As in Recent walruses, the only remaining incisors, upper or lower, are the I^3's. In *G. pugnax,* the I^3's are large and procumbent, whereas, in the Recent walrus they are small, premolariform, and have migrated to a position medial to the upper canine (Fay, 1982). No pinniped, fossil or living, has been described with large, procumbent upper tusks like those of *G. pugnax,* although *D. santacruzensis* has smaller upper canines that are nearly as procumbent. No walrus-like fossil has been described with the lower canines developed as tusks also. Only *D. santacruzensis* shows any tendency for elongation of both the upper and lower canines (Repenning and Tedford, 1977); although elongated, these remained caniniform and certainly would not be described as tusks (Kellogg, 1927; Mitchell, 1975). What remains of the cheek teeth of *G. pugnax* indicates that they were peglike. Their crowns are unknown, obliterated on the holotype by random breakage in life and subsequent massive wear.

Clearly *G. pugnax* was not eating fish, as do most species of living otariids (King, 1983), which have normal-sized canines and pointed cheek teeth that do not normally incur such severe wear and breakage. *Gomphotaria pugnax* did not have large eyes, as do sea lions and seals and, therefore, probably did not dive to great depths in search of food. For this reason, and also because its teeth do not resemble those of the living elephant seals (*Mirounga* spp.), it is also unlikely that it was a squid eater. The wear on the upper and lower canines, especially the anterior surfaces, indicates that these teeth probably contacted the ocean substrate during feeding. The substrate could have been fine sediments or even rocky surfaces, but in either case, the prey items would have been benthic invertebrates. The closest living analogy to this type of food item would be the prey of the Recent walrus (see Fay, 1982), although the method of feeding must have been different. Living walruses have highly vaulted palates, no anterior incisors, and vertically oriented tusks. They feed in relatively shallow water (being the shallowest divers among the otariids) by probing sandy or silty substrates with the sensitive muzzle and vibrissae, and eat mostly bivalved mollusks as well as a variety of soft-bodied invertebrates such as tunicates, polychaete annelid worms, priapulid worms, and sea cucumbers (Fay, 1982). The soft-bodied animals are ingested whole. Walruses, however, do not chew up the shells of mollusks to get at the soft parts. The shells are held with the large lips, and using the tongue like a piston within the highly vaulted mouth, the soft inner tissues are sucked out. The shells are mostly discarded empty and nearly intact; they are not masticated by the cheek teeth and are not found in stomach contents (see Fay, 1982).

Unlike walruses, however, *G. pugnax* does not have a highly vaulted palate, indicating that it probably was unable to suck out the soft parts of shelled mollusks using its tongue as a piston. The extensive breakage and wear of its teeth indicate either that the food items with hard parts were ingested whole and chewed or that rocks were ingested with the food. It would seem that *G. pugnax* probably had a diet that included hard-shelled benthic invertebrates such as mollusks. Because the canine tusks are very procumbent and are present in both the upper and lower jaws, the angle of approach that *G. pugnax* took to the bottom and the way it probed the substrate must have been quite different from that of walruses. Because the rostrum is shaped more like that of a sea lion than a walrus, it probably did not have a broad muzzle with specialized vibrissae such as modern walruses use to locate food.

In life, *G. pugnax* was apparently a huge, heavy-bodied pinniped, with a high forehead (at least in the males, like the California sea lion, *Z. californianus*) and small eyes. It probably had a very fleshy mouth, but no proboscis like an elephant seal and no broad muzzle like a walrus. The lower lips might have been as large as the upper lips of living walruses. Its long, procumbent anterior teeth must have projected outward from its mouth, there being no way that its lips could have covered them. The large upper canines curved outward and downward with the smaller pair of procumbent I^3's between them. The lower canine tusks curved upward and outward between the upper tusks.

The extensive pathology of the right elbow joint indicates that the animal probably lived with its disability for a considerable period of time prior to its death at an extremely old age. The pathologic fusion of the joint may have inconvenienced the animal but apparently did not prevent it from swimming and feeding. Even if there was some swimming impairment, the postulated mode of feeding in shallow water on bottom-dwelling invertebrates would not have required such agile swimming as does the capture of fish or squid.

PHYLOGENY AND CLASSIFICATION

The carnivore family Otariidae, used here in the broad sense (see Mitchell, 1968, 1975; Barnes, 1979, 1987, 1989; Barnes, Domning, and Ray, 1985:table 1), includes the living sea lions, fur seals, walruses, and their extinct fossil relatives. This broadly constructed family is equivalent to the superfamily Otarioidea as it was used by Tedford (1976), Repenning (1976), Repenning and Tedford (1977), Muizon (1978), and King (1983). The fossil record of this family, dating back to the latest Oligocene or earliest Miocene (Barnes, 1979, 1989), documents a surprising diversity of taxa. This diversity affects the classification of the extant species and our interpretation of their phylogeny.

As new fossil discoveries provided evidence of past diversity among the extinct otariids, various family groups were established to recognize the lineages (see Barnes et al., 1985). Mitchell (1968) recognized six subfamilies in a single family, the Otariidae (*sensu lato*), including walruses. In this arrangement, the dusignathines were separate from the odobenines. Later, Mitchell and Tedford (1973) added another, very primitive subfamily, the Enaliarctinae. When Repenning and Tedford (1977) reviewed the group, they merged the Dusignathinae with the subfamily Imagotariinae, a group of animals with walrus-like and dusignathine-like characters (principally postcranial) and sea lion-like dentitions and skulls. Repenning and Tedford regarded Dusignathinae as the senior synonym of Imagotariinae on the basis of page priority and classified the Dusignathinae within the family Odobenidae (walruses). Barnes (1989) presented a classification of Otariidae, to include Odobenidae, with separate subfamilies (e.g., Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Dusignathinae, Imagotariinae, and Odobeninae), much as they were recognized by Mitchell (1968). We follow Mitchell (1968) in recognizing both Imagotariinae and Dusignathinae as subfamilies in the family Otariidae (including Odobenidae, see also Hall, 1981).

In reviewing the literature regarding fossil walrus-like pinnipeds from the west coast of North America, one finds that the species in the subfamilies Imagotariinae, Dusignathinae, and Odobeninae have been classified separately or together in a variety of subfamilies or families. Such varying classifications can be traced back as far as the original description of the type genus of the Dusignathinae, *D. santacruzensis*. Kellogg (1927) originally recognized that it had both sea lion-like and walrus-like features, but classified it in the family Otariidae, rather than in the Odobenidae. In using it to establish the new subfamily Dusignathinae, Mitchell (1968) pointed out its unique derived characters. Repenning and Tedford (1977), influenced by its walrus-like features, assigned it to the subfamily Dusignathinae (including Imagotariinae) in the family Odobenidae with modern walruses.

Uniting *G. pugnax* with *D. santacruzensis* in the Dusignathinae, and excluding them from the Imagotariinae are the following shared characters: sagittal crest present; vertical median crest present near apex of occipital shield; tympanic bulla inflated, not flat; stylomastoid foramen round, its aperture angled anterolaterally toward external acoustic meatus; mandibular condyle located at level of alveolar border of dentary; horizontal ramus of dentary relatively short, deep dorsoventrally, and bent upward at posterior part; coronoid process recumbent; enamel on teeth relatively thin and smooth; tendency toward extreme wear on tooth crowns; tendency for accretion of cementum to tooth roots; very long I^3, with long slender roots; loss of lower incisors; procumbent, elongate canines; absence of posterior crista on canine crowns; lower canine crowns with wear on anterior surfaces; lower canine roots three-sided in cross section; four premolars and one molar in each dentary; presence of a smooth lingual cingulum on cheek teeth.

Clearly, with their specialized morphologies, *D. santacruzensis* and *G. pugnax* are not walruses, although they have some walrus-like features. They also have some sea lion-like features that are derivable from the imagotariines. As Kellogg (1927) noted, *D. santacruzensis* also is intermediate in its features (see Mitchell, 1968). Dusignathinae may share a common ancestry with Odobeninae, but none of the known species could have been ancestral to them because true odobenines are contemporaneous with both *D. santacruzensis* and *G. pugnax*. Imagotariinae are still morphologically the most likely antecedents for both the Dusignathinae and the Odobeninae (Repenning and Tedford, 1977).

The work of Mitchell (1966, 1968, 1975) showed that a great number of extinct fossil animals in different lineages have acquired a sea lion-like habitus. The work of Repenning and Tedford (1977) demonstrated that an otariid need not have tusks to be related to walruses. The present study indicates that the fossil dusignathines were a relatively diverse group with members that were at least partly convergent upon walruses.

FOSSIL WALRUSES AND FOSSIL WALRUS-LIKE PINNIPEDS

Because several latest Miocene and/or Pliocene fossil pinnipeds with varying degrees of walrus affinities have been classified in the subfamilies Imagotariinae, Dusignathinae, or Odobeninae (walruses), they are summarized in Table 4 and their differences from *G. pugnax* are discussed in the following text. Although the systematics and relationships of several of these taxa remain obscure

Table 4. Nominal species of fossil Odobeninae and Dusignathinae, listed alphabetically within originally assigned genera.

Taxon	Age	Type material	Subfamily assignment
Alachtherium cretsii	Pliocene	Dentary	Odobeninae
Alachtherium antverpiensis	Pliocene	Dentary	Odobeninae
Aivukus cedrosensis	Latest Miocene	Skull, forelimb	Odobeninae
Dusignathus santacruzensis	Latest Miocene	Skull	Dusignathinae
Gomphotaria pugnax	Latest Miocene	Skeleton	Dusignathinae
Odobenus mandanoensis	Pleistocene	Dentary	Odobeninae
Pliopedia pacifica	Latest Miocene	Forelimb	Uncertain
Pontolis magnus	Latest Miocene	Braincase	Imagotariinae
Prorosmarus alleni	Pliocene	Dentary	Odobeninae
Trichecodon huxleyi	Pleistocene	Tusk	Odobeninae
Trichecodon koninckii	Pleistocene	Tusk	=*T. huxleyi*
Valenictus imperialensis	Latest Miocene	Humerus	Uncertain

because they are not known by comparable anatomical parts, *G. pugnax* can be distinguished from each of them.

Alachtherium spp.

Two nominal species from Europe have been assigned to the primitive odobenine walrus genus, *Alachtherium* DuBus, 1867: *Alachtherium cretsii* DuBus, 1867; and *A. antverpiensis* (Rutten, 1907). There are problems with the typology of these species of *Alachtherium* and the identification of referred specimens (Repenning and Tedford, 1977: 12–13). Both species have an unfused mandibular symphysis and mandibular morphology indicating that the upper canine was a tusk. The type species of the genus is *A. cretsii* DuBus, 1867. Its holotype dentary, from Early Pliocene (*ca.* 4 Ma) deposits in Belgium, may be compared directly with the type material of *G. pugnax*, and has been illustrated by Van Beneden (1877) and Berry and Gregory (1906).

Gomphotaria pugnax differs from *A. cretsii* by having a more horizontally elongate dentary in which the posterior end is not elevated above the cheek tooth row, a straighter horizontal ramus, a larger coronoid process, a broader symphyseal surface, by having a smaller pterygoid process, by lacking lower incisors, having an unreduced lower canine, and retaining the M_1.

Aivukus cedrosensis Repenning and Tedford, 1977

The primitive odobenine walrus, *Aivukus cedrosensis*, is known from the latest Miocene part of the Almejas Formation on Isla Cedros, Mexico. Its holotype cranium, mandible, and forelimb bones may be compared directly with those of *G. pugnax*. Cranial characters of *G. pugnax* that distinguish it from *A. cedrosensis* are: presence of the sagittal crest; broader rostrum; border of anterior narial opening relatively rounded, not so sharply edged; frontal–maxillary suture forming a broad V, not nearly straight across; cheek surface of maxilla not so flat or so deep dorsoventrally; zygomatic process of jugal more slender with relatively smaller postorbital process, and longer posterior process extending posteriorly beneath squamosal; orbit smaller; palate not so highly vaulted; lateral margins of palate not extended so far ventrally; preglenoid process present (to more firmly hold mandibular condyle); external acoustic meatus more compressed anteroposteriorly between mastoid and postglenoid processes; more prominent crest projecting laterally dorsal to external acoustic meatus; exoccipital directed more posteriorly and lacking a rather well-formed lateral border that projects posteriorly; mandibular symphysis relatively much larger, more rounded in shape, and extending much further posteriorly (to a point ventral to the P_4); presence of an elongate ridge along the ventrolateral margin of the dentary; horizontal ramus of dentary nearly straight, not bowed laterally; presence of only one upper incisor in each premaxilla instead of two; I^3 not so round in cross section, but more compressed transversely; upper and lower canines relatively larger and of large diameter, more procumbent, and having fluted roots; P_1 much more shallowly rooted; and M_1 with a large round root instead of a small bilobed root. In *A. cedrosensis* the frontal–maxillary suture is nearly transverse and is aligned with the posterior part of the nasal bones (the restoration in Repenning and Tedford, 1977: fig. 1A is idealized), instead of being in the form of a splint of the maxilla projecting posteriorly into the frontal and paralleling the posterior part of the nasals as in *G. pugnax* (the primitive condition in Carnivora and Otariidae).

Dusignathus santacruzensis Kellogg, 1927

The only other species that we now assign to the subfamily Dusignathinae, *D. santacruzensis*, is from the latest Miocene part of the Purisima Formation near Santa Cruz, California. The holotype consists of a rostral fragment, a squamosal, part of the roof of the braincase, two dentaries, and teeth, all belonging to one individual. All of these parts may be compared directly with the type material of *G. pugnax*. The generic diagnosis of *Gomphotaria* lists characters differentiating it from *Dusignathus,* and need not be repeated here.

Subsequent to Kellogg's original (1927) publication, Mitchell (1966:34–36, 1968:1888, 1894–1895, 1975:18–19) and Repenning and Tedford (1977:43–48) have discussed *D. santacruzensis,* and Mitchell (1968:fig. 16, 1975:fig. 1) and Repenning and Tedford (1977:fig. 6) showed it on phylogenies. Mitchell (1975:fig. 7) reillustrated the holotype squamosal and (1975:fig. 8) showed a possible skull reconstruction. Repenning and Tedford (1977:pl. 5, fig. 3a, b) published photographs of the holotype dentary, and (1977:pl. 15, figs. 10–17, 19, 20, 22; pl. 16, figs. 1, 3, 5) of referred and questionably referred postcranial bones from other localities. These referrals are of course subjective, because the holotype included no postcranial bones, and for our purposes, we have restricted our comparisons to the holotype.

The holotype of *G. pugnax,* which includes a baculum, is a male, and the holotype of *D. santacruzensis,* based on its small-diameter canines, might be a female. We do not believe that the two specimens represent different sexes of the same species because the relative size differential between the two holotypes is greater than the sexual size dimorphism among other species of otariids. Additionally, compared with that of *G. pugnax,* the dentary of *D. santacruzensis* is thinner transversely, less massive in overall build, the horizontal ramus is deep dorsoventrally rather than elongate as in *G. pugnax,* and the differential between the diameter of the canine and the diameters of the cheek tooth alveoli is proportionally much less.

***Odobenus* spp.**

Although living walruses, *Odobenus rosmarus,* are Arctic in distribution (Fay, 1982), it and/or similar species were distributed farther south in both the North Atlantic and the North Pacific oceans in prehistoric, Pleistocene, and Pliocene time (e.g., Ray, 1960:137–138, 1977). One extinct Pleistocene species has been well founded on a mandible: *Odobenus mandanoensis* Tomida, 1989, from Japan.

Recent and Pleistocene *Odobenus* differ from all fossil odobenines by lacking (in adulthood) upper I^{1-2} and the lower incisors, by having an I^3, which is premolariform and in line with the upper premolar row, by having reduced or absent posterior premolars, and by having a fused mandibular symphysis. *Gomphotaria pugnax* differs from *Odobenus* spp. by having an unfused mandibular symphysis, large, procumbent I^3's, more procumbent upper canines, enlarged lower canines, and the suite of cranial characters used here to diagnose the genus *Gomphotaria* and the subfamily Dusignathinae.

***Pliopedia pacifica* Kellogg, 1921**

Pliopedia pacifica, a problematic and poorly known latest Miocene, walrus-like pinniped from the Paso Robles Formation near Santa Margarita, central California, was based only on forelimb bones, formerly Stanford University No. C. 537, now USNM 13627 (the holotype). The holotype humerus and ulna of *P. pacifica,* illustrated and described by Kellogg (1921:figs. 1a–d, 4a–c), are reillustrated here in lateral views (Fig. 3b, c). The forelimb bones of *G. pugnax* differ from the comparable bones of *P. pacifica* in the following ways: (1) the deltoid crest of the humerus is narrower transversely with a more abrupt change of slope along its anterior border than in *P. pacifica;* (2) the humerus lacks the prominent lateral crest that is confluent with the lateral epicondyle in *P. pacifica;* (3) the posterior surface of the distal end of the shaft of the humerus is distinctly convex, not flat to concave as in *P. pacifica;* (4) the shaft of the ulna is broader anteroposteriorly, with a thicker and more curved posterior border; and (5) the olecranon process is larger than it could possibly have been in *P. pacifica,* judging by the width of the ulna of the latter. The homologous bones of the two species are sufficiently different to indicate that they are not synonymous and are probably not even very closely related. Upon reexamination, the partial skeleton from the Kettleman Hills that Repenning and Tedford (1977) referred to *Pliopedia pacifica* appears (Barnes and Perry, in prep.) not to be *P. pacifica,* and we limit our consideration of *P. pacifica* to its holotype.

***Pontolis magnus* (True, 1905a)**

Another large pinniped, of the same geologic age as *G. pugnax,* is *Pontolis magnus.* The holotype of this species is an incomplete posterior part of a cranium (see True, 1905a, b, 1909; Mitchell, 1975; Repenning and Tedford, 1977) from the latest Miocene part of the Empire Formation at Coos Bay in central coastal Oregon. At first, Mitchell (1968) was equivocal, indicating that *P. magnus* might be either an imagotariine or an odobenine. Later (1975) he considered it to be a derived imagotariine otariid (and see Barnes, 1989:23), and we agree with this. In an alternative classification, Repenning and Tedford (1977) classified it as a dusignathine (Dusignathinae including Imagotariinae) odobenid otarioid. Significantly, the broad relationships understood by Mitchell (1975) and Repenning and Tedford (1977) for this species are similar, but the hierarchical levels of their classifications differed.

Mitchell (1968:1878–1879) has suggested that an isolated squamosal and ear region (LACM 8915) from the latest Miocene part of the Capistrano Formation in Orange County, California, might represent *P. magnus* or some other large otariid pinniped. On comparing this squamosal with the more completely prepared and reillustrated holotype of *P. magnus* (see Mitchell, 1975:fig. 9; Repenning and Tedford, 1977:pl. 18, fig. 5), we concluded that the two specimens are conspecific. Therefore, the holotype and this referred squamosal serve as the basis for our comparisons between *P. magnus* and *G. pugnax.* This comparison is especially relevant because the species are contemporaneous, and both occur in the Capistrano Formation.

The holotypes of *P. magnus* and *G. pugnax* both represent large, fully adult individuals. *Gomphotaria pugnax* differs from *P. magnus* in the following ways: (1) its mastoid process is relatively smaller, more vertically oriented, and it is broad and not tapered dorsally; (2) the lateral surface of the zygomatic process of the squamosal is nearly vertically oriented, not sloping, the process is more tapered anteriorly, and is less deep dorsoventrally; (3) a shelf of squamosal bone dorsal to the external acoustic meatus is broader (i.e., extends farther laterally) and is confluent with a deeper, more anteroposteriorly elongate squamosal fossa; (4) the lateral part of the nuchal crest is broadly flaring where it merges with the squamosal bone above the mastoid process, a condition that is absent in *P. magnus;* (5) the tympanic bulla is much more inflated and extends ventrally well below the postglenoid process, whereas it is extremely flat (even somewhat concave) in *P. magnus;* (6) the aperture of the stylomastoid foramen is more round, more anterolaterally directed, and not so distinctly separated by a ridge of bone from the posteroventral border of the external acoustic meatus; (7) the dorsal part of the nuchal crest is thin and sloping posteriorly in contrast with the thickened and more vertically oriented crest of *P. magnus;* (8) a prominent, broad, vertical crest is present on the occipital shield, but is absent in *P. magnus;* (9) the occipital shield is broader than in *P. magnus;* and (10) the braincase is relatively narrower and lower vaulted than in *P. magnus.* The two species are clearly distinct and the differences cited here indicate that their separation at the subfamily level is warranted.

Prorosmarus alleni **Berry and Gregory, 1906**

Prorosmarus alleni, a primitive odobenine (Mitchell, 1968:1897), is known only by the holotype dentary from the Early Pliocene age (4 to 5 Ma) Yorktown Formation in Virginia. Subsequent to its original description, the species has been discussed and shown on phylogenies by Mitchell (1966:34–36, 1968:fig. 16, 1975:fig. 1) and Repenning and Tedford (1977:13–14, fig. 6). A very accurate cast of the dentary was illustrated by Repenning and Tedford (1977:pl. 2, fig. 4; pl. 5, fig. 4a, b). *Prorosmarus alleni* has an unfused mandibular symphysis, two lower incisors in a common otariid arrangement anteromedial to the lower canine, a small and premolariform lower canine, lower premolars with large, round roots, and a medial constriction of the anterior part of the dentary that indicates that the upper canine was a tusk.

Gomphotaria pugnax differs from *P. alleni* by having a differently shaped dentary, larger symphysis, no lower incisors, the lower canine developed as a tusk, and the M_1 present.

Trichecodon huxleyi **Lankester, 1865**

This is a large Pleistocene odobenine walrus, originally described on the basis of tusks from Great Britain and subsequently known by specimens from elsewhere in Europe and in eastern North America (see Ray, 1960). The species is sometimes classified in the genus *Odobenus* (e.g., Repenning and Tedford, 1977:55). Another nominal species, *Trichecodon koninckii* Van Beneden, 1877, is of doubtful validity (see Repenning and Tedford, 1977:55). *Gomphotaria pugnax* differs from *T. huxleyi* by having tusks that are smaller, less curved, and which lack elongate sulci on the medial sides.

Valenictus imperialensis **Mitchell, 1961**

Another problematical walrus-like pinniped of uncertain affinities is *V. imperialensis* Mitchell, 1961. This species is based solely on an isolated humerus, of latest Miocene age, from the Imperial Formation in Imperial County in the extreme southern part of California. Repenning and Tedford (1977:pl. 16, figs. 1, 2, 7) also illustrated and discussed the holotype and a referred humerus from the latest Miocene San Joaquin Formation in California's San Joaquin Valley. *Valenictus imperialensis* is not particularly closely related to *G. pugnax,* nor to any of the other described walrus-like otariids for that matter. It has definite walrus affinities, but more precise determination of its relationships is not possible at this time.

The humerus of *G. pugnax* is very different from that of *V. imperialensis* by: (1) being more elongate and less stout; (2) having a thinner and higher deltoid crest; (3) having a smaller deltoid tuberosity located more distally (at the midpoint) on the shaft; and (4) having the greater tuberosity extending farther proximally relative to the head (in *V. imperialensis* the greater tuberosity is more equal to the height of the lesser tuberosity and of the head).

CONCLUSIONS

Gomphotaria pugnax is a new genus and species of large fossil pinniped that inhabited the North Pacific Ocean off the coast of southern California in latest Miocene time between approximately 5 and 8.5 million years ago. We classify this remarkable new animal in the extinct subfamily Dusignathinae of the pinniped carnivore family Otariidae, and it shares some convergently acquired derived characters with Odobeninae (walruses). The species is based on a pathologic adult male skeleton found in the Capistrano Formation at San Clemente in southern California, U.S.A. (about 33 degrees north latitude). Its rarity as a fossil suggests that this pinniped may have been rare when it lived. The nearly complete holotype skeleton includes all bones necessary to differentiate *G. pugnax* from all previously named otariid pinnipeds. Most importantly, *G. pugnax* is clearly distinguishable from type and referred specimens of all previously described odobenines and dusignathines. Some of these others, however, continue to be known only by fossil bones that are not directly comparable, and there may be some as yet unresolved synonymies among the odobenines and dusignathines.

Gomphotaria pugnax and the approximately contemporaneous *D. santacruzensis* Kellogg, 1927, are the only species that we assign to the subfamily Dusignathinae. *Dusignathus santacruzensis* is known from the Purisima Formation, which is exposed in the sea cliffs near Santa Cruz in central California. *Gomphotaria pugnax* is the more highly derived of the two species. Its cranial and mandibular features are among the most highly derived of any pinniped, but its postcranial osteology is relatively generalized. The suite of characters that distinguishes the Dusignathinae from other otariid groups includes the following: dentary deep, with broadly rounded angle, broad and low coronoid process; I^{1-2} and I_{1-2} reduced or lost; upper and lower canines procumbent and greatly elongated; and cheek teeth with relatively smooth enamel crowns and single, large, round roots.

Gomphotaria pugnax was a huge pinniped, with large procumbent upper and lower canine tusks and upper incisors projecting from its mouth, relatively small eyes, and a highly arched forehead. It probably fed in shallow water mostly on hard-shelled invertebrates such as mollusks. The wear on the anterior surfaces of its tusks indicates that it probably probed the sea floor for food, and extensive tooth breakage and wear indicate that either the food items had hard parts or that rocks were ingested with the food. The inferred food items are similar to those in the diet of Recent walruses. Unlike walruses, however, *G. pugnax* has a relatively flat palate, indicating that it did not employ a specialized method of sucking out the soft parts of shelled mollusks using its tongue as a piston. (Walruses do not chew up the shells of mollusks to get at the soft parts.)

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Two New Species of *Ophidion* (Pisces: Ophidiidae) from Remote Islands of the Eastern Pacific

C. Richard Robins

Natural History Museum of Los Angeles County

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TWO NEW SPECIES OF *OPHIDION* (PISCES: OPHIDIIDAE) FROM REMOTE ISLANDS OF THE EASTERN PACIFIC[1]

C. RICHARD ROBINS[2]

ABSTRACT. Two dwarf species of *Ophidion* are described from islands in the eastern Pacific Ocean. One occurs at Easter Island and in the Marquesas, the other at Mas A Tierra in the Juan Fernandez Islands and at Isla San Felix. The two are sister species differing principally in meristic characters and they appear to be most closely related to American Pacific species. Zoogeographic implications are discussed. Dwarfism in this instance probably is an adaptive response to a predator-rich environment. The loss of sexual dimorphic features in the swim bladder and associated supportive structures is correlated with dwarfism and life in high energy, noisy environments. These shared losses muddle the phylogenetic picture.

INTRODUCTION

Ophidiid fishes occur peripherally in the Pacific Ocean. Species of many genera (*Genypterus, Lepophidium, Cherublemma, Ophidion,* and *Otophidium*) occur in coastal waters of the Americas, but very few are known from the vast reaches of the Pacific. The southern genus *Genypterus* reaches southern Australia, New Zealand, and the Chatham Islands. *Ophidion muraenolepis* described from the Arafura Sea is common around Hawaii in fairly deep waters (Robins, unpublished) and probably is widely distributed. *Ophidion asiro* occurs in the extreme western Pacific and an undescribed species occurs around Samoa. Finally, there is at least one species of *Ophidion* along the eastern coast of Australia. Basically, the family is largely absent from the Pacific Plate. Robins (1961, 1962) reviewed the eastern Pacific species of *Lepophidium* and *Cherublemma* (=*Brotuloides*), Robins and Lea (1979) commented further on *Lepophidium,* and Lea (1980) revised the species of *Ophidion* and *Otophidium* from the Pacific Coast of the Americas, including the Galapagos Islands.

Three expeditions collected the same undescribed species of cusk-eel at Easter Island: Ramsey Parks and the crew of the ketch CHIRIQUI collected nine specimens in 1958; the medical expedition under the direction of Ian E. Efford in 1965 obtained it at five stations; and John E. Randall and G.R. Allen collected it twice in 1969. Randall and D.B. Cannoy obtained three specimens at the Marquesas Islands in 1971. Material of a second undescribed species, from the Juan Fernandez Islands and Isla San Felix, was obtained by divers from the Southeastern Pacific Biological and Oceanographic Program (SEABOP). This report describes these two species and comments on their distribution and relationships.

For material, notes, and other assistance, I am indebted to Ian E. Efford of the University of British Columbia (BC), David K. Caldwell, Jack Grove, and Robert J. Lavenberg, and Daniel M. Cohen of the Natural History Museum of Los Angeles County (LACM), Don E. McAllister of the National Museum of Canada (NMC), Richard H. Rosenblatt, and the late Carl L. Hubbs of the Scripps Institution of Oceanography (SIO), William N. Eschmeyer of the California Academy of Sciences (also for Stanford University (SU) material now housed at this institution (CAS)), Ernest A. Lachner, W.R. Taylor, and Stanley H. Weitzman of the National Museum of Natural History (USNM), Myvanwy Dick and Karsten Hartel of the Museum of Comparative Zoology, Harvard University (MCZ), Alfred W. Ebeling and Keith S. Thomson of Yale University (BOC), P.H. Greenwood of the British Museum (Natural History) (BMNH), and John E. Randall of the Bernice P. Bishop Museum (BPBM). Randall has made special efforts to obtain specimens and has generously provided notes of life colors and habitat, and photographs. Material from the Smithsonian Oceanographic Sorting Center was made available

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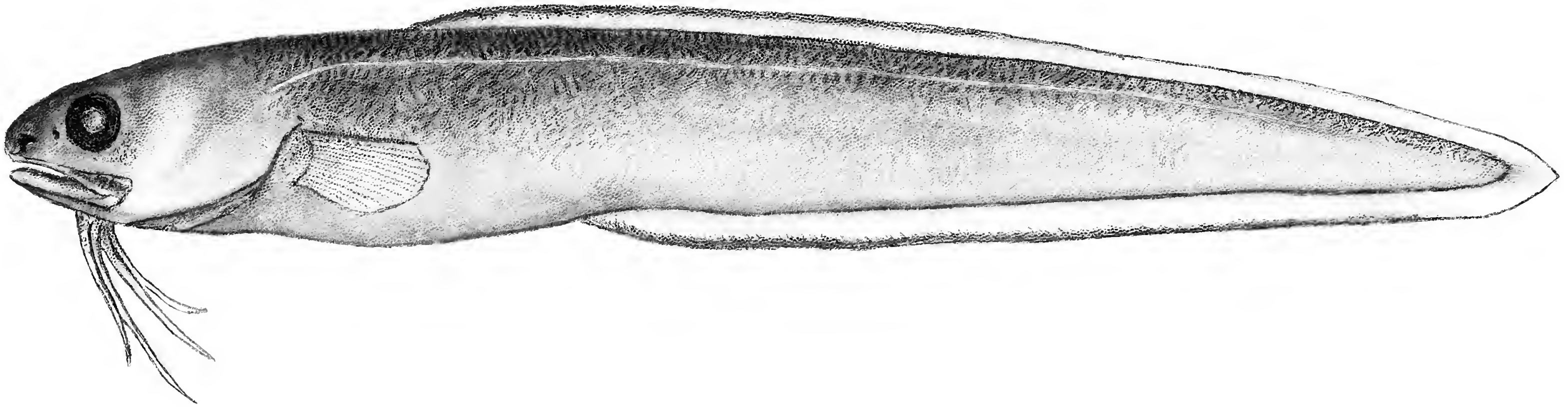

Figure 1. *Ophidion exul,* holotype, NMC 74-524, a male, 93.2 mm SL from Easter Island. Drawn by Catherine H. Robins.

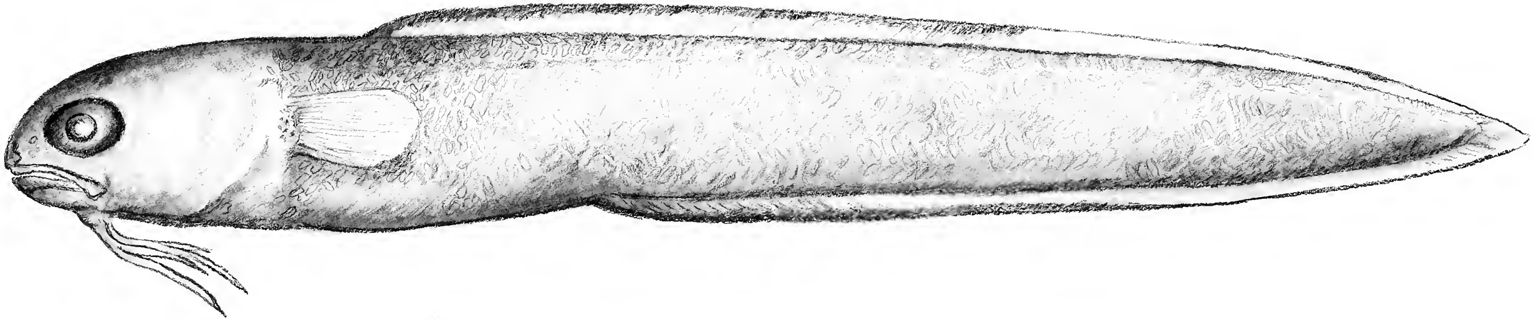

Figure 2. *Ophidion metoecus,* paratype, SIO 65-637, a female, 76.0 mm SL from Isla Robinson Crusoe, Juan Fernandez Islands. Drawn by Catherine H. Robins.

by Leslie Knapp and its advisory committee. Catherine H. Robins prepared Figures 1 and 2 and also commented on the manuscript. This study is part of a program supported by the National Science Foundation (NSF-GB28440X2). Abbreviations in parentheses above are those used in reference to material in the text. Most of this research was done at the author's home laboratory in Miami, Florida.

Ophidion exul new species

Figure 1, Tables 1, 2

No published literature refers to this species.

DIAGNOSIS. Scales ovoid, in staggered rows as in *Anguilla,* head naked, the 2 pelvic-fin rays unequal. Ethmoid process absent. No pyloric caeca. Gill rakers 6 (2 rudiments and 4 developed rakers) on first arch. Vertebrae 69–72 (usually 70–71, anal-fin rays 118–131, dorsal-fin rays 140–152, and pectoral-fin rays 21–24. Longer pelvic ray 13–15 percent of standard length, shorter 9–12 percent. Gas bladder small; a simple sac lacking posterior opening and major bony modifications. Coloration brownish, paler below, without distinctive markings, except margins of vertical fins dark, especially anteriorly and especially in the anal fin.

DESCRIPTION. Frequency distributions of various counts are given in Table 1; Table 2 treats morphometry for the type series. All specimens examined have 9 caudal rays (arranged as is usual in ophidiid fishes [*sensu stricto*], 4 dorsal and 5 ventral) and 7 branchiostegal rays (4 attached to the outer surface of the epihyal and ceratohyal and 3 to the ventral surface of the ceratohyal). Gill rakers were counted on 40 specimens and, with one exception, all have 2 rudiments on the upper arm and 4 short rakers on the lower arm of the first arch for a total of 6 elements. The exception (LACM 6560-2, 113.6 mm SL) has 3 rudiments above and thus a total of 7 rakers. The longest raker generally equals about half the pupil diameter.

There is a single row of small fixed teeth on each palatine bone and a single V-shaped row along anterior edge of head of vomer. Premaxillary and dentary teeth are arranged in a band, best developed in outer row.

The anguilloid squamation covers the entire body except for the head and the course of the lateral line along side of body. However, the scales are deeply imbedded in some areas and, at first glance, the belly, pectoral-fin base, and flanks appear to be naked.

Ophidion exul is elongate, the body being little deeper at the dorsal-fin origin than at occiput or anal-fin origin (Table 2). The two rays of each pelvic fin are unequally developed. The longer (outer) averages 14.8 percent of SL and is possibly proportionally longer in smaller specimens. The shorter (inner) ray averages 10.5 percent of SL. In all instances except one, the pectoral fin was shorter than the shorter pelvic ray.

Life colors are noted from a Kodachrome kindly provided by John E. Randall. Body behind anus and the anterior dorsal half are brown with the lateral line a distinct, pale streak throughout its length. Dorsal and anal fins are pale except for the dark brown edge. Belly and lower half of the sides of head and anterior part of body are whitish with silvery reflections. Pelvic fins are pale except at the basal peduncle. Juveniles are "pale yellowish gray, silvery on head and abdomen, with some dark pigment along base of dorsal and anal fins" (Randall, personal communication). In preservative (see Fig. 1), all are dusky, particularly on the dorsum in smaller specimens, but otherwise without much paling below. Orbit outlined with a narrow dark ring. Dorsal fin is narrowly and sharply edged with dark brown in all specimens. Anal fin is marked similarly in males and small females but is almost unmarked in the series of nine large females (LACM 6560-2). It is unlikely that this mark could have faded in this one series and the dark anal edge probably is a character of males and juveniles. The peritoneum, digestive tract, and oral cavity are pale. The posterior end of the swim bladder is often blackish.

Small specimens (less than 60 mm SL) have the anterior gular region blackish with large scattered melanophores behind and have some deep-seated dark pigment anterior to the eye. One, 45 mm SL, is extreme in these features and has the general facies of the pelagic prejuvenile stage. Presumably, 45 mm SL is about the size at which transformation occurs and a benthic habit is assumed.

The head-pore arrangement does not depart much from that described by Robins (1960:87 and Fig. 2) for *Lepophidium pheromystax.* The supratemporal canal bears 3 pores (the second median), each at the caudal end of very short side canals. The lateral canal contains 1 pore above the posterior half of the dorsal edge of the opercle. The supraorbital canal has 5 pores, 1 above the upper posterior quadrant of orbit, the second a median coronal pore, the third above the anterior edge of orbit, and numbers 4 and 5 above and in front of the anterior nostril. There are 8 pores in each infraorbital canal, 3 on the descending portion of the canal, numbers 4 and 5 below orbit, 6 under the posterior nostril, and 7 and 8 along the preorbital rim behind the anterior nostril. The preoperculomandibular canal bears 8 pores, the first 2 from the end of caudally projecting side canals behind lower half of preopercle, the third at the end of a side canal about halfway forward to corner of mouth, the fourth under the posterior part of maxilla, and the fifth to eighth on alternate sides of mandible near the anterior end of the canal. The anterior pores are difficult to locate in some specimens. The snout tip is ridged and bears a few short papillae at its rim.

All nine specimens collected at Anakena Cove on October 1 (LACM 6560-2) were ripe females. None of those collected in February was ripe.

The swim bladder is a simple, thin-walled sac. It

Table 1. Fin-ray and vertebral counts of *Ophidion exul* (A, B)[1] and *Ophidion metoecus* (C, D).[1]

	Dorsal rays (*O. exul*)												
	140	141	142	143	144	145	146	147	148	149	150	151	152
A	2	4	2	1	3	5	1	1†	2	1	1	3	1
B	—	—	—	—	—	—	2	—	—	2	—	1	—
Total	2	4	2	1	3	5	3	1†	2	3	1	4	2

	Dorsal rays (*O. metoecus*)												
	158	159	160	161	162	163	164	165	166	167	168	169	170
C	1	2	—	1	—	—	—	1	1	5	2	5	6
D	—	—	—	—	—	1	—	—	1	—	—	—	—
Total	1	2	—	1	—	1	—	1	2	5	2	5	6

	Anal rays (*O. metoecus*)												
	129	130	131	132	133	134	135	136	137	138	139	140	141
C	1	2	1	—	2	3	5†	3	4	5	8	5	3
D	—	—	—	—	—	2	—	—	1	—	1	—	—
Total	1	2	1	—	2	5	5†	3	5	5	9	5	3

	Pectoral rays[2]							Vertebrae								
								Precaudal				Caudal				
	21	22	23	24	25	26	27	15	16	17	18	54	55	56	57	58
A	16†	23†	11	2	—	—	—	7	29†	—	—	11	19†	6	—	—
B	—	1	2	5	—	—	—	—	5	—	—	2	3	—	—	—
Total	16†	24†	13	7	—	—	—	7	34†	—	—	13	22†	6	—	—
C	—	—	1	12†	28	15	1	—	5	39†	2	—	—	—	—	1
D	—	—	—	2	6	—	—	—	—	4	—	—	—	—	—	—
Total	—	—	1	14†	34	15	1	—	5	43†	2	—	—	—	—	1

[1] A, Easter I., B, Marquesas Is., C, Juan Fernandez Is., D, Isla San Felix.

[2] Both fins recorded.

† Count includes that of holotype.

is small, confined mostly to the anterior third to half of the body cavity. There is no median rocker bone nor bony encasement of the bladder. The winglike process of the first vertebra (see Rose, 1961) is expanded and is closely associated with the anterior end of the swim bladder.

MATERIAL EXAMINED. Easter Island: HOLOTYPE: NMC 74-524 (formerly BC 65-451), a male, 93.2 mm SL, collected off Hanga Roa, 27°08′37″S, 109°26′10″W in 1–5 m, 2 Feb. 1965. PARATYPES: NMC 74-525 (4 specimens, 71–80 mm SL) and UMML 32674 (3, 79–92 mm SL) collected with the holotype. BC 65-428 (1, 44 mm SL) tide pool at Hanga Piko, 27°08′37″S, 109°26′10″W, 7 Jan. 1965. USNM 213841 (formerly BC 65-453) (2, 71–95 mm SL) also at Hanga Piko, 4 Feb. 1965. BC 65-457 (1, 83 mm SL) at Hanga Roa, date unknown (presumably early Feb. 1965). BC 65-458 (1, 65) at Hanga Roa, 6 Feb. 1965. All material listed above was collected by Ian E. Efford and Jack A. Mathias. LACM 6560-2 (9, 79–131 mm SL) Anakena Cove, east side, 30 m NE of sand beach, 27°03′50″S, 109°19′50″W, in 1–4.5 m, by Ramsey Parks and crew of ketch CHIRIQUI, 1 Oct. 1958 (original field number W58-386). BPBM 6765 (5, 45–81 mm SL) Mataveri o Tai in 6 m, J.E. Randall and G.R. Allen, 2 Feb. 1969. BPBM 6766 (9, 45–73 mm SL) off Aku Akapu in 11 m, J.E. Randall, G.R. Allen, B. Baker, 7 Feb. 1969. BPBM 30546 (1, 91.7 mm SL) off east end of Anakena in 6 m, J.E. Randall, 14 February 1985. BPBM 30547 (1, 40.7 mm SL) off east end of Anakena in 21 m, J.E. Randall and Louis H. Di Salvo, 14 Feb. 1985.

Marquesas Islands (not paratypes): BPBM 10864 (2, 41–45 mm SL) Nuku Hiva, Anaho Bay, in 38–40 m, J.E. Randall, D.B. Cannoy, 2 May 1971. BPBM 11932 (1, 42 mm SL) Tahuata, south end of Vaitahu Bay in 30 m, J.E. Randall, D.B. Cannoy, J. Haywood, 23 April 1971. BPBM 16426 (1–34 mm SL) Tahuata, Haava Straits between Tahuata and Hiva Oa in 68 m, Sta. TH X, crew of the PELE, 1 October 1967. BPBM 17714 (1, 64 mm SL) Nuku Hiva I., in 73–82 m, Sta. NH 7, crew of the PELE, 17 September 1967.

Table 1 Continued.

Anal rays (*O. exul*)

118	119	120	121	122	123	124	125	126	127	128	129	130	131
1	4	1	1	1	4	1	3	4†	4	1	4	1	1
1	1	2	—	—	—	—	—	—	1	—	—	—	—
2	5	3	1	1	4	1	3	4†	5	1	4	1	1

Dorsal rays (*O. metoecus*)

171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
3	4†	2	3	2	—	2	—	3	2	—	—	—	—	1
—	—	1	—	—	1	—	—	—	—	—	—	—	—	—
3	4†	3	3	2	1	2	—	3	2	—	—	—	—	1

Anal rays (*O. metoecus*)

142	143	144	145	146
2	—	2	1	1
—	—	—	—	—
2	—	2	1	1

Vertebrae

Caudal					Total											
59	60	61	62	63	69	70	71	72	73	74	75	76	77	78	79	80
—	—	—	—	—	2	12	19†	3	—	—	—	—	—	—	—	—
—	—	—	—	—	—	2	3	—	—	—	—	—	—	—	—	—
—	—	—	—	—	2	14	22†	3	—	—	—	—	—	—	—	—
1	13†	25	5	1	—	—	—	—	—	—	1	1	15†	25	4	1
1	1	1	1	—	—	—	—	—	—	—	—	1	1	1	1	—
2	14	26	6	1	—	—	—	—	—	—	1	2	16†	26	5	1

NAME. *Exul,* from the common gender Latin noun *exul* (also *exsul*) meaning exile, alluding to the isolated geographic position of this species.

DISTRIBUTION. *Ophidion exul* is known from Easter Island and the Marquesas Islands. It occurs in sandy areas at the base of the rocky shores of these islands from tide pools to about 50 m. It should be looked for at Sala y Gomez, Ducie, Henderson, and Pitcairn islands, but Randall (personal communication) has commented that sandy areas especially near reefs in the Tuamotus and other island groups toward the Central Pacific have been well collected compared to Easter Island and that it is doubtful that O. *exul* or any other shallow dwelling cusk-eel occurs in that region.

GEOGRAPHIC VARIATION. Considering the remoteness of its two known populations, *Ophidion exul* exhibits remarkably little variation. Table 1 separates the meristic data for specimens from Easter Island and the Marquesas. Pectoral-ray counts are lower from Easter Island but there are too few specimens from the Marquesas and they are too small for further morphometric comparison. Additional material may indicate that the two merit subspecific recognition. Because of these considerations, specimens from the Marquesas are not designated as paratypes.

Ophidion metoecus new species

Figure 2, Tables 1, 3

DIAGNOSIS. Very similar to *Ophidion exul* in its size and color but more slender. Gill rakers 6 (2 rudiments and 4 developed rakers) on first arch (also as in O. *exul*). Vertebrae 75–80 (usually 75–78), anal-fin rays 129–146, dorsal-fin rays 158–185, and pectoral-fin rays 23–27 (usually 24–26). Longer pelvic ray 10–13 percent of SL, shorter 7–9 percent. Gas bladder small, without posterior opening or bony modifications.

DESCRIPTION. Frequency distributions of numbers of fin rays and vertebrae are given in Table 1. Morphometric data are given in Table 3. All specimens have 9 caudal rays and 7 branchiostegal

Table 2. Measurements[1] of body parts expressed in percent of SL for the holotype and 19 paratypes of *Ophidion exul* from Easter Island.

Collections[2]	458	453	NMC	NMC	NMC	UMML	NMC	457	UMML
Standard length (mm)	65.2	70.8	70.8	71.5	78.0	78.6	80.5	83.1	87.3
Head length[3]	19	19	20	19	19	18	18	19	19
Snout tip to:									
Dorsal fin	27	28	26	27	27	26	25	27	25
Anal fin	37	38	41	36	37	38	38	37	36
Occiput	16	16	15	15	15	15	15	15	14
End of lateral-line	83	83	84	84	78	90	84	85	81
Tip maxilla	8.3	9.0	8.9	9.0	8.8	8.8	8.7	8.4	8.7
Body depth at:									
Occiput	12	12	13	12	12	12	12	12	12
Dorsal-fin origin	12	13	13	13	14	13	13	13	13
Anal-fin origin	12	13	13	12	13	13	12	11	13
Pectoral fin	8.9	9.7	9.2	9.4	8.7	8.9	9.6	9.4	8.4
Pelvic ray:									
Outer	15	15	17	16	16	16	14	13	16
Inner	10	10	11	11	11	10	11	11	11
Caudal fin	3.1	3.1	2.1	3.5	2.9	3.2	2.7	3.2	3.0
Orbit diameter	5.5	6.5	5.8	5.7	5.4	5.2	5.7	5.4	5.2
Bony interorbit	2.8	2.8	3.1	3.1	2.7	2.5	2.6	2.4	2.6
Snout length	4.8	4.6	4.4	4.2	4.4	4.2	4.0	4.4	4.6
Postorbit[3]	11	11	11	10	10	10	9.4	11	10

[1] For definition of measurements see Robins (1960:90–91).

[2] All numbered collections are in the University of British Columbia 65 series. LACM is Los Angeles County Museum 6560-2, NMC is National Museum of Canada 74-524 (holotype) and 74-525, UMML is UMML 32674.

[3] To tip of opercular flap.

† Holotype.

rays arranged as described above for *O. exul.* All 31 specimens examined have 4 developed gill rakers on the lower limb of the first arch and 29 have 2 rudiments above (total 6); one each has 1 and 3 rudiments above (total 5 and 7, respectively). The developed rakers are somewhat longer than half the pupil diameter. Dentition is as described for *exul* but the scales are more imbedded and many individuals appear almost naked. The head-pore system is the same as in *exul.*

Life colors are unrecorded but likely are similar to those of *O. exul.* The lateral line may not be whitish, however, for it is more solidly pigmented and less conspicuous in preserved specimens than in *O. exul.* Some collections appear darker with the border of the vertical fins bolder but this probably reflects more the ecology at these stations than any specific difference. The gular pigment of juveniles is the same as in *O. exul.*

The swim bladder is small, as in *O. exul,* not extending as far caudally as the tip of the depressed pectoral fin. The winglike process on the first vertebra again is the only bony modification associated with the swim bladder.

The longest specimen, 86 mm SL, is much shorter than the 131 mm recorded for *O. exul*; *O. metoecus* probably is a smaller species.

MATERIAL EXAMINED. Juan Fernandez Islands: Isla Robinson Crusoe: HOLOTYPE: USNM 204246, an adult, probably female, 79.4 mm SL, 33°38′20″S, 78°48′50″W in 6–11 m, ANTON BRUUN Cr. 12, Field No. MV 65 IV 41, 11 Dec. 1965. PARATYPES: SIO 65-634 (6, 72–81 mm SL), Cumberland Bay, *ca.* 33°38′20″S, 78°48′50″W in 6–11 m, MV 65 IV 41, 11 Dec. 1965. SIO 65-636 (1, 86 mm SL) Cumberland Bay, *ca.* 33°38′20″S, 78°49′00″W in 64 m, MV 65 IV 43, 11 Dec. 1965. SIO 65-637 (23, 67–80 mm SL), north side, 800 m NW of San Carlos Pt., 33°37′18″S, 78°50′20″W in 24–27 m, MV 65 IV 44, 12 Dec. 1965. SIO 65-645 (18, 64–80 mm SL) and UMML 32938 (3, 73–76 mm SL) northwest side of Punta Suroeste, *ca.* 33°37′15″S, 78°55′05″W in 20–23 m, 13 Dec. 1965. SIO 65-655 (17, 60–86 mm SL), west end Carvajal Bay, 33°41′10″S, 78°58′30″W in 9–12 m, MV 65 IV 65, 15 Dec. 1965. SIO 65-657 (1, 74 mm SL), west end of Villagra Bay, 33°39′45″S, 78°52′50″W, in 7.5–9 m, MV 65 IV 66, 15 Dec. 1965. SIO 65-659 (6, 68–81 mm SL) off Bacalao Pt. *ca.* 33°38′20″S, 78°47′15″W, to 26 m, MV 65 IV 69, 16 Dec. 1965. MCZ 46159 (1, 82 mm SL) West Bay in 0–2 m, ANTON BRUUN Cr. 13, coll. 15, 1 Dec. 1966. MCZ 46170 (4, 66–77 mm SL) west coast in 0–20 m, ANTON BRUUN Cr. 13, coll. 37, 27 Jan. 1966.

Table 2. Continued.

LACM	LACM	UMML	NMC†	LACM	453	LACM	LACM	LACM	LACM	LACM
89.8	91.5	92.0	93.2	94.4	95.0	112.1	113.6	116.0	129.5	130.9
18	20	19	19	18	18	20	19	18	20	18
27	28	27	25	25	27	27	28	26	26	26
37	39	39	37	39	39	37	39	37	40	40
14	15	15	14	14	14	14	14	14	14	14
85	88	89	86	87	85	84	86	86	88	89
8.6	9.7	8.3	8.8	7.2	8.6	8.9	8.4	8.0	8.4	8.0
12	12	13	12	12	12	12	12	11	12	12
13	14	14	14	12	—	13	13	12	13	—
12	12	13	13	11	11	13	11	12	13	13
9.6	9.0	11	8.6	9.2	9.3	8.6	8.6	8.5	8.0	8.8
16	17	14	13	14	14	15	15	14	14	13
10	12	10	10	9	10	11	10	9	10	10
3.2	3.0	2.3	3.1	2.8	2.9	2.8	2.6	2.8	2.7	2.8
5.2	6.2	5.5	5.7	4.8	5.5	5.7	5.8	5.6	6.0	5.5
2.0	2.1	2.6	3.2	2.0	2.3	2.1	1.9	2.2	2.1	2.1
3.9	4.3	4.3	4.3	3.7	3.9	4.0	4.2	4.0	4.2	4.0
10	10	11	10	9.5	10	10	10	8.9	11	10

Isla San Felix: SIO 65-629 (1, 72 mm SL), Cathedral Rocks, 26°16′10″S, 80°06′30″W, MV 65 IV 36, 7 Dec. 1965. SIO 65-625 (1, 75 mm SL) northwest side, 26°17.1′S, 80°05.2′W, MV 65 IV 31, 5 Dec. 1965. SIO 65-624 (2, 66–74 mm SL) *ca.* 26°17′30″S, 80°05′40″W, 5 Dec. 1965.

NAME. *Metoecus,* from the masculine Greek noun meaning a sojourner, settler.

DISTRIBUTION. *Ophidion metoecus* is known only from Isla Robinson Crusoe (=Mas A Tierra) in the Juan Fernandez Islands and from Isla San Felix. Its depth range is from the waters edge to 30 m in sandy bottom. Bottom temperatures were 15°C. There have been few collections made by divers using ichthyocides in steep-sloped, high energy island environments. The occurrence of *O. metoecus* only on the principal island in the Juan Fernandez group probably reflects nothing more than collection effort. It should occur on the various islands and near surface sea mounts from the eastern end of the Easter Island seamount chain south to the Juan Fernandez group.

COMPARISONS AND RELATIONSHIPS

Ophidion exul and *O. metoecus* are sister species. Substantial differences between them in numbers of fin rays and vertebrae are easily derived from the diagnoses and from Table 1. Also, comparisons of Tables 2 and 3 indicate differences in 9 morphometric features. There is almost no overlap in the distance from snout tip to dorsal fin (smaller in *O. metoecus*), in lengths of both pelvic-fin rays (shorter in *O. metoecus*), but there are average differences in body depth (*O. metoecus* is more slender throughout) at occiput, dorsal-fin origin, and anal-fin origin, and in distance from snout tip to anal-fin origin (smaller in *O. metoecus*). Also, *O. metoecus* has a larger orbit and shorter postorbit. These differences coupled with the consistency of both species throughout their respective ranges, point to their recognition as species.

Table 4 lists the data obtained from examination of the holotypes of *Ophidion muraenolepis* (Günther), *Ophidion iris* Breder, *Ophidion nigracauda* Breder, and *Ophidion fulvum* (Hildebrand and Barton). These species represent the closest geographic neighbors, in different directions, in *Ophidion,* to *O. exul* and *O. metoecus* and each is discussed below.

Ophidion muraenolepis has been known only from the holotype, BMNH 1879.5.14.46, a specimen collected at CHALLENGER st. 192 in the Ki (or Kai) Islands in the Arafura Sea north of Australia, and described by Günther (1880:46, Plate XX, fig. A). I have completed a study of many spec-

Table 3. **Measurements[1] of body parts expressed in percent of SL for the holotype and 21 paratypes of *Ophidion metoecus* from the Juan Fernandez Islands and San Felix.**

Collection	MCZ 46170	MCZ 46170	SIO65 624*	MCZ 46170	MCZ 46170	SIO65 634	SIO65 629	SIO65 634	SIO65 634	SIO65 634
Standard length (mm)	65.5	65.6	66.5	67.2	67.2	71.5	71.9	71.9	72.7	72.3
Head length[2]	16	16	19	16	16	17	19	19	19	18
Snout tip to:										
Dorsal fin	22	21	22	21	21	22	24	22	23	22
Anal fin	35	36	36	35	35	33	37	36	35	34
Occiput	14	14	15	13	14	14	16	14	15	14
End of lateral-line	85	87	85	87	88	87	87	89	90	86
Tip maxilla	8.2	8.4	8.4	9.1	10	8.1	8.9	8.3	8.7	7.8
Body depth at:										
Occiput	10	10	11	9.4	10	10	11	11	11	11
Dorsal-fin origin	12	10	12	11	11	11	13	12	12	12
Anal-fin origin	10	10	11	9.2	9.1	10	11	12	10	10
Pectoral fin	9.0	9.0	9.3	7.9	8.3	8.1	9.4	8.3	8.8	8.2
Pelvic ray:										
Outer	13	10	12	10	11	11	13	11	12	12
Inner	8.1	7.5	9.5	7.0	6.8	8.1	9.0	7.5	8.1	7.1
Orbit diameter	6.4	5.8	5.9	5.6	5.4	5.9	6.2	6.2	6.0	5.9
Bony interorbit	2.6	2.6	2.2	2.5	2.8	2.6	2.8	2.5	3.4	2.7
Snout length	3.8	3.6	4.1	3.9	3.4	3.8	4.4	3.9	4.6	4.0
Postorbit[2]	9.3	10	9.0	9.1	9.8	9.2	9.2	9.2	9.8	8.6
Sex	—	—	♀	—	—	♀	—	♀	♂?	♂

[1] For definition of measurements see Robins (1960:90–91).

[2] To tip of opercular flap.

* Isla San Felix.

† Holotype.

imens of this species, which occurs as far to the northeast as Hawaii, and this analysis will be published elsewhere. *Ophidion muraenolepis* is a large species with a thick-walled swimbladder with posterior opening and an anterior bony encasement; it is not closely related to *O. exul* or *O. metoecus.*

Analysis of species of *Ophidion* from the Pacific shore of America was done by Robert N. Lea (1980). Comments on a few holotypes are in order. *Ophidion nigracauda* and *O. iris* were both described (Breder, 1936:44–47, figs. 15, 16) from single specimens collected at Refugio Bay and Gonzago Bay, Gulf of California, Mexico, respectively. Study of columns C and D in Table 4 shows that these nominal species are almost identical in their counts and measurements. They are here synonymized and, as first reviser, I select *O. iris.* (Cohen and Nielsen, 1978:16, list *nigracauda* as a synonym of *iris* without comment but based on personal communication from Robins and Lea. It is not clear whether this action qualified them as first revisers.) Although *O. nigracauda* has page priority and its holotype is in better condition, the name is based on an anomalous condition. The black area at the caudal end of the body is overemphasized in the original illustration and appears to be the result of physical damage such as a burn from a hot deck. No melanophores are evident (personal observation, and Lea 1980). It is inappropriate to saddle this very pallid species that never has a black tail with this name when an alternate is available. Basically, *O. iris* is much like *O. exul* and *O. metoecus.* The swim bladder of *iris,* though larger, is similar, its head-pore system is identical, and it has 2 rudiments and 4 developed rakers on its first gill arch. However, it has fewer dorsal- and anal-fin rays, its scales are smaller, and it is longer and more robust. Among described species, *O. iris* and *O. fulvum* are the smallest from the American Pacific.

Ophidion fulvum was known only from the holotype, USNM 144257, collected at Talara, Peru, and described by Hildebrand and Barton (1949:32–34, fig. 9), but Lea (1980) reports it from Costa Rica to Peru. The counts given in the original description are incorrect. There are 142 (not about 115) dorsal-fin rays, 114 (not about 83) anal-fin rays, and 25 (not 26 or 27 pectoral-fin rays). *Ophidion fulvum* also has fewer caudal vertebrae than *O. exul* or *O. metoecus.* In body proportions it generally agrees with *O. exul* except that the pelvic rays are decidedly shorter (outer 10 vs. 13–17 percent of SL, inner 6.4 vs. 9–11 percent SL). Its pelvic-fin rays are more like those of *O. metoecus.* In general form *O. exul* and *O. motoecus* most closely resemble *O. fulvum.*

Table 3. Continued.

SIO65 657	SIO65 624*	SIO65 634	SIO65 625*	SIO65 655	USNM 204246†	SIO65 634	SIO65 655	MCZ 46159	SIO65 655	SIO65 655	SIO65 655
73.8	73.8	74.6	75.4	78.5	79.4	80.8	81.3	82.0	82.9	84.2	86.3
17	18	18	19	19	20	18	19	21	19	18	20
22	24	23	24	23	24	24	24	26	24	22	24
33	36	34	37	37	38	37	36	38	36	35	38
14	16	15	16	15	16	15	15	16	16	14	16
85	92	86	90	87	82	86	88	88	82	86	89
7.3	7.7	8.0	8.4	8.7	9.1	8.0	8.8	9.5	9.5	8.7	9.4
10	12	11	11	11	12	12	12	—	11	11	13
11	13	13	14	11	15	13	13	13	12	11	14
10	12	11	12	10	14	12	11	13	11	10	12
8.1	8.9	9.5	9.4	9.2	10	9.2	9.0	11	10	8.9	10
11	12	12	13	11	12	12	12	13	11	12	12
7.5	8.8	8.0	9.2	7.9	8.8	9.0	7.6	8.2	7.6	8.0	8.3
6.2	5.4	6.3	6.2	6.0	6.7	6.2	6.9	7.1	6.6	5.7	6.6
2.7	2.4	2.8	2.2	2.8	2.6	2.5	2.7	2.7	2.6	2.4	2.7
3.9	4.0	3.8	3.9	3.9	4.2	4.0	4.4	4.9	4.1	3.8	4.4
8.2	9.2	9.2	9.9	10	9.9	9.0	10	10	10	10	10
♀	♀	♂	♀	—	♀?	♂	♂?	—	—	—	♂

ZOOGEOGRAPHY

The origin of a stock of *Ophidion* on the islands and sea mounts of the Nazca Plate is unclear. Rendahl (1921:59–60) analyzed his findings on Easter Island fishes and concluded that the Easter Island fish fauna was derived from the west across the Pacific by dispersion. A western origin is not supported by *Ophidion.* One must go to the Arafura Sea or Hawaii, or Samoa to find the first representative of *Ophidion* in that direction and neither O. *muraenolepis* nor the undescribed species from Samoa belong to species groups closely related to O. *exul* or O. *metoecus.* The Nazca species appear to have been derived from the American fauna. Springer (1982) reviewed in detail the distributional patterns of genera and species of shorefishes occurring on the Pacific Plate and its immediate periphery as well as representative genera and species that avoided the Pacific Plate. His evidence does not support a close relationship between shorefish faunas of the Pacific and Nazca plates although (his fig. 60) he shows a new genus as occurring from the Tuamotus to Easter Island and this pattern is expanded over much of the Pacific Plate for one species of the mollusk genus *Strombus* (his fig. 47).

Bonatti and Harrison (1976), in their discussion of hot spots and hot lines, concluded that Easter Island is over a hot line and that the small Easter Plate possibly resulted from (p. 404) "complex interaction of two patterns of mantle flow at the intersection of the Easter line and the East Pacific Rise." Easter Island is thought to have formed about 3 million years ago at the earliest (Bonatti et al., 1977:2471). What vicariant event led to isolation of the Nazca stocks and speciation of O. *exul* and O. *metoecus* is unclear. The occurrence of O. *exul* in the Marquesas could simply be the result of dispersal as these islands lie downstream in the Southeast Trade Wind Belt. Current patterns also could explain the dispersal of O. *metoecus* to Isla San Felix since this island lies downstream of the Juan Fernandez group.

The geology of the Nazca Plate is complex (as clearly discussed by Bonatti et al. (1977). Also, collections of the kind that yielded the Nazca cusk-eels are few and largely confined to the very islands where these species were found. Such collections are nonexistent for the many sea mounts whose tops may reach sufficiently close to the surface to be populated by cusk-eels. Only in the Tuamotus and nearby islands on the Pacific Plate has there been sufficient collecting effort (Randall, personal communication) to have confidence about the ab-

Table 4. Measurements[1] of body parts expressed in percent of SL and fin-ray and vertebral counts[2] for the types[4] of selected Pacific species of ophidiid fishes.

	A	B	C	D
Standard length (mm)	69.1	169.8	111.1	127.5
Head length[3]	20	22	20	21
Snout tip to:				
Dorsal fin	24	29	27	26
Anal fin	39	45	39	38
Occiput	14	16	15	15
End of lateral-line	87	76	86	85
Tip maxilla	7.8	10.3	9.0	9.1
Body depth at:				
Occiput	11	14	12	12
Dorsal-fin origin	11	14	—	14
Anal-fin origin	11	13	12	12
Pectoral fin	8.0	9.5	8.3	8.9
Pelvic ray:				
Outer	10	14	12	13
Inner	6.4	9.2	8.3	9.5
Caudal fin	2.7	3.2	2.6	2.8
Orbit diameter	5.6	6.1	6.2	5.8
Body interorbit	2.0	2.5	2.4	2.7
Snout length	5.6	4.6	4.4	4.2
Postorbit[3]	11	12	10	11
Dorsal rays	142	160	133	137
Anal rays	114	132	109	110
Pectoral rays	22–25	26–26	24–24	23–23
Gill rakers	2 + 4	2 + 4	2 + 4	2 + 4
Precaudal vertebrae	15	17	16	16
Caudal vertebrae	51	56	54	55
Sex	♂	♂	♂	♀

[1] For definition of measurements see Robins (1960:90–91).

[2] All specimens have 9 caudal rays, 4 above and 5 below.

[3] To tip of opercular flap.

[4] Holotypes: A = USNM 144257, *Ophidion fulvum* (Hildebrand and Barton); B = BMNH 79.5.14.46, *Ophidion muraenolepis* (Günther); C = BOC, *Ophidion iris* Breder; D = BOC, *Ophidion nigracauda* Breder.

sence of these species. It is to be expected that both *O. exul* and *O. metoecus* have more extensive distributions, especially if they occur deeper than here reported. Based on submarine research, in which I have participated, on steep island slopes in the tropical western Atlantic, a depth distribution of 200 m can be expected.

Recent studies on the Juan Fernandez Islands include that by Zeiss and Hermosilla (1970) and the collection of reports in Arana E. (1985). No cusk-eels were included in the list of fishes known from the Archipelago by Sepúlveda V. and Pequeño R. (1985). The geological history of the region relative to events on the Nazca Plate were reviewed by Morales G. (1986). Stuessy et al. (1984) use potassium–argon dating of basalts to age various islands in the Juan Fernandez group. Isla Robinson Crusoe (their "Masatierra") was estimated to be about 4.23 million years old and was intermediate in age among their islands. Thus, these islands are distinctly older than Easter Island.

Both *O. exul* and *O. metoecus* are dwarf species. Dwarfism is a common evolutionary pathway among benthic shore fishes from tropical oceanic islands. Small species can utilize the smaller and abundant food organisms, especially autochthonous plankton, which occurs very close to the bottom along steep slopes (personal observation), and utilize the limited shelter afforded by sandy substrata. Larger size invites predation from insular and oceanic species (e.g., *Polyprion oxygeneios* is common in the Juan Fernandez Islands). Böhlke and Robins (1959) and Robins and Böhlke (1959) described six dwarf species of cusk-eels from the tropical western Atlantic. Like the Nazca species, all six are unusual among ophidiine cusk-eels in lacking strong sexual dimorphism in the swim bladder. This dimorphism involves development of special bony structures and tympanic windows that play various roles in sound production. The small size of the fish and the noisy, surfy environment may be related to the loss of specialized structures associated with sound production since the sound producing ability is diminished and ambient noise may render sound ineffective as a signalling device. The absence of such important and distinctive derived structures makes it difficult to demonstrate relationships of dwarf cusk-eels.

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Contributions in Science

Studies of Neotropical *Amblyopone* Erichson (Hymenoptera: Formicidae)

John E. Lattke

Natural History Museum of Los Angeles County

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STUDIES OF NEOTROPICAL *AMBLYOPONE* ERICHSON (HYMENOPTERA: FORMICIDAE)

JOHN E. LATTKE[1]

ABSTRACT. Two new species of neotropical *Amblyopone* are described: *A. falcata* from Puerto Rico and *A. lurilabes* from northern South America, southeastern Peru, and northern Argentina. *Amblyopone tropicalis* Brown is synonymized under *A. orizabana* Brown, and the previously unknown worker of *A. mystriops* Brown is described. *Amblyopone degenerata* Borgmeier is reported from southeastern Peru. A key for the identification of the workers and females of New World *Amblyopone* is included.

RESUMEN. Se describen dos nuevas especies de *Amblyopone* del neotrópico: *A. falcata* de Puerto Rico y *A. lurilabes* del norte de Sud América, sureste Peruano y el norte de La Argentina. *Amblyopone tropicalis* Brown se convierte en un sinónimo menor de *A. orizabana* Brown y se describe la casta obrera de *A. mystriops* Brown, previamente desconocida. Se reporta la presencia de *A. degenerata* Borgmeier en el sureste del Perú. Se incluye una clave para la identificación de las obreras y hembras de *Amblyopone* del Nuevo Mundo.

INTRODUCTION

Amblyopone is a cosmopolitan genus of primitive ants belonging to the subfamily Ponerinae. It consists, at present, of 50 species, 13 of which occur in the New World. Brown revised the group in 1960 and described an additional neotropical species in 1962. Aspects of *Amblyopone* biology are presented in Gotwald and Levieux (1972), Baroni Urbani (1978), Masuko (1986), and Ward (1988). Recent improvements in collecting methods such as leaf litter sifting and the use of Berlese funnels or Winkler sacks have permitted the capture of more specimens of *Amblyopone* and other cryptic ground nesting ants than was previously possible. New species have been discovered and the status of known taxa can be better evaluated. The measurements used in this study are as defined by Taylor (1978: 830), except for HW, which here includes the gular teeth.

SPECIMENS EXAMINED

During the course of this study I have studied material from the following collections:

BMNH—British Museum of Natural History, London, England
CASC—California Academy of Sciences, San Francisco, California, U.S.A.
CFFB—Colección Fernando Fernández, Bogotá, Colombia
IZAV—Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
JTLC—Jack T. Longino Collection, The Allyn Museum, Sarasota, Florida, U.S.A.
LACM—Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
MCZC—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MZUSP—Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
USNM—U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Amblyopone falcata Lattke, new species

(Fig. 1)

TYPE MATERIAL. Holotype worker: PUERTO RICO, Guayama, carr. 7740, km 4 (8 km N Guayama, 18°04′N 66°07′W, 985 m), San Lorenzo, 22-IV-1980, J.A. Torres, col., no. 33. Deposited in the LACM. Paratypes: (1) Eight nidoparatypic workers with same collection data as holotype. Three deposited in the LACM, 2 in IZAV, 1 in MCZC, 1 in BMNH, 1 in MZUSP. (2) One worker: PUERTO RICO, Aguas Buenas Forest at Aguas Buenas Cave, 18°14′N 66°07′W, 250 m, 7–17 May 1973, S. Peck, leg. Deposited in MCZC.

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WORKER. Holotype (paratypes) dimensions: HL 1.12 (0.73–1.10), ML 0.98 (0.41–0.98), HW 1.00 (0.57–1.00), SL 0.63 (0.37–0.65), WL 1.32 (0.85–1.32) mm, CI 0.89 (0.75–0.91), MI 0.98 (0.72–0.98), SI 0.63 (0.65–0.66); n = 6.

Head in full face view with concave posterior margin, sides weakly convex and diverging anterad. Anterior clypeal margin convex, with 6–8 teeth: 2 median teeth may be separate or fused to variable degree, 2 intermediate teeth and 2 lateral triangular teeth. Gular teeth small and sharply pointed. Mandibles elongate with concave outer margins: apical tooth long and sharp, preapical tooth very small and subquadrate (sometimes slightly emarginate medially and in small specimens tubercle-like), followed by 5 double teeth fused basally, and a large and triangular innermost tooth. Mandibles in small specimens relatively broader and with more convex inner preapical border; double teeth tend to be more fused basad.

Frontal carinae contiguous, separated only by slight suture. Apex of antennal scape reaching back ⅔ of head and narrowest medially. Funiculus 10-merous, each segment constricted one from another and incrassate apicad, not forming distinct club. Funicular segments I–V, X longer than broad; VI–IX long as broad. Anterior one-third to one-fourth of head with parallel longitudinal rugae that diverge slightly posterad, very weakly impressed median longitudinal sulcus reaches vertex or a little before it. Eyes absent. Dorsum of head densely punctate-reticulate, each puncture with central piligerous tubercle. Punctures slightly less dense on lateral and ventral sides of head. Occiput shining and with sparse shallow punctures.

Mesosoma laterally with pronotum convex and separated by deep suture from straight and slightly descending mesonotum. Metanotum and dorsal propodeal face slightly convex, gently curving down to feebly convex declivitous face. Most of mesosoma smooth and shining with numerous piligerous punctures except for narrow median longitudinal band that extends caudad over mesosomal dorsum with fewer punctures, appearing smoother. Mesonotum transverse and dorsally narrowest part of mesosoma; metanotal suture sometimes impressed as fine shallow transverse sulcus. Propodeum with posterolateral striae, declivitous face with almost glabrous inferomedian area and with superolateral punctures and inferolateral transverse striae. Mesepisternum with horizontal rugulae. Sides of procoxa with oblique rugulae and dispersed punctures. Sides of metepisternum and propodeum with few punctures. Propodeal spiracle oval.

Petiole laterally with fairly straight anterior margin, meeting the weakly convex face at sharp angle. Gaster smooth and shining, with numerous piligerous punctures; acrotergite with very fine transverse striae; base of gastric segment II scrobiculate; postpetiolar sternite with larger punctures and appearing roughened. Gastric sternite II with boomerang-shaped, beige to yellow patch, outlined in brown. Pygidium densely punctate, with some longitudinal rugae. Subpetiolar process is translucent rounded lobe anteriorly directed. Petiole and postpetiole dorsally broader than long. Tibiae and femora smooth and shining with abundant punctures. Empodia present, claws simple. Large pectinate spur on protibial apex, none on mesotibia and one long pectinate spur plus smaller, slender straight spur at metatibial apex.

Most of body covered with short and dilute appressed pubescence; antennae, tibia, and gastric apex with some decumbent hairs, erect hairs present on gastric apex. No pubescence on mes- and metepisterna. Color mostly ferruginous-yellow, legs and gaster slightly paler.

QUEEN, MALE. Unknown.

ECOLOGY. The holotype series was taken from leaf litter in the Carite subtropical wet forest.

DISCUSSION. *Amblyopone falcata* may be confused with the Cuban *A. bierigi* Santschi, a species known only from the holotype. *Amblyopone bierigi,* however, lacks the yellow spot on gastric sternite II of *A. falcata* and has 12-merous antennae rather than 11, and sparser punctulae on the body. The combination of 11 antennal segments and the distinctive spot on the gastric ventrum sets *A. falcata* apart from all other known species of the genus. Reduced antennal segmentation is known in *A. degenerata* Borgmeier (6 or 7) from SE Brazil and SE Peru, and *A. gnoma* Taylor (10) from Guadalcanal Island. SEM examination of the unique gastric spot at 150× failed to reveal openings or other sculpturing of taxonomic interest, only smooth integument.

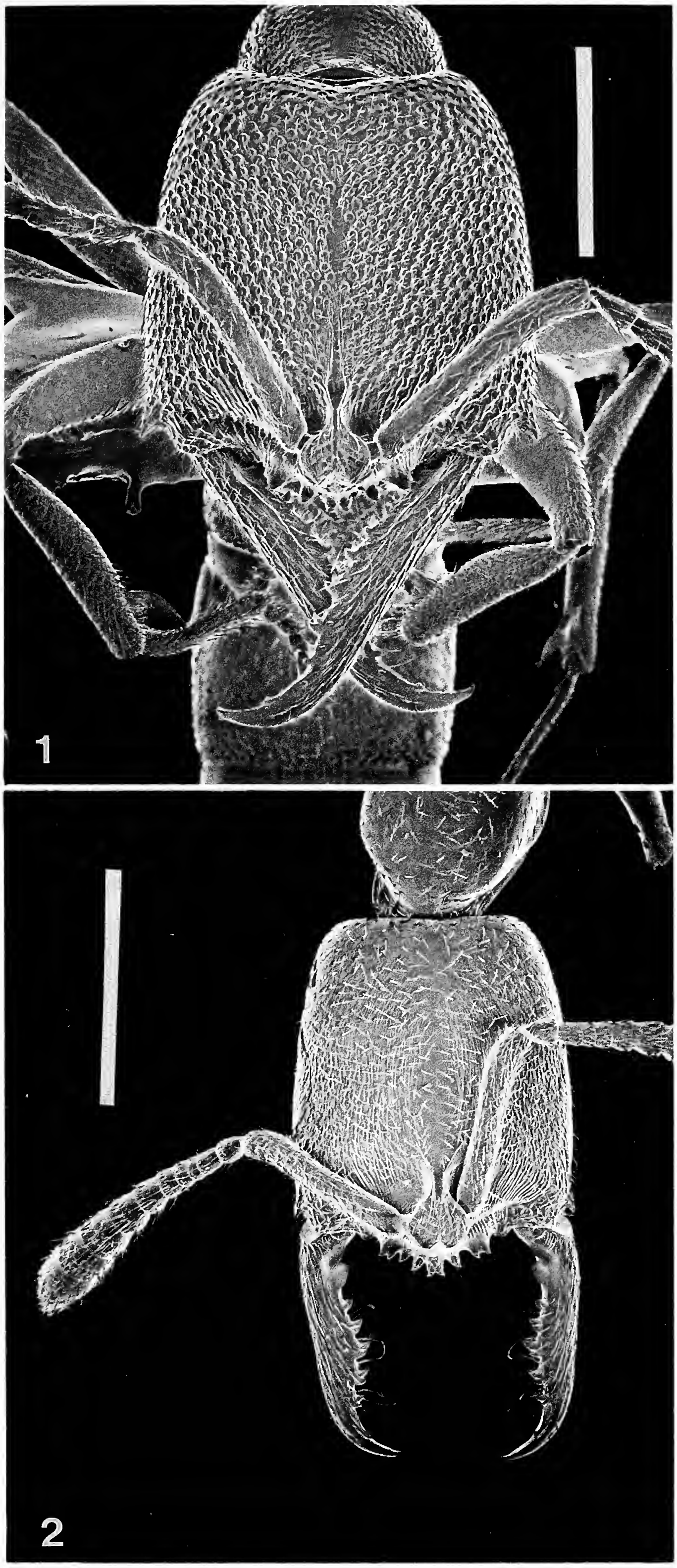
ETYMOLOGY. The species epithet *falcata* is derived from the Latin adjective *falcatus* and alludes to the sickle-shaped mandibles of the ant.

Amblyopone lurilabes Lattke, new species

(Fig. 2)

Amblyopone armigera Lattke 1985:82, 84 (misidentification).

TYPE MATERIAL. Holotype worker: VENEZUELA, Portuguesa, 6 km SE Biscucuy, 9°18′N 70°01′W, 1000 m, 18-VIII-1983, J. Lattke, leg. no. 438. Deposited in IZAV. Paratypes: (1) Eleven nidoparatypic workers and queen with the same collection data as the holotype. One worker each in MCZC, LACM, MZUSP. (2) COLOMBIA, Guajira, Serranía de Macuira, 6–8 km S Nazareth, 70–200 m, 13-VI-75, W.L. Brown & C. Kugler, leg. MCZC. (3) COLOMBIA, Magdalena, Parque Tayrona near Pueblito, 200 m, 15-X-77, C. Kugler, leg. CASC. (4) COLOMBIA, Antioquia, Providence Biological Station, Zona Buenos Aires, 600–800 m, 30-XII-77, C. Kugler, leg. MCZC. (5) COLOMBIA, Meta, Villavicencio, 3-III-72, S. & J. Peck, leg. MCZC. (6) ECUADOR, Pichincha, Tinalandia, 16 km SE Santo Domingo de los Colorados, 4-VI-76, S. & J. Peck, leg. MCZC. (7) ECUADOR, Manabí,



Figures 1 and 2. *Amblyopone* species. **1.** *Amblyopone falcata* frontal view of head. **2.** *Amblyopone lurilabes* frontal view of head. Scale bar equals 0.5 mm.

73 km NE Chone, 300 m, 12-VI-76, S. & J. Peck, leg.

Additional studied material (not types): (1) TRINIDAD, Tortuga Estate, 1943, Strickland & Mc.C. Calley, leg. MCZC. (2) ARGENTINA, Buenos Aires, Zelaya, III-1956, J. Daguerre, leg. USNM. (3) COLOMBIA, Magdalena, Cañaveral, 200 m, 11°19′N 73°56′W, 11-VII-85, J. Longino 708-15. JTLC.

S.P. Cover (pers. comm.) reports a dealate queen from: PERU, Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, 23-VI-89, S. Cover & J. Tobin, leg. CA-423. MCZC.

WORKER. Holotype (paratypes) dimensions: HL 0.76 (0.72–0.80), ML 0.54 (0.50–0.56), HW 0.60 (0.57–0.70), SL 0.34 (0.35–0.40), WL 0.90 (0.94–1.00) mm, CI 0.79 (0.79–1.00), SI 0.57 (0.57–0.63); n = 5.

Head in full face view with straight to gently convex posterior border, sides slightly convex and diverging anterad. Gular teeth small and acute. Anterior clypeal border convex, usually with 6 teeth: median pair may be separate or fused to a variable degree, single tooth on each side, and heavy, usually bidentate lateral teeth. Sometimes a single tooth may be present between median teeth and lateral tooth; one specimen with small denticle between median teeth. Inner mandibular margin with large basal triangular tooth, smaller subbasal tooth, series of four basally fused double teeth. A small preapical, usually bicuspid tooth present before long, sharp apical tooth. Dorsal and ventral mandibular surfaces longitudinally rugose. Scape with longitudinal rugulae and low oval depressions.

Cephalic dorsum densely reticulate-punctate and with noticeable longitudinal rugulae on anterior one-fourth to one-third of head, much weaker rugulae, sometimes barely discernible, extend caudad toward vertex. Some oblique striae on gular area. A narrow longitudinal median strip of smoother sculpture present, extending from behind frontal carinae to vertex. Microsculpture on posterior cephalic dorsum coriarious. Head ventrum smooth, with scattered piligerous punctures; occiput smooth and shining with some punctures. Eyes consisting of single ommatidium situated behind cephalic midlength.

Mesosoma laterally with nearly flat dorsal margin, promesonotal suture marked, metanotal suture totally effaced. Propodeal dorsum slightly higher than rest of mesosomal dorsum, broadly curving into gently convex declivitous face. Propodeal dorsum smooth and shining, with scattered punctures, declivitous face glabrous. Mesosoma widest at pronotum, narrowest at mesonotum, which is transverse; propodeum has broadly convex sides that diverge caudad. Pronotal sides smooth and shining with scattered punctures. Metepisternal and lateral propodeal faces glabrous, except for inferoposterior transverse striae with some punctures below propodeal spiracle. Katepisternum with transverse rugulae, anepisternum smooth and shining.

Petiole laterally with straight to slightly concave anterior face, meeting the flat to slightly convex dorsal face at right angle. Petiole dorsally longer than wide, postpetiole transverse. Subpetiolar process elongate, with slightly concave inferior margin. Gaster smooth and shining with scattered piligerous punctures. Femora and tibia, especially middle and hind, laterally compressed. Apex of fore tibia with large pectinate spur, mesotibia with small slender spur and metatibia with large curved pectinate spur and an accompanying smaller, more slender one. Empodia present, claws simple.

Head very dark brown; antennae, mandibles, petiole, and posterior pronotal margins dark ferruginous yellow. Mesosoma mostly black; gaster light to dark yellowish-brown. Legs ferruginous yellow. Lateroposterior corners of propodeum with oblong patch usually testaceous to dark ferruginous yellow. Body with short standing hairs on mesosoma, longer on anterior face of pronotum, posterior margin of propodeal dorsal face and toward apex of gaster. Pubescence mostly sparse and appressed.

QUEEN. HL 0.72, 0.71; ML 0.44, 0.47; HW 0.58, 0.56; SL 0.35, 0.35; ED 0.10, 0.11; WL 1.00, 1.00 mm; CI 0.81, 0.79; MI 0.76, 0.84; SI 0.60, 0.63. Two paranidotypes with same collection data as holotype. Deposited in IZAV. Significant differences from the workers are the usual: presence of compound eyes, ocelli, and more mesosomal development, plus wing stumps. Punctures of cephalic dorsum are shallower than in worker, and the longitudinal rugulae are more noticeable. Pilosity more abundant than worker.

MALE. Unknown.

ECOLOGY. The holotype nest consisting of two queens and 17 workers was found beneath a stone in a coffee plantation. Beneath the same stone and apparently with overlapping nest limits was a colony of *Basiceros discigera* (Mayr). Other samples come from leaf litter samples taken mostly in humid and wet forests, between elevations of 70–1000 m. The Peruvian specimen was captured in clay soil at the base of a large tree growing in mature "tierra firme" forest.

DISCUSSION. The dense anterior sculpturing on the cephalic dorsum separates this species from *A. elongata* (Santschi) and *A. monrosi* Brown, which are predominantly smooth and shining. *Amblyopone lurilabes* is apparently sympatric with *A. elongata* in northern Argentina, and *A. monrosi* is an endemic Chilean ant. *Amblyopone armigera* Mayr is larger in size, with proportionally much larger gular teeth, and larger punctures and more prominent rugae on the cephalic dorsum than *A. lurilabes.* An apparently exclusive character that separates *A. lurilabes* from the rest of New World *Amblyopone* is the spot on each posterolateral propodeal face.

Most of the records for this species are concentrated in northern South America, with the exception of a specimen from northern Argentina and the Peruvian record. The large gaps in its distribution is unexpected considering the fact that this species is apparently not uncommon, judging from the number of specimens available for study.

ETYMOLOGY. The name of this species is a conjugation of the Latin adjective for pale yellowish, *luridus*, and the Latin noun for spot, *labes*. The name alludes to the unique propodeal spots.

Amblyopone degenerata Borgmeier

Amblyopone degenerata Borgmeier, 1957:111.

S.P. Cover (pers. comm.) reports capturing this rare species, previously known only from SE Brazil: PERU, Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, 13-IV-89, S. Cover & J. Tobin, leg. Samples CA-129 and CA-119. Both samples were taken from clay soil at the base of a large tree, and each sample yielded two workers. All are deposited in MCZC. These specimens compare well with the *degenerata* type, however all 4 have 6 antennomeres, and not 7 as does the type.

Amblyopone mystriops Brown

Amblyopone mystriops Brown, 1960:185–188, fig. 19 (female).

WORKER. Dimensions: HL 1.18–1.35, ML 1.14–1.29, HW 1.08–1.24, SL 0.72–0.77, ED 0.06–0.08, WL 1.63–1.88 mm, CI 0.92, MI 1.03–1.07, SI 0.62–0.67; n = 3. Cephalic dorsum reticulo-punctulate with short smooth and shiny median strip, bordered laterally by longitudinal carinae that extend from between frontal carinae and fusing at cephalic midlength. Anterior cephalic margins with longitudinal parallel rugulae that diverge from antennal fossae. Frontal carinae separated by smooth and shining median depression, and also by small clypeal lobe. Head without gular teeth, only blunt corners present. Mandibles between dorsal carinae and teeth with oblique rugulae, becoming smooth and shining apicad. About 7 denticles on anterior clypeal margin. Mandibles with 2 separate ranks of teeth, a short apical tooth and a rounded preapical process. Eyes small and situated behind cephalic midlength. Antennae 12-merous.

Promesonotal suture deep, mesometanotal suture also well defined; mesonotum narrow, transverse rugulose to punctate. Rest of nota tend to be smooth and shining, with sparse punctures.

Mesosoma laterally with anterior pronotal margin convex and broadly convex dorsally; metanotum straight; dorsal propodeal face slightly convex, declivitous face straight to slightly convex. Propodeal spiracle oval and directed lateroposteriorly. In dorsal view lateral pronotal margin and metanotum + propodeum form two broad convexities. Anepisternum with some longitudinal rugulae, but rest of lateral mesosomal sculpture as on dorsum, but with fewer punctures posteriorly. Declivitous propodeal face smooth and shining. Anterior nodal face of petiole straight to slightly concave, dorsal face broadly convex. Subpetiolar process an anteriorly directed rounded lobe with oval fenestra. Gaster smooth and shining with sparse punctures. Legs mostly smooth and shining, but with numerous punctures. Apex of protibia with pectinate spur, mesotibia with 2 simple spurs and metatibia with pectinate spur and simple spur.

Head, legs, antennae, and ventral mandibular face with abundant decumbent pubescence, thinner on rest of body. Suberect hairs on interior mandibular margin, antennae, and to a lesser degree on legs. Abundant subdecumbent hairs on tarsi. Sparse decumbent pilosity on mesosoma, gaster and longer suberect hairs on pygidium. Mandibles, antennae, legs reddish brown, rest of body black.

QUEEN. As in Brown's original description except that space between the dorsal mandibular carina and teeth is mostly convex.

COMMENTS. The Gorgona locality is a new southern range extension of this species. The island is located approximately 56 km NNW of the town of Guapi on the southwestern Colombian coast and has extensive forest cover.

MATERIAL EXAMINED. COSTA RICA, Reserva Biológica Hitoy-Cerese, 9°40′N 83°02′W, 200 m, 29-VIII-85, J. Longino no. 942-s. Five workers and 1 queen from wet forest litter sample. Deposited in JTLC. COLOMBIA, Isla Gorgona, 1-X-1987, G. Andrade, leg. *Amblyopone mystriops* was previously known only from the types series from Los Amates, Guatemala.

Amblyopone orizabana Brown

Amblyopone orizabana Brown, 1960:198, worker and female (examined).

Amblyopone tropicalis Brown, 1962:73, worker (examined) NEW SYNONYMY.

WORKER. Dimensions: HL 0.58–0.62, ML 0.38–0.42, HW 0.48–0.55, SL 0.31–0.34, WL 0.70–0.79 mm, CI 0.81–0.90, MI 0.76–0.88, SI 0.58–0.65; n = 8.

The recent increase of specimens in collections has permitted a new assessment of the status of *A. tropicalis* as a valid species. Brown (1962:76) separated *A. tropicalis* from *A. orizabana* by the following characters: (1) reduced number of clypeal teeth, (2) configuration of the median clypeal tooth, (3) diminished dorsal members of the mandibular double teeth, (4) larger size, (5) broader head, and (6) longer and more slender mandibles. These characters, as well as others taken into account during the present studies, all show an overlapping continuum of variability. In particular, the use of the disposition and number of clypeal teeth as a species difference can be misleading if one is comparing only a few specimens; especially variable is the degree of fusion of the median pair of teeth. The number of mandibular teeth in the examined material is 7 (2 single basal teeth, 4 double teeth, and a reclinate preapical tooth), except for the holotype of *A. orizabana*, which apparently has 6 (as its mandibles are closed tightly against the clypeus another tooth could be hidden).

MATERIAL EXAMINED. COLOMBIA, Chocó, 10 km SW San José del Palmar, Rio Torito, 610 m, 1–4 June 1978, C. Kugler; COSTA RICA, Puntarenas, Monteverde, 1500 m, 10°18′N 84°48′W, 10-XII-87, J. Longino no. 1972-s; EL SALVADOR, Cerro Verde, 1760 m, 14-V-1971, S. Peck, Ber. 201; MEXICO, Veracruz, Pico Orizabana, 2750 m, 24-VIII-53, E.O. Wilson; MEXICO, Veracruz, Córdoba, Paraje Nuevo, El Nacimiento, 7-VIII-69, S. & J. Peck no. B-176; MEXICO, Oaxaca, 14.5 km NE Oaxaca on Mex. 175, 1890 m, 20-VIII-1973, A. Newton; PANAMA, Barro Colorado Island, 6-I-60, W.L. Brown; PANAMA, Barro Colorado Island, II-14-76, A. Newton.

KEY TO NEW WORLD SPECIES OF *AMBLYOPONE*—WORKERS AND FEMALES

The following key is modified from Brown (1960: 191–192).

1. Antenna with 12 segments 3
– Antenna with <12 segments 2
2. Antenna with 11 segments; HW > 0.70, WL > 1.10 mm (Puerto Rico) .... *falcata* n. sp.
– Antenna with 6 or 7 segments; HW < 0.70, WL < 1.10 mm (SE Brazil, SE Peru) .... *degenerata* Borgmeier
3. Lobes of frontal carinae separated by a distinct gap 4
– Lobes of frontal carinae contiguous or fused 7
4. Mandibles on inner surfaces each with 2 separate rows of small, sharp sparse teeth (C. America–SE Colombia) ... *mystriops* Brown
– Mandibles on inner surfaces with much larger teeth, those near midlength fused at bases to form heavy double teeth 5
5. Inner borders of mandible angularly produced, so that the blades are triangular in shape without the apices; large double teeth with rounded apices; genal teeth reduced to inconspicuous obtuse angles (N. Carolina, U.S.A.) .... *trigonignatha* Brown
– Inner borders of mandibles straight to convex, not angularly produced, the blades linear; large double teeth prominently acute; genal teeth acute and projecting 6
6. Inner borders of mandibles and anterior clypeal margin straight (N California to British Columbia) .... *oregonensis* (Wheeler)
– Inner borders of mandibles, and usually also the anterior clypeal margin convex in outline (temperate N. America at least to Arizona) .. .. *pallipes* (Haldeman)
7. At least the anterior ⅗ of the head (full-face view) predominantly densely sculptured and opaque 8
– Entire or nearly entire cephalic dorsum smooth and shining, with spaced punctures 12
8. Anterior ⅓–¾ of cephalic dorsum longitudinally striate with intermixed punctures and/or posterolateral propodeal corners each with testaceous to ferrugineous yellow spot; color of body mostly black or brown 9
– Cephalic dorsum densely and uniformly punctate or striolate-punctate (except for shining border of median frontal groove in some cases); longitudinal striae on anterior ⅓–¾ of head absent; yellowish posterolateral propodeal spots always absent; color of body mostly yellow or ferruginous 10
9. Longitudinal striae on anterior ½–¾ of cephalic dorsum well developed; sculpture on remainder of cephalic dorsum consisting of distinct punctures only, with spaces between them smooth and shining; propodeum completely black (SE Brazil–N Argentina) .... *armigera* Mayr
– Longitudinal striae usually confined to anterior ¼–⅓ of head, sometimes weakly extending further toward vertex, sometimes very feebly developed and difficult to see; sculpture on remainder of cephalic dorsum consisting of moderately dense punctures, the spaces between them, if present, shining; propodeum with a testaceous to ferrugineous yellow spot on each of its posterolateral corners (N South America, SE Peru, N Argentina) .... *lurilabes* n. sp.
10. Mesosoma smooth, punctation sparse; propodeum with very few punctures on dorsum, and its lateral striation restricted to the lower third; color yellow (Mexico–Choco, Colombia) .... *orizabana* Brown
– Punctures more abundant and distinct on mesosoma; sculpture of propodeal lateral faces covers one-half or more of surfaces 11
11. Unique holotype worker 4.5 mm long (according to original description) (Cuba) .... *bierigi* (Santschi)
– Worker TL 3.0–4.1 mm; female TL 4.1–4.5 mm (Chile) .... *chilensis* Mayr
12. HW > 0.70 mm; straight anterior clypeal margin with small median tooth, not advanced beyond the larger lateral teeth (Chile) .... *monrosi* Brown
– HW < 0.70 mm; convex anterior clypeal margin with median tooth advanced beyond lateral teeth (SE Brazil–N Argentina) .... *elongata* (Santschi)

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SPECIES LIMITS WITHIN THE *ARBORIMUS LONGICAUDUS* SPECIES-COMPLEX (MAMMALIA: RODENTIA) WITH A DESCRIPTION OF A NEW SPECIES FROM CALIFORNIA

MURRAY L. JOHNSON[1] AND SARAH B. GEORGE[2]

ABSTRACT. Karyotypic and morphologic variability was assessed in populations of red tree voles, *Arborimus longicaudus* species-complex, from Oregon and California. Diploid numbers vary from 52 in the north to 40 in the south. Populations from Oregon and California, separated by the Klamath Mountains, are strongly differentiated based on morphometric data, with individuals from southern populations smaller. Laboratory breeding studies demonstrated a reproductive barrier between northern and southern populations, and a new species is proposed for the red tree voles from California.

INTRODUCTION

The red tree vole, *Arborimus longicaudus* (True, 1890), formerly referred to *Phenacomys longicaudus* was described late in the sequence of taxonomic studies in North America. Frederick True (1890) provided the type description on the basis of a single specimen from Coos County, Oregon. A closely related species, *Arborimus* [*Phenacomys*] *silvicola* (Howell, 1921), described from Tillamook County, Oregon, has subsequently been classified as a subspecies of *A. longicaudus* (Johnson, 1968; Hall, 1981). Originally proposed as a subgenus of *Phenacomys, Arborimus* (Taylor, 1915) was elevated to generic rank by Johnson (1973); included within it are the red tree vole and the white-footed vole, *A. albipes* (Johnson and Maser, 1982).

The range of *A. longicaudus* was thought to extend from northwestern Oregon, south along the Pacific coast to Sonoma County, California (Benson and Borrell, 1931; Hall, 1981; Fig. 1). Coastal Oregon populations (*A. l. silvicola*) are characterized by their larger size and darker color than populations of *A. l. longicaudus* to the south and east. Johnson (1973) suggested that the California populations of the red tree vole represent an undescribed sibling species. Laboratory breeding studies, karyotypic analyses, and morphometric analyses were conducted to examine the systematic relationships among populations within this species complex. We report here the results of those investigations, update the taxonomy of the species group, and describe the previously unrecognized sibling species in California.

MATERIALS AND METHODS

CHROMOSOMAL ANALYSES

Nineteen wild-caught and four captive Oregon × California cross individuals were karyotyped using the procedures of Hsu and Patton (1969) and Lee and Elder (1980). Karyotypes from two Oregon individuals were published by Hsu and Benirschke (1974). Collecting localities are listed in Table 1. Negatives are deposited in the laboratory of Dr. T.C. Hsu at M.D. Anderson Hospital in Houston, Texas (TCH). Voucher specimens are deposited in the collections of mammals at the University of Puget Sound, Tacoma, Washington (PSM), the Thomas Burke Memorial Washington State Museum, Seattle (UW), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); TCH specimens are not cataloged (Table 1).

CAPTIVE BREEDING STUDIES

From 1955 to 1986, red tree voles were maintained in captivity. Cages were made of Douglas fir (*Pseudotsuga menziesii*) plywood and had plexiglas fronts and tops of vinyl-coated, half-inch screen. Three sizes were used: 60 cm deep × 20 cm wide × 38 cm high, 60 cm deep × 38 cm wide × 20 cm high, and for breeding, 60 cm deep × 114 cm wide × 40 cm high. Cage floors were covered with coarse Douglas fir sawdust. A cedar nest box with two openings and a removable top was provided in each unit; usually two nest boxes were kept in the breeding cages. An excess of Douglas fir terminal branches was kept in an earthenware bowl in each cage at all times; the bowl also provided water to the mice at all times.

Based on the report of Hamilton (1962), a more intensive breeding program was begun in 1965. Breeding encounters were arranged by placing an adult male with an adult female in a cage for 30 hours. In some cases, males and females were left in cages for up to 10 days. There was no significant difference between results of encounters that lasted less than 30 hours and those lasting

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Natural History Museum of Los Angeles County, 1991

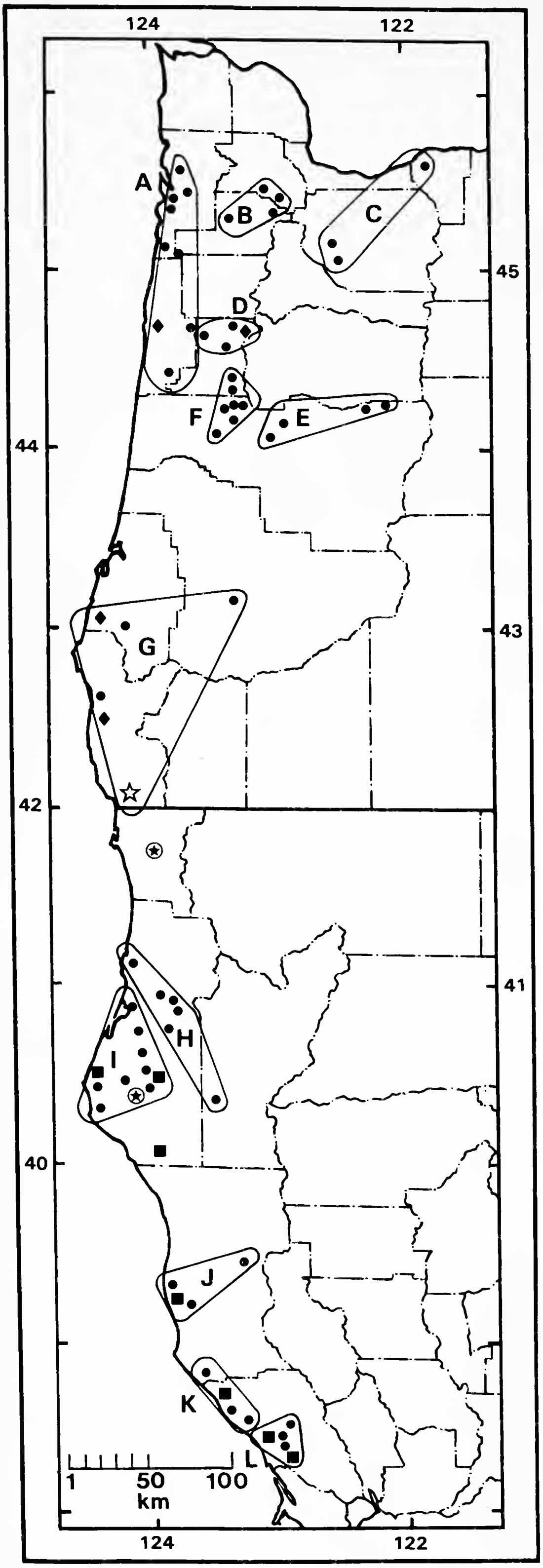

Figure 1. Locations of specimens in Oregon and California used in morphometric analyses are noted by dots. Diamonds denote karyotyped specimens with 2N = 52; open star denotes specimen with 2N = 48; stars enclosed in circles denote specimens with 2N = 42; squares denote specimens with 2N = 40. Enclosures denote localities lumped for statistical purposes; letters refer to samples listed in the appendix.

between 30 hours and 10 days (*G*-test, $P > 0.10$), therefore all results were considered together. This time was chosen as a reasonable biological period that a free-ranging male might court a receptive female in the wild. This optimized the chance of success with minimal risk to the males, which we observed to suffer a significant time-related mortality rate when caged with adult females (i.e., male mortality rose after 10 days with females).

Males and females were classified as being of Oregon (O) or California (C) origin; control encounters consisted of O × O and C × C arrangements, whereas test encounters consisted of O × C and C × O encounters. Based on the localities from which the animals were taken, it is assumed that the Oregon animals (with the exception of those from the Winchuk River area) had 2N = 52 and the California animals had 2N = 40. There may have been a California animal with 2N = 42, as not all individuals were karyotyped. There was no significant difference between results of encounters in which an individual from the Winchuk River area participated (*G*-test, $P > 0.10$), and therefore all encounters (including animals from the Winchuk River area) were combined.

Results of encounters were classified as negative (no known pregnancy), successful (production of litter surviving beyond 1 week), or as a pregnancy-related death (PRD). The latter category included maternal deaths (occurring during pregnancy or shortly after parturition), fetal deaths (aborted fetus(es) found in cage; abortion of fetuses early in pregnancy and resorption of fetuses are likely to be occult in occurrence, thus our estimates are probably low), and perinatal deaths (newborn litter dying in the arbitrarily set period of 1 week after parturition). Results were analyzed with an R × C test of independence using the *G*-test (Sokal and Rohlf, 1969) to determine if the number of successful pregnancies and PRDs were independent of the type of parental cross.

MORPHOMETRIC ANALYSES

A total of 306 adult specimens was examined from California and Oregon. These specimens are deposited in the collections listed in the acknowledgments. Specimens were aged on the basis of toothwear. An individual was classified as a juvenile if the reentrant angles of the molars were not evident above the alveolus, as an adult if molar roots were evident above the alveolus, and as an old adult if wear had obliterated the enamel pattern on the molar faces (Johnson, 1973). Juveniles and old adults were excluded. Three external measurements were recorded from specimen tags: head and body length (HB), tail length (TL), and hind foot length (HF). Five cranial measurements were taken using dial calipers, accurate to 0.1 mm: greatest length of skull (GLS), zygomatic breadth (ZB), least interorbital width (IOC), mastoid breadth (MB), and depth of braincase (DB). Nine cranial measurements were taken using an ocular micrometer, accurate to 0.1 mm: length of nasals (LN), length of maxillary toothrow (MT), distance from the posteriormost point of nasals to posteriormost point of maxillaries (PW), width of interparietal (IPW), length of interparietal (IPL), M2–M2 width (MW), length of diastema (LD), width of upper M2 (TW), and length of palatal foramen (PF).

Table 1. Collecting locality, sex, and diploid number of 23 specimens of *Arborimus* karyotyped. In the case of the hybrid individuals, the collecting localities of the parents are listed with the female first.

Locality	Voucher catalog no.	Sex	2N
OR: Benton Co.; McDonald Forest	PSM 10916	F	52
OR: Benton Co./Lane Co. line	PSM 10915	M	52
OR: Coos Co.; 2 mi. (3.2 km) W Bandon, Bill's Peak	PSM 10920	M	52
OR: Curry Co.; 1 mi. (1.6 km) S Humbug Mt.	PSM 23922	M	52
OR: Lincoln Co.; no specific locality	PSM 23928	F	52
OR: Curry Co.; Winchuk River	TCH 2447	F	48
CA: Del Norte Co.; S Fork Smith River, Big Flat	PSM 24934	M	42
CA: Humboldt Co.; 2 mi. (3.2 km) W Bridgeville	TCH 2448	M	42
CA: Humboldt Co.; 4.3 mi. (6.9 km) N Bridgeville	MVZ 140633	F	40
CA: Humboldt Co.; 3 mi. (4.8 km) N Capetown	MVZ 140517	M	40
CA: Humboldt Co.; 5 mi. (8 km) S Garberville	PSM 20937	M	40
CA: Mendocino Co.; Albion	PSM 20943	M	40
CA: Sonoma Co.; 1 mi. (1.6 km) E Stewart's Point	PSM 10943	M	40
CA: Sonoma Co.; Jenner	PSM 21019	F	40
CA: Sonoma Co.; Jenner	PSM 24040	F	40
CA: Sonoma Co.; Jenner	PSM 21017	M	40
CA: Sonoma Co.; Jenner	PSM 21024	M	40
CA: Sonoma Co.; Jenner	UW 34476	F	40
CA: Sonoma Co.; Freestone	PSM 21260	M	40
OR: Lane Co.; 6 mi. (9.7 km) NNE Coburg × CA: Mendocino Co.; Albion	PSM 24008	F	46
OR: Lane Co.; 6 mi. (9.7 km) NNE Coburg × CA: Mendocino Co.; Albion	PSM 24009	M	46
OR: Benton Co.; Monroe × CA: Mendocino Co.; Albion	PSM 24010	M	46

Standard statistics (mean, standard deviation, standard error, and coefficient of variation) were calculated for sample measurements using STATS of SYSTAT (1985). Twelve samples were pooled on the basis of subspecific classification and geographic locality (Fig. 1; see Specimens Examined in the appendix for sample sizes and specific localities). The four largest samples (A, F, I, and L; Fig. 1) were selected to test for significant differences between sexes using Student's *t*-test (SYSTAT, 1985). Females averaged larger in most cases, and for each sample, at least three measurements were significantly different between the sexes. Subsequently, males and females were analyzed separately. Far fewer males than females were available for study, and it was necessary to further pool male geographic samples. Thus male sample B includes samples B, D, and F; C includes C and E; and H includes H and I; J includes J, K, and L.

Tests of normality, Student–Newman–Keuls multiple range tests, and a one-way analysis of variance (*F*-test) for significant differences among means were done using BIOSTAT II (Pimentel and Smith, 1986). Multivariate analyses of variance (MANOVAs) and canonical analysis were used to assess the extent of morphometric divergence among samples. These were performed using PROC GLM of SAS for the MANOVAs (SAS Institute, 1985) and BIOSTAT II for the discriminant analysis (Pimentel and Smith, 1986).

RESULTS

CHROMOSOMAL ANALYSES

Four diploid numbers were documented in wild-caught individuals: 52, 48, 42, and 40 (Table 1). Northern specimens were characterized by a diploid number of 52 (Table 1; Fig. 1; Hsu and Benirschke, 1974; with reexamination by V.R. Rausch, personal communication), with 22 pairs of acrocentric or subtelocentric autosomes, three pairs of small submetacentric autosomes, a large submetacentric X chromosome, and a small submetacentric Y chromosome. Southern individuals have a diploid number of 40 (Table 1, Figs. 1 and 2A), 5 pairs of large metacentric autosomes, 1 pair of large submetacentric autosomes, 11 pairs of small acrocentric or subtelocentric autosomes, 2 pairs of small submetacentric autosomes, and a small subtelocentric Y chromosome (not figured) and two morphologically distinct X chromosomes. One is a large submetacentric, similar in size and shape to that of northern population, the other is a large subtelocentric (Fig. 2). The 2N = 48 individual has a chromosomal morphology similar to the 2N = 52 individuals except that the former has four fewer acrocentric pairs and two additional pairs of large metacentric autosomes. The X chromosome is a large submetacentric. Specimens possessing 2N = 42 differ from the 2N = 40 individuals in having one less pair of large metacentric autosomes and two additional pairs of acrocentric or subtelocentric autosomes. All X chromosomes in these specimens are large telocentrics.

The F_1 hybrid individuals have 46 chromosomes (Fig. 2B). As would be predicted from the morphology of the parental karyotypes (Hsu, *in litt.*), there are 6 large metacentrics, 1 large submetacentric (which is probably the X chromosome from its northern mother), 35 acrocentric or subtelocentric

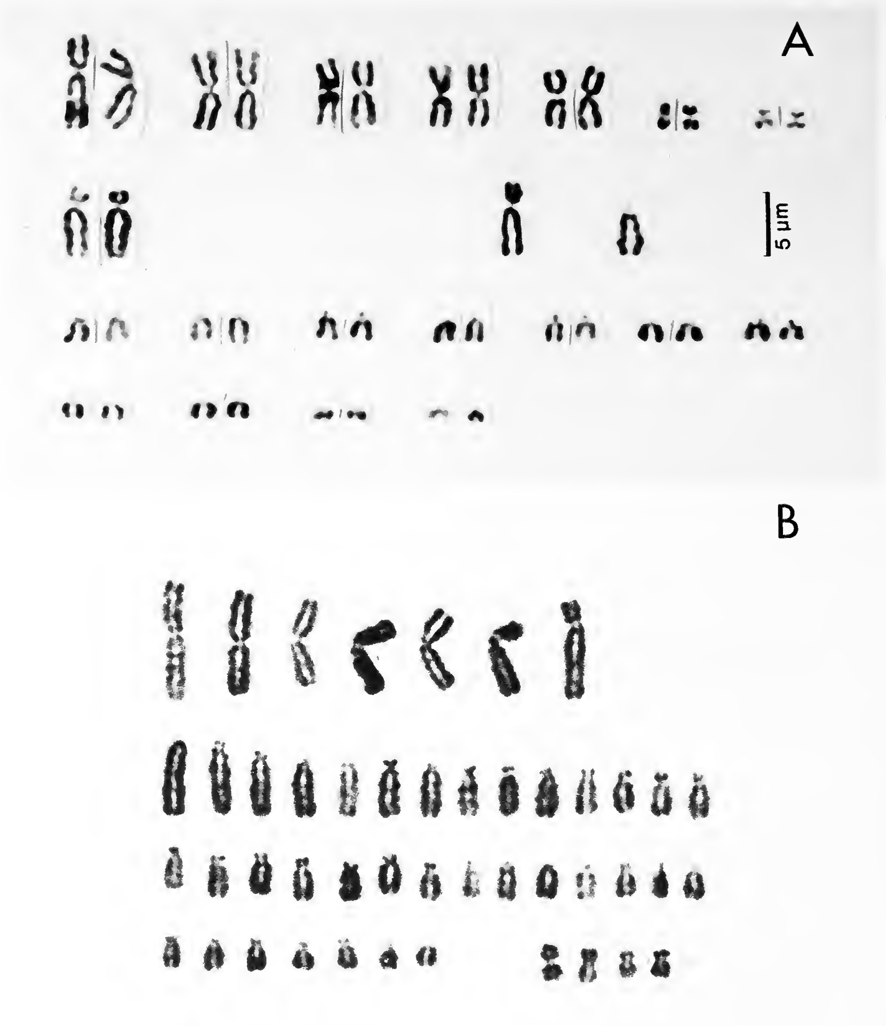

Figure 2. **A.** Karyotype of the holotype of *Arborimus pomo* n. sp., with 2N = 40, from Jenner, Sonoma Co., California. **B.** Karyotype of a male F_1 hybrid, provided by T.C. Hsu. The mother was from 6 mi. (9.7 km) NNE Coburg, Lane Co., Oregon, and the father was from Albion, Mendocino Co., California.

chromosomes (one of which is probably the Y chromosome from its southern father), and 4 small metacentric or submetacentric chromosomes.

CAPTIVE BREEDING STUDIES

Of 250 encounters recorded, 27 were Oregon × California crosses (Table 2). The *G*-value is 206.0, which is significant (df = 6; $\chi^2 = 18.6$), suggesting that results of encounters are not independent of the type of parental cross. The successful pregnancy rate for all Oregon–California crosses was 23%, slightly lower than that for the average of the within-state crosses (28%). The success of crosses between California females and Oregon males was strikingly lower than the reciprocal cross, suggesting a directional barrier to reproduction between northern and southern populations. When Oregon and California individuals were crossed, the number of PRDs was much higher than for within-state crosses (17% vs. 3%), further indicating a barrier to reproduction between northern and southern populations.

MORPHOMETRIC ANALYSES

All *F*-values were significant ($P < 0.05$; Table 3). Oregon samples of both sexes averaged larger than California samples for variables HB, TL, HF, GLS, ZB, MT, LD, and TW for both sexes (Table 3). Variable IOC measured larger in Oregon males than California males, but the same was not true for females. For variable IPW, sample G individuals were as small as the California samples. Only for variable PW were California individuals larger than Oregon individuals.

Table 2. Results of breeding experiments. C denotes a California origin; O denotes an Oregon origin; PRD indicates pregnancy-related deaths. Proportions are in parentheses.

f × m	Negative	Successful	PRD	Total encounters
O × O	83 (0.66)	39 (0.31)	4 (0.03)	126 (1.00)
C × C	69 (0.73)	22 (0.23)	3 (0.03)	94 (1.00)
O × C	6 (0.46)	5 (0.38)	2 (0.15)	13 (1.00)
C × O	12 (0.70)	2 (0.12)	3 (0.18)	17 (1.00)
Total	160	61	12	250 (1.00)

The results of the Student–Newman–Keuls multiple range test (Table 3) indicate that there are few significant subgroups of samples. The exceptions are all in the male samples as follows: samples A and G are significantly larger for HF; California males are significantly larger than Oregon males for PW; sample J is significantly larger for PF; sample H is significantly smaller for LD; and for MT, males break in three significant subgroups (H/J, B/G/C, and H).

Results of the MANOVAs (Wilks' criterion, Pillai's trace, Hotelling–Lawley trace, and Roy's maximum root criterion) were significant ($P < 0.0001$; upper bound for Roy's) for both males and females. The canonical vectors expressed the following percentages of the morphometric variation (female/male): first—73.60/76.84; second—8.36/9.28; third—5.88/8.38. The first three canonical vectors are listed in Table 4. Characters with percentages of their variance over 80% explained by the first vector in females are HB, GLS, ZB, MB, LN, DB, PW, IPL, LD, and PF, whereas for males they are GLS, MT, DB, PW, IPL, LD, and PF. On the second vector, no characters had more than 50% of their variance explained for females, whereas for males, TL, HF, and ZB had more than 50% variance explained.

Two-dimensional plots of the first two canonical vectors for females and males (showing the sample mean and 95% confidence limits; Pimentel and Smith, 1986) are illustrated in Figure 3. The third vector is not illustrated as it accounts for a relatively small portion of the variability. For both sexes, Oregon samples (A–G) are separated from California samples (H–L) along the first vector. There appears to be some geographic pattern of alignment along the second vector within the cluster of Oregon populations. For example, for females, the samples align from A (the northernmost sample) to G (the southernmost sample in the left of Figure 3A, whereas the male populations do not fall out in any discernable geographic pattern. The same is seen in the clusters of male samples (Fig. 3B).

The degree of phenetic overlap of the samples was assessed further by comparing the proportion of individuals from each locality that were misclassified by the discriminant function analysis (Table 5). Of 306 individuals, 234 (76.5%) were classified correctly to their *a priori* designated samples by the discriminant function; 72 (23.4%) were classified incorrectly. Of the latter, only three (1.0%) were classified to populations in the other state (i.e., two California individuals misclassified to an Oregon sample, and one Oregon individual misclassified to a California sample). The remainder were misclassified to a within-state population.

DISCUSSION

Chromosomal analyses suggest that there are two distinct groups within specimens previously recognized as *A. longicaudus.* The northern (Oregon) group is typified by 2N = 52, and a single type of X chromosome (a large submetacentric); the southern (California) group has a 2N of 40 or 42 and two types of X chromosomes. The differences in morphology between the two X chromosomes may be due to heterochromatic additions or losses. This variability is commonly seen in arvicolid voles (Modi, 1987), but its existence in *Arborimus* cannot be substantiated without C-banded karyotypes. The autosomal variability may be due to Robertsonian fission–fusion events. However, banded chromosomes and larger sample sizes are needed to test this hypothesis.

Morphometric results reflect a similar pattern distinguishing Oregon and California groups. Although the univariate statistics do not demonstrate easily discernable differences between the groups, Oregon individuals tend to be larger than California individuals. Also, the maxillaries in California individuals tend to project more posteriorly relative to the nasals than do the maxillaries in Oregon individuals. The multivariate results provide incontrovertible patterns of distinctness of the two groups. Laboratory breeding studies are concordant with the karyologic and morphologic results and demonstrate a strong reproductive barrier between Oregon and California populations.

Additional data on morphologic distinction between the two groups may be found in Kesner (1986). In an examination of the myology of the microtine manus, he demonstrated that individuals from California populations (referred to as *A. longicaudus*) possess a muscle (*M. adductor digiti secundi*) that is absent in individuals from northern populations (referred to as *A. silvicola*). In addition, California specimens possess the full complement of *Mm. lumbricales,* whereas Oregon specimens do not.

Table 3. Variation in 17 measurements (mm) for populations of *Arborimus*. Population samples and measurements are explained in the materials and methods section. Vertical lines alongside each geographic sample indicate statistically homogeneous subsets derived from a Student–Newman–Keuls multiple range test. All *F*-tests are highly significant ($P < 0.001$), except depth of braincase ($P < 0.05$ for both sexes), and tail length ($P < 0.05$ for males).

Sample	Mean	S.D.	Sample	Mean	S.D.
	Head and body length (HB)				
	Females ($F = 7.32$)			Males ($F = 6.38$)	
C	112.56	3.94	A	105.11	5.00
A	112.23	4.67	C	104.44	5.70
G	107.00	6.30	G	102.14	6.83
B	107.00	2.31	B	98.38	2.67
E	106.25	3.30	J	98.11	6.38
D	106.17	5.81	H	94.58	7.75
F	103.58	5.27			
I	103.29	7.30			
K	102.90	5.26			
H	102.60	6.13			
L	102.46	5.66			
J	101.50	6.95			
	Tail length (TL)				
	Females ($F = 4.12$)			Males ($F = 2.80$)	
E	79.25	9.32	G	71.14	5.87
D	79.00	5.44	B	70.75	4.93
C	78.89	5.35	C	70.00	4.18
B	75.43	7.37	J	68.27	5.92
A	75.23	5.44	A	66.89	5.31
G	74.75	5.31	H	64.17	5.22
F	74.21	6.55			
L	73.26	6.73			
H	70.80	8.23			
I	68.95	9.32			
J	68.17	7.52			
K	65.90	9.28			
	Hind foot length (HF)				
	Females ($F = 15.19$)			Males ($F = 14.80$)	
C	22.78	0.83	A	21.72	1.13
A	22.19	0.75	C	21.56	0.88
B	22.00	1.41	G	20.57	0.79
E	21.50	1.00	B	20.44	1.09
G	21.00	0.76	J	19.95	0.81
F	20.95	1.87	H	19.42	0.90
D	20.83	1.17			
L	20.18	0.83			
K	19.90	0.88			
I	19.57	1.33			
H	19.40	1.43			
J	19.33	0.52			
	Greatest length of skull (GLS)				
	Females ($F = 8.40$)			Males ($F = 13.07$)	
A	26.08	0.71	A	25.38	0.58
C	25.81	0.71	G	24.89	0.37
B	25.36	0.53	C	24.69	0.69
E	25.30	0.80	B	24.42	0.57
D	25.28	0.61	J	24.15	0.60
F	24.99	0.80	H	24.03	0.66
J	24.92	0.84			
G	24.81	0.62			
I	24.70	0.93			
L	24.54	0.72			
H	24.49	0.89			
K	24.49	0.98			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
		Zygomatic breadth (ZB)			
	Females ($F = 6.63$)			Males ($F = 8.66$)	
C	14.72	0.30	G	14.50	0.34
A	14.55	0.48	A	14.20	0.41
E	14.40	0.40	C	13.96	0.41
B	14.36	0.49	B	13.80	0.40
D	14.28	0.29	J	13.70	0.36
J	14.18	0.53	H	13.63	0.50
G	14.13	0.37			
F	14.11	0.43			
H	14.10	0.59			
I	14.03	0.59			
L	14.02	0.39			
K	13.99	0.25			
		Least interorbital width (IOC)			
	Females ($F = 6.81$)			Males ($F = 5.74$)	
B	3.59	0.20	A	3.48	0.13
H	3.47	0.18	C	3.44	0.14
A	3.46	0.10	B	3.44	0.19
C	3.41	0.13	G	3.37	0.21
K	3.34	0.18	H	3.33	0.22
D	3.32	0.18	J	3.28	0.14
G	3.31	0.21			
I	3.31	0.14			
L	3.27	0.14			
F	3.27	0.21			
E	3.22	0.17			
J	3.12	0.18			
		Mastoid breadth (MB)			
	Females ($F = 8.28$)			Males ($F = 4.66$)	
C	8.86	0.21	J	8.69	0.30
E	8.77	0.54	C	8.64	0.26
L	8.77	0.30	A	8.63	0.21
A	8.71	0.20	G	8.57	0.24
G	8.70	0.36	B	8.43	0.18
J	8.68	0.54	H	8.36	0.25
B	8.63	0.38			
K	8.62	0.25			
I	8.57	0.32			
D	8.53	0.21			
H	8.50	0.44			
F	8.47	0.45			
		Length of nasals (LN)			
	Females ($F = 5.59$)			Males ($F = 4.96$)	
A	6.85	0.35	G	6.84	0.31
C	6.82	0.33	A	6.61	0.27
I	6.72	0.46	H	6.43	0.52
G	6.68	0.50	C	6.32	0.36
H	6.67	0.39	J	6.29	0.38
E	6.65	0.31	B	6.26	0.19
J	6.58	0.31			
D	6.53	0.24			
K	6.51	0.44			
F	6.51	0.25			
B	6.50	0.33			
L	6.42	0.38			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
		Length of maxillary toothrow (MT)			
	Females ($F = 18.40$)			Males ($F = 20.40$)	
A	5.90	0.16	A	5.86	0.16
C	5.77	0.18	C	5.70	0.19
B	5.76	0.15	G	5.63	0.13
E	5.75	0.29	B	5.56	0.17
D	5.58	0.23	J	5.43	0.17
G	5.55	0.19	H	5.41	0.17
F	5.50	0.23			
K	5.49	0.17			
L	5.47	0.19			
I	5.46	0.27			
J	5.45	0.19			
H	5.33	0.20			
		Depth of braincase (DB)			
	Females ($F = 1.98$)			Males ($F = 2.84$)	
H	7.26	0.37	J	7.19	0.29
J	7.23	0.52	A	7.16	0.20
A	7.23	0.20	G	7.11	0.21
L	7.23	0.29	H	7.08	0.24
B	7.20	0.08	C	7.01	0.27
I	7.16	0.28	B	6.93	0.25
F	7.15	0.32			
K	7.13	0.28			
E	7.12	0.17			
D	7.12	0.20			
G	7.03	0.23			
C	7.02	0.28			
		Nasal–maxillary distance (PW)			
	Females ($F = 19.58$)			Males ($F = 8.28$)	
I	1.11	0.25	J	0.89	0.30
L	0.99	0.24	H	0.86	0.33
J	0.98	0.17	B	0.56	0.26
H	0.89	0.35	A	0.56	0.28
K	0.82	0.11	C	0.53	0.15
B	0.66	0.22	G	0.44	0.19
D	0.58	0.15			
F	0.57	0.19			
A	0.53	0.17			
C	0.44	0.18			
E	0.35	0.17			
G	0.30	0.40			
		Width of interparietal (IPW)			
	Females ($F = 15.36$)			Males ($F = 5.59$)	
C	9.02	0.24	A	8.64	0.29
A	8.86	0.31	B	8.43	0.30
D	8.60	0.27	C	8.32	0.37
B	8.54	0.30	H	8.31	0.30
F	8.54	0.24	G	8.17	0.72
I	8.44	0.34	J	8.14	0.35
E	8.40	0.52			
H	8.37	0.35			
J	8.37	0.30			
K	8.27	0.50			
L	8.15	0.35			
G	7.83	0.37			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
		Length of interparietal (IPL)			
	Females ($F = 7.71$)			Males ($F = 6.20$)	
C	3.72	0.25	J	3.54	0.31
K	3.72	0.40	C	3.40	0.24
L	3.68	0.28	H	3.31	0.30
H	3.62	0.50	B	3.27	0.26
E	3.58	0.13	G	3.24	0.36
I	3.55	0.31	A	3.16	0.19
J	3.52	0.41			
F	3.33	0.25			
G	3.29	0.23			
B	3.27	0.24			
A	3.21	0.25			
D	3.20	0.30			
		M2–M2 width (MW)			
	Females ($F = 15.47$)			Males ($F = 12.50$)	
C	5.84	0.17	A	5.78	0.16
A	5.84	0.19	C	5.69	0.17
E	5.70	0.08	G	5.54	0.24
B	5.64	0.19	H	5.52	0.19
D	5.60	0.20	B	5.49	0.20
J	5.53	0.21	J	5.39	0.19
G	5.47	0.16			
H	5.46	0.18			
I	5.46	0.18			
F	5.41	0.23			
L	5.40	0.18			
K	5.38	0.14			
		Length of diastema (LD)			
	Females ($F = 8.56$)			Males ($F = 13.91$)	
C	7.54	0.43	A	7.14	0.20
A	7.45	0.33	C	7.02	0.19
B	7.17	0.21	G	6.84	0.24
E	7.10	0.26	B	6.84	0.21
F	6.98	0.35	J	6.76	0.28
D	6.98	0.22	H	6.45	0.22
G	6.90	0.33			
L	6.83	0.36			
K	6.82	0.46			
J	6.82	0.48			
H	6.71	0.43			
I	6.67	0.37			
		Width of upper M2 (TW)			
	Females ($F = 9.89$)			Males ($F = 8.26$)	
E	1.35	0.06	C	1.31	0.08
C	1.33	0.07	A	1.31	0.07
A	1.31	0.05	B	1.26	0.05
D	1.30	0.06	G	1.23	0.08
F	1.25	0.06	H	1.23	0.06
B	1.24	0.05	J	1.22	0.06
J	1.23	0.08			
L	1.22	0.06			
K	1.22	0.08			
G	1.21	0.04			
I	1.20	0.05			
H	1.20	0.05			

Table 3. Continued.

Sample	Mean	S.D.	Sample	Mean	S.D.
		Length of palatal foramen (PF)			
Females ($F = 7.15$)			Males ($F = 17.85$)		
L	4.71	0.23	J	4.61	0.19
A	4.69	0.18	A	4.50	0.11
J	4.68	0.26	H	4.40	0.14
I	4.59	0.22	C	4.33	0.19
K	4.58	0.29	G	4.31	0.14
C	4.56	0.22	B	4.18	0.20
B	4.51	0.11			
H	4.47	0.24			
D	4.45	0.26			
E	4.40	0.18			
F	4.27	0.26			
G	4.24	0.42			

The tree voles obtained from Curry County, Oregon (2N = 48), and Del Norte County, California (2N = 42) represent new locality records located in a long-recognized hiatus in the distribution of "*Arborimus longicaudus.*" Each was from a very small isolated and restricted population. When these populations were last monitored in 1985, evidence of persistence was poor, restricted to several inaccessible (to us) nests. These individuals do not represent either F_1 or F_2 hybrids (Fig. 2B; T.C. Hsu, personal communication). Based upon the morphology of the X chromosome and the results of the morphometric analyses, the affinity of the population represented by the 2N = 48 individual is with other Oregon samples, whereas the affinities of the populations represented by the 2N = 42 individuals is with other California samples.

One may argue that the morphological gap between the Oregon and California samples (Fig. 3) reflects nothing more than a lack of specimens from that geographic area, and should specimens exist from that area, the gap would be filled in. We refute this argument by pointing out that within both Oregon and California there are geographic gaps not represented by any samples (e.g., between F and G, or between H/I and J) that are as large as or larger than the geographic gap between samples G and H (Fig. 1). Clustering of within-state samples (Fig. 3)

Table 4. First three canonical vectors and percent of overall morphometric variation explained by each vector for 17 variables in both females and males.

	Females			Males		
Variable	CV1	CV2	CV3	CV1	CV2	CV3
HB	−0.010	−0.004	−0.009	0.001	−0.001	−0.006
TL	−0.002	0.010	−0.004	0.001	0.016	−0.012
HF	−0.047	0.050	0.055	−0.020	−0.107	−0.028
GLS	−0.151	−0.143	−0.077	−0.169	−0.089	0.148
ZB	0.117	0.104	−0.042	0.073	0.416	−0.136
IOC	−0.028	−0.334	0.004	−0.091	0.145	−0.074
MB	0.304	0.217	0.107	0.155	−0.240	−0.219
LN	0.259	−0.235	−0.247	0.224	0.268	0.201
MT	−0.118	−0.084	0.204	−0.311	−0.072	−0.270
DB	0.196	0.038	0.060	0.078	−0.065	0.021
PW	0.514	−0.443	0.002	0.268	0.043	0.210
IPW	−0.164	−0.288	−0.052	−0.093	−0.085	0.206
IPL	0.206	0.097	0.093	0.244	0.011	−0.259
MW	−0.280	−0.333	0.127	−0.030	−0.218	0.658
LD	−0.251	0.197	0.229	−0.372	−0.159	−0.365
TW	−0.318	0.502	0.702	−0.351	−0.241	−0.181
PF	0.415	−0.231	0.547	0.615	−0.712	0.196
Percent	73.60	8.36	5.88	76.84	9.28	8.38

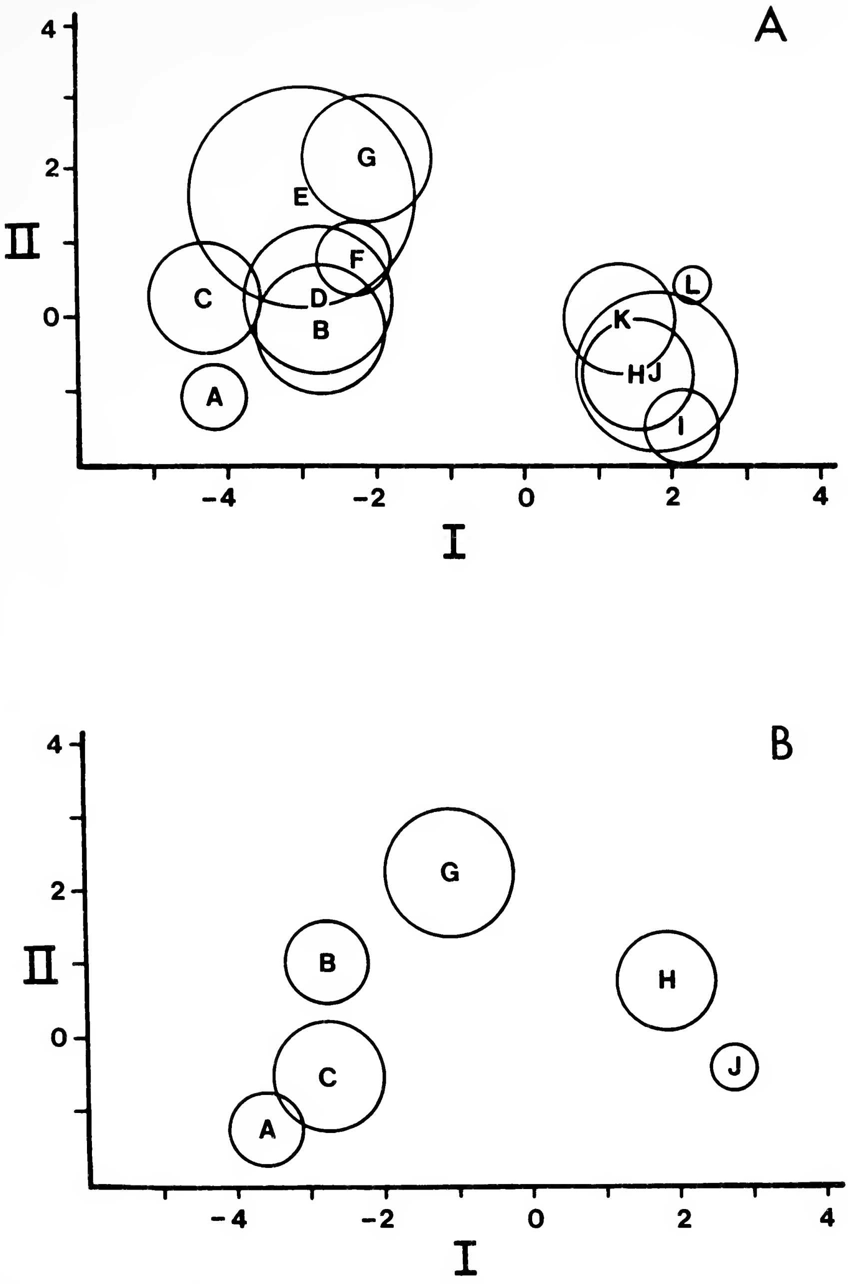

Figure 3. Plot of the mean and one standard deviation of the first two canonical variates for 12 samples of females (top) and six samples of males (bottom) belonging to the *Arborimus longicaudus* species-complex. Letters refer to samples identified in the appendix.

does not reflect these geographic gaps, further suggesting a genetic component to the gap between Oregon and California samples.

In light of the data presented here (Tables 1, 2, and 5; Figs. 1–3), we recognize the California populations as a distinct biological species. By Mayr's (1969) discrimination grid, the two species are grossly morphologically identical, are allopatric, and are reproductively isolated, therefore they may be considered sibling species. The name *A. longicaudus* in the broad sense (type locality, Marshfield, Coos County, Oregon) must be applied to the Oregon group, leaving the California species without an available name; it is described and named below.

The hiatus between the northern and southern species of red tree voles exists in the Klamath Mountains area. This region is significantly higher in altitude and geologically older than the Coast

Table 5. Geisser classification of individual red tree voles (n = 306). Rows are actual groups and columns are predicted groups. Asterisks indicate specimens classified to a sample outside of the state (see results section). See appendix for explanation of sample acronyms.

Actual group	n	Percent classified correctly	Predicted locality											
			A	B	C	D	E	F	G	H	I	J	K	L
A) Females														
A	26	92	24			2								
B	7	71		5		1		1						
C	9	89	1		8									
D	6	67			1	4		1						
E	4	50			1		2		1					
F	19	63		1	1	3	1	12				1*		
G	8	88				1			7					
H	10	50				1*				5	2	1		1
I	21	71								3	15	1	1	1
J	6	67										4	2	
K	9	70										1	7	2
L	74	70								2	4	5	11	74
B) Males														
A	18	89	16	1	1									
B	16	75	1	12	3									
C	8	56	3	1	5									
G	7	71		1					5				1*	
H	12	92								11			1	
K	44	91								4			40	

Ranges to the north and south, and is dissected by rivers running through narrow, steep-walled canyons (Bailey, 1966; Wright and Frey, 1965). The climate and vegetation of this region reflect the geology and geography, in that the area is more arid, with a rain shadow closer to the coast, and therefore has a more compressed mesic vegetation belt. The flora is diverse and rich in narrowly endemic species (Whittaker, 1961), lacking large continuous stands of Douglas fir and associates (*Tsuga heterophylla, Picea sitchensis, Abies grandis,* and *A. concolor*), which are primary food sources for red tree voles. Distributions of a number of species-complexes of animals reflect this fragmentation of the mesic forest (Maser et al., 1981; Nussbaum et al., 1983). An example is the *Eutamias townsendi* species-complex, where sibling species of chipmunks appear to be separated geographically by the Rogue, Klamath, and Eel rivers in the Klamath Mountains area (Levenson et al., 1985; Sutton, 1987). Isolation by the combination of these environmental factors may be an important factor in speciation within the *A. longicaudus* species-complex as well.

There is not any strong morphometric or karyologic differentiation between *A. l. longicaudus* and *A. l. silvicola* in Oregon. The two taxa have been distinguished primarily on the basis of color (Hall, 1981) but now can be properly delineated geographically. The darker race, *A. l. silvicola,* is restricted to the Pacific slope of the coast ranges in Tillamook and Lincoln counties in Oregon (sample A in Fig. 1). The nominotypical subspecies is distributed to the east and south (samples B–G in Fig. 1).

Arborimus pomo new species

HOLOTYPE. Adult female, skin, skeleton, and karyotype, no. 34476, mammal collection, Thomas Burke Memorial Washington State Museum, University of Washington; from Jenner Ridge, 0.8 km (0.5 mi.) north of Jenner, Sonoma County, California (T7N, R11W, NW¼, Sec. 18; 38°27′30″N, 123°6′W). Taken on 24 February 1984 by M.L. and S. Johnson, sacrificed for karyotyping 13 March 1985, original number R. Rausch 46529. Skull is drawn in Figure 4.

PARATYPES. Several collections have series of specimens from the area of the type locality, including the Museum of Vertebrate Zoology, University of California at Berkeley; the University of Puget Sound; the Burke Museum, University of Washington.

DISTRIBUTION. All California populations formerly included within *A. longicaudus* (Fig. 1). The most southern record is from Freestone, Sonoma County, California. Specimens are available from scattered localities in Sonoma, Mendocino, Humboldt, and western Trinity counties. The northernmost population was collected from the South Fork of the Smith River, Del Norte County, California.

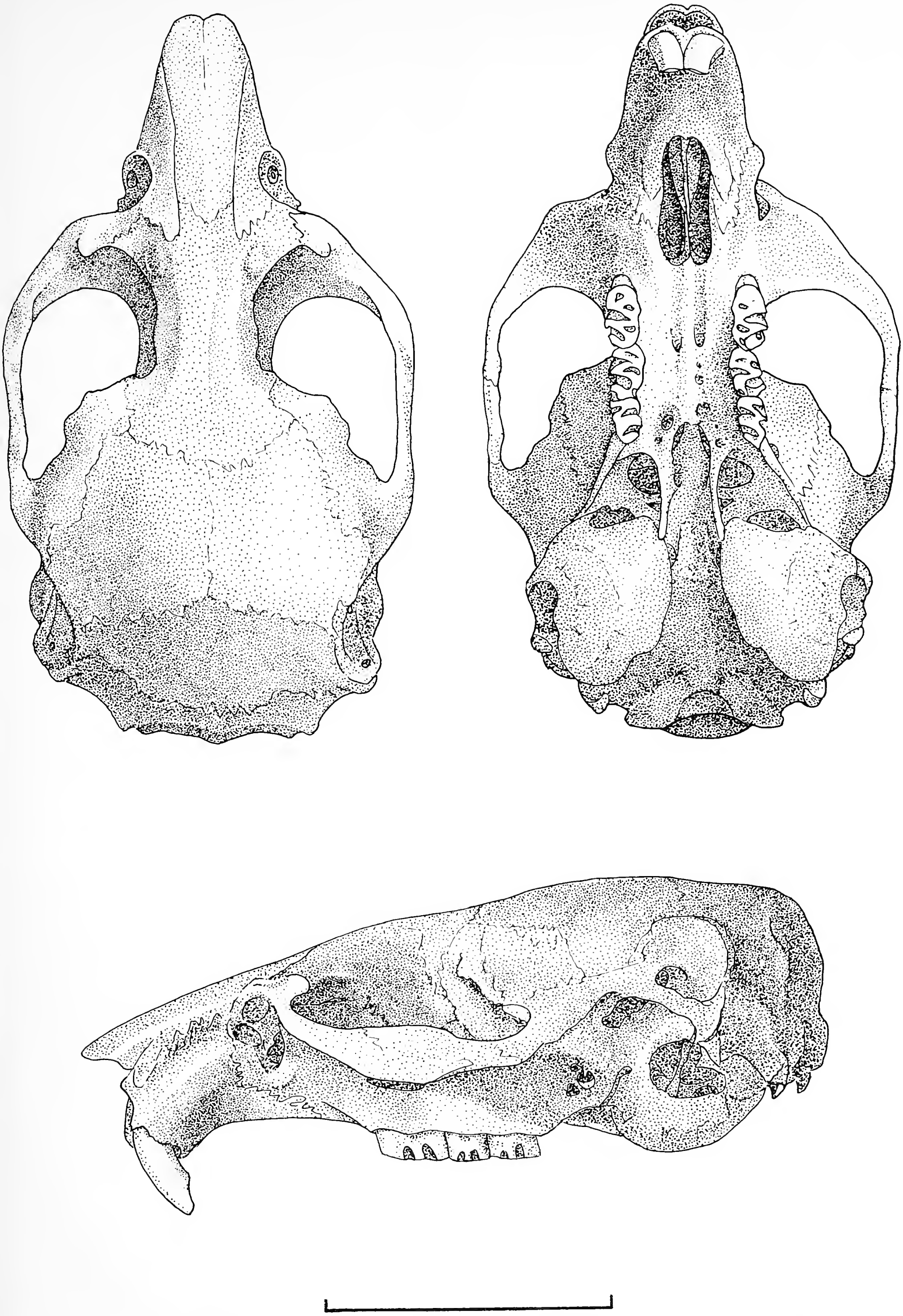

Figure 4. Dorsal, ventral, and side view of cranium of holotype of *Arborimus pomo* n. sp. (UW 34476). Bar is 1 cm.

DIAGNOSIS. *Arborimus pomo* has a diploid number of 40 or 42, with a large submetacentric and/or a large subtelocentric X chromosome, and a small subtelocentric Y chromosome. Specimens are smaller in overall size than those of *A. longicaudus,* the nasals do not extend as far posteriorly relative to the maxillaries as do the nasals in *A. longicaudus,* and specimens have a full set of *Mm. lumbricales* and *M. adductor digiti secundi.*

DESCRIPTION. *Arborimus pomo* is a true sibling species to *A. longicaudus,* the former being identical in coloration and external morphology to *Arborimus l. longicaudus* in southwestern Oregon. The color above is nearly uniform, bright rusty brown; the undersurfaces are white, slightly tinged with rusty brown, especially on the abdomen. The tail is dusky brown above, somewhat paler below. Measurements of the holotype (in mm) are: total length, 180; length of tail, 75; length of hind foot, 23; ear, 11.5; greatest length of skull, 25.9; zygomatic breadth, 14.5; least interorbital width, 3.4; mastoid breadth, 8.7; length of nasals, 6.9; length of maxillary toothrow, 5.4; depth of braincase, 7.2; distance from the posteriormost point of nasals to posteriormost point of maxillaries, 0.7; width of interparietal, 8.7; length of interparietal, 4.0; M2–M2 width, 5.3; length of diastema, 7.2; width of upper M2, 1.2; length of palatal foramen, 4.7.

ETYMOLOGY. The specific name refers to the Pomo peoples, indigenous to northern coastal California. The Pomo had a subsistence culture based on acorn processing and are widely respected for their basketry work. The name is a noun in apposition.

ECOLOGY. The habitat of *A. pomo* has been compared by repetitive monitoring and field studies to plant communities inhabited by *A. longicaudus* in Oregon (C. Maser and M.L. Johnson, *in litt.*). We can distinguish no particular pattern of difference. These mice inhabit a wide variety of mesic habitats, including those dominated by: (1) Douglas fir (*Pseudotsuga menziesii*), (2) grand fir (*A. grandis*), (3) Sitka spruce (*P. sitchensis*), or (4) western hemlock (*T. heterophylla*). Within the geographic range of these trees in northern California, those areas that have sufficient moisture (from ocean fog, increased precipitation, and permanent ground water such as along streams or around lakes) appear suitable for red tree voles. Habits of *A. pomo* were described in detail by Howell (1926; as "*Phenacomys longicaudus*").

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APPENDIX

Single letters in parentheses are sample designations used in morphometric analyses. Sample sizes are indicated by numbers following specific localities. Complete names for collections in which specimens are housed are given in the acknowledgments; LACM refers to specimens housed at the Natural History Museum of Los Angeles County.

Arborimus longicaudus silvicola

OREGON: (**A**; 26 females, 18 males) Lincoln Co.: near Grande Ronde (UW 34494, PSM 23928–9); near Nashville (FMNH 51496); Tillamook Co.: 3 mi. (4.8 km) E Cape Lookout, headwaters Tillamook River (PSM 21506, 21517, 21521, 22745–6); Cape Meares (PSM 22719); Cascade Head (PSM 21592); Foley Creek (UW 34487); Netarts (PSM 22723); ¾ mi. (1.2 km) SE Netarts Summit (UW 34490); approximately 1 mi. (1.6 km) SE Netarts Summit (UW 34493); Netarts Watershed, Crown Zellerbach Logging Area (PSM 21590, 21594–5, 21597–8); Oceanside (PSM 6781, 6784); Neskowin (MVZ 104979); 5 mi. (8 km) NW Pleasant Valley (PSM 21519–20); 3–4 mi. (4.8–6.4 km) E Tillamook, Bay Ocean Road (PSM 21515); 3 mi. (4.8 km) SW Tillamook, past Eckloft Road (PSM 21522); vicinity of Tillamook (UW 34484, PSM 21507, 21510–1, 21513); south Tillamook Bay (UW 34486, PSM 21553, 21587, 21709–10, 21712, 21715–7, 22716–8, 22720).

Arborimus longicaudus longicaudus

OREGON: (**B**; 7 females, 2 males) Washington Co.: 3 mi. (4.8 km) E Gaston (AMNH 175922); 5 mi. (8 km) E Gaston (AMNH 183335); 1½ mi. (2.4 km) SE Laurelwood (PSM 23926, 23970); Yamhill Co.: 9 mi. (14.5 km) W Carlton (MVZ 126859–60); 4 mi. (6.4 km) N Newburg, Ribbon Ridge (AMNH 183338, 183341, 183343).

(**C**; 9 females, 4 males) Clackamas Co.: Molalla (PSM 5871, 5873); 7½ mi. (12.1 km) SE Molalla (PSM 5870); 8 mi. (12.9 km) SE Molalla (PSM 10378, 10380, 10382, 10414, 23963, 23969); 8½ mi. (13.7 km) SE Molalla (PSM 8387); near Molalla, Schoenborn Ranch (PSM 5859, 10381); Hood River Co.: 1 mi. (1.6 km) E Cascade Locks, Oxbow Fish Hatchery (PSM 7019).

(**D**; 6 females, 5 males) Benton Co.: Alsea River, Seely Creek (PSM 23962); near Blodgett (FMNH 51495); 3¾ mi. (6 km) WNW Camp Adair (PSM 10400); 6 mi. (9.7 km) N Corvallis, Nettleton Road, McDonald Forest (OSU 5030, 5050, 5069); McDonald Forest (UW 34497, OSU 5048, 5075, PSM 10906); Prairie Mt., 3200 ft. (975 m) (T14S, R7W, SW¼, Sec. 7) (PSM 13107).

(**E**; 4 females, 5 males) Lane Co.: 6.8 km N, 7.6 km E Blue River (T15S, R5E, Sec. 32) (USNM 557648, 560412); 6 mi. (9.7 km) NNE Coburg (PSM 10441, 10927); 2½ mi. (4 km) SW Donna (PSM 10437); Eugene, Spencer Butte (OSU 5038); 6.4 km N, 0.6 km E McKenzie Bridge (T15S, R5E, Sec. 25) (USNM 558062); 6 km N, 0.6 km E McKenzie Bridge (T15S, R5E, Sec. 25) (USNM 557645); Linn Co.: 4½ mi. (7.2 km) S Sodaville (OSU 5079).

(**F**; 19 females, 9 males) Benton Co.: 5 mi. (8 km) S Alpine, Ferguson Creek (PSM 10404); NW Bellfountain (PSM 23904); 4 mi. (6.4 km) S Monroe (PSM 23906–7); 4.5 mi. (7.2 km) SW Monroe (OSU 5072, PSM 10383, 10389, 10399, 10406, 10409, 10411, 10917, 13104, 13109, 23892); Lane Co.: 6 mi. (9.7 km) NW Cheshire (PSM 10926); 6.75 mi. WNW Cheshire (OSU 5045); 3 mi. (4.8 km) W Cheshire (PSM 10433); 2¾ mi. (4.4 km) W Cheshire, near Jones Creek (OSU 5071); 5½ mi. (8.9 km) SW Cheshire (PSM 10436); 11 mi. (17.7 km) W Junction City (T5S, R5W, SE¼, Sec. 15) (PSM 23910, 23912, 23915); 6 mi. (9.7 km) SW Monroe (OSU 582, PSM 23913, 23916); 1½ mi. (2.4 km) NW Noti (PSM 10434); ¼ mi. (0.4 km) NE Walterville (PSM 10922).

(**G**; 8 females, 7 males) Coos Co.: 7 mi. (11.3 km) SW Bandon, Bill's Peak (PSM 23919–20); 1 mi. (1.6 km) NW Bill's Peak, 1200 ft. (366 m) (PSM 10920); 3 mi. (4.8 km) SW Broadbent (T30S, R13W, Sec. 12) (PSM 14498–9); Curry Co.: 1.1 mi. (1.8 km) SE Humbug Mt., along Hwy 101 (PSM 23924); Winchuk River at Wheeler Creek (PSM 23936–7, 23945, 23947, 23951–2, 23954, 23957–8).

Arborimus pomo

CALIFORNIA: (**H**; 10 females, 5 males) Humboldt Co.: 4 mi. (6.4 km) N, 11 mi. (17.7 km) E Arcata (PSM 20941); 8 mi. (12.9 km) E Blue Lake, Snow Camp Road (HSU 2338, 2370, 2372, 2376, 2378); Maple Creek, 1 mi. (1.6 km) N junction Mad River (MVZ 99616–8, 99621, 99624); Patrick Point State Park (PSM 10425, 20938); Trinity Co.: Mad River, South Fork Mountain, 2500 ft. (762 m) (MVZ 57039); Reilley's Ranch, South Fork Mountain, 3000 ft. (915 m) (MVZ 57042).

(**I**; 21 females, 7 males) Humboldt Co.: Arcata, Fickle Hill Road (HSU 3770); 5 mi. (8 km) E Arcata on Fickle Hill Road (CSULB 10497); Big Bend, Mad River (MVZ 19130); 8½ mi. (13.7 km) N Bridgeville (HSU 1410, 1427, 1612, 1614); 4.5 mi. (7.2 km) N Bridgeville (MVZ 140635); 4.3 mi. (6.9 km) N Bridgeville (MVZ 140633); 2 mi. (3.2 km) E Bridgeville (MVZ 47133); 5.3 mi. (8.5 km) NE Capetown, Morrow Ranch (MVZ 120595); Carlotta (MVZ 21148–54, USNM 206376, 206378–80, 206382–3); Cuddeback (MVZ 19174); 1.3 mi. (2 km) N Hydesville on Rohnerville Road (PSM 10423); 0.75 mi. (1.2 km) W Kneeland, New Kneeland Rd. (HSU 969); 1.5 mi. (2.4 km) S Kneeland, Old Kneeland Rd. (MVZ 165902).

(**J**; 6 females, 4 males) Mendocino Co.: 1½ mi. (2.4 km)

N Albion (AMNH 178883–7); Albion (PSM 10929); ¼ mi. (0.4 km) E Albion (PSM 10420, 10930); Mendocino City (MVZ 19973); 5 mi. (8 km) S Mt. Sanhedrin, Emandal Ranch (PSM 20945).

(K; 10 females, 4 males) Mendocino Co.: Anchor Bay (CM 16427); Sonoma Co.: 3 mi. (4.8 km) N Fort Ross (PSM 10934); 2.8 mi. (4.5 km) S Fort Ross (PSM 21088, 21101, 24036); 0.3 mi. (0.5 km) E Stewarts Point (PSM 10944); 0.4 mi. (0.6 km) E Stewarts Point (PSM 10942); ½ mi. (0.8 km) E Stewarts Point (MVZ 112394, PSM 21121); 1 mi. (1.6 km) E Stewarts Point (PSM 10940, 10943, 21098); 1¼ mi (2 km) E Stewarts Point (PSM 21481); 1 mi. (1.6 km) SSE Stewarts Point (MVZ 112424).

(L; 74 females, 36 males) Sonoma Co.: 1 mi. (1.6 km) N, 0.2 mi. (0.3 km) E Bridgehaven (MVZ 128791); 3.5 mi. (5.6 km) N Camp Meeker (MVZ 94759); 1 mi. (1.6 km) N Camp Meeker (PSM 21438–9, 21442, 21444–5); 3½ mi. (5.6 km) W Duncan Mills (MVZ 70189); 3 mi. (4.8 km) W Duncan Mills (MVZ 94760); 2 mi. (3.2 km) W Duncan Mills, Russian River (MVZ 94716, 94721); 3 mi. (4.8 km) E Duncan Mills (MVZ 70190); ½ mi. (0.8 km) SE Duncan Mills (PSM 21464); between Duncan Mills and Jenner (PSM 21167, 21256, 21258); near Duncan Mills, Rien's Beach (PSM 21491, 21496); ½ mi. (0.8 km) NW Freestone (PSM 21089–90, 21099–100, 21125, 21260); ½ mi. (0.8 km) N Freestone (PSM 21116, 21118–9, 21168–70); Freestone (PSM 21263); 3 mi. (4.8 km) N Jenner, Willig Ranch (PSM 21406, 21408); 2 mi. (3.2 km) N Jenner, Willig Ranch (PSM 21399, 21401); ½ mi. (0.8 km) NW Jenner (PSM 21384, 21386, 21397–8); ½ mi. (0.8 km) N Jenner (PSM 21499); Jenner Ridge, 0.8 km (½ mi.) N Jenner (T7N, R11W, NW¼, Sec. 18) (UW 34458, 34462, 34476, LACM 85688–92, PSM 20970, 20973, 20976–8, 21016, 21019–20, 21025, 21028, 21412, 21415–6, 24037, 24040, 24048); 1 mi. (1.6 km) E Jenner (MVZ 103482, PSM 21349, 21352, 21354–62); 1.5 mi. (2.4 km) E Jenner (PSM 21347–48); 2 mi. (3.2 km) E Jenner (PSM 21363, 21365–6, 21368); Jenner area (PSM 21466); 1 mi. (1.6 km) W Monte Rio (CM 16426); 2 mi. (3.2 km) SE Monte Rio (CM 16425); 2.3 mi. (3.7 km) S Monte Rio (MVZ 70191, 70195, 70197); 3 mi. (4.8 km) S Monte Rio (PSM 21450, 21452, 21468); 4 mi. (6.4 km) S Monte Rio (MVZ 70201); 1 mi. (1.6 km) S Occidental (MVZ 94761); near Occidental, Camp Meeker (PSM 21426, 21429, 21432–4); Russian River (PSM 21172); lower Russian River, halfway between Duncan Mills and highway junction (PSM 21261–2, 21264); S side Russian River, ¼ mi. (0.4 km) upriver from Duncan Mills (PSM 21093, 21369, 21418, 21421); S side Russian River, ½ mi. (0.8 km) S Duncan Mills, Cassini Ranch (PSM 21376, 21379–80); ¼ mi. (0.4 km) W junction Sheephouse Creek and Russian River (MVZ 122096).

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THREE NEW SPECIES OF THE *PAGURUS LEPIDUS* COMPLEX (DECAPODA, ANOMURA, PAGURIDAE) FROM THE EASTERN PACIFIC

JANET HAIG[1] AND ALAN W. HARVEY[2]

ABSTRACT. Three new species reported as *Pagurus lepidus* (Bouvier), or included in the *Pagurus lepidus* complex by the senior author in earlier publications, are now described and illustrated. *Pagurus rhabdotus* appears to be endemic to the outer coast of the Baja California peninsula and *Pagurus nanodes* is known only from Central and northern South America, whereas *Pagurus virgulatus* has a broad geographic range from central Mexico to Ecuador. *Pagurus rhabdotus* and *P. virgulatus,* like *P. lepidus,* possess the striped ambulatory legs so typical of most of the *provenzanoi* group species. In contrast, *P. nanodes* is distinctive in having banded walking legs.

INTRODUCTION

The Gulf of California, Mexico, more popularly referred to as the "Sea of Cortez" (Steinbeck and Ricketts, 1941), has been an area of carcinological interest for more than a century. The early "Albatross" expeditions of the late 1880s (cf. Townsend, 1901) provided much of the material upon which Benedict (1892) based his descriptions of new pagurid species from the Gulf. The fauna of the Gulf and west coast of Baja ("Lower") California was investigated in the 1930s by the Templeton Crocker Expedition ("Zaca", New York Zoological Society) (Beebe, 1937; Glassell, 1937) and in the 1930s and early 1940s by the Allan Hancock Foundation ("Velero III," University of Southern California) (Fraser, 1943). The outer coast of the Baja California peninsula was also the focus of the 1964 "Magbay" Expedition (cf. Haig et al., 1970). More recently, Brusca (1973, 1980) provided a summation of 24 months of field collecting in the Gulf. Hermit crabs have also been included in numerous reports of decapods from Central and South America (e.g., Rathbun, 1910; Boone, 1931; Holthuis, 1954; Bott, 1955; Del Solar et al., 1970). However, few species of *Pagurus* have received more than brief attention. Ball and Haig (1974) reported that of the 27 species of hermit crabs collected during the 1968 Stanford Oceanographic Expedition's survey of the intertidal and shallow subtidal regions from Paita, Peru to Bahía Magdalena, Baja California, Mexico ("Te Vega" Expedition 18), only nine were pagurids and seven of those represented species of the *provenzanoi* group. Although the authors indicated that these latter species would be treated separately, the report they had planned was never completed.

Since the description of *Pagurus lepidus* (Bouvier, 1898), virtually all small pagurid species from the Gulf of California and/or the west coast of Baja California were routinely assigned to this taxon or to a complex of species confounded under this name (e.g., Haig et al., 1970; Ball and Haig, 1974; McLaughlin, 1975; Snyder-Conn, 1980). Following Haig and McLaughlin's (1991) redescription of *P. lepidus* several species of the complex have been described (i.e., Haig and McLaughlin, 1991; Harvey and McLaughlin, 1991). In the present report three of the species referred to by Haig et al. (1970) as *P. lepidus,* and by Ball and Haig (1974) as *Pagurus* spp., are now described as new species closely allied to, but distinct from, *P. lepidus.*

MATERIALS

Materials for this study have come from the Crustacea collections of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), the National Museum of Natural History, Smithsonian Institution (USNM), and the Natural History Museum of Los Angeles County (LACM). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. Specimens will be returned to depositories of origin and paratypes also deposited in the Naturhistoriska Riksmuseet, Stockholm (NHRM), Nationaal Natuurhistorisch Museum, Leiden (RMNH), and Muséum National d'Histoire Naturelle, Paris (MNHN). One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

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SYSTEMATICS

Pagurus rhabdotus new species

Figure 1A–G

Pagurus lepidus: Haig et al., 1970:19 (in part, see remarks); Ball and Haig, 1974:103 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.4 mm), AHF 6410 (LACM 64-178.1). **Type locality.** Bahía San Hipólito, W. Baja California, Mexico, "Magbay" Expedition, 10–13 m, February 9, 1964, collectors T. Hopkins and T. Scanland.

PARATYPES. W. Baja California, Mexico: Bahía San Hipólito, 2 ♀, 1 ovigerous ♀ (SL = 1.5–2.2 mm), "Magbay" Expedition, 10–13 m, February 9, 1964, collectors T. Hopkins and T. Scanland, AHF 6411 (LACM 64-179.1); outside Punta Hughes, 3 ♂, 2 ♀ (SL = 1.6–2.5 m), "Magbay" Expedition, 20 m, January 30, 1964, collectors T. Hopkins and T. Scanland, USNM 244078, RMNH D 38109, NHRM 4179; Bahía Magdalena, 1 ♂, 1 ♀ (SL = 2.0, 2.2 mm), "Te Vega" station 18-23, 5–7 m, June 2, 1968, collector E. Ball, AHF 6817 (LACM 68-407.1); Bahía Magdalena, 1 ♂ (SL = 2.0 mm), "Te Vega" station 18-23, 3–8 m, June 2, 1968, collectors J. Yarnall and E. Ball, MNHN.

DIAGNOSIS. Shield slightly longer than broad. Ocular peduncles one-half to two-thirds shield length; acicles multispinose. Articles of antennal flagella each with 2 or 3 short setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with row of 3–5 spines on dorsomesial margin. Left chela with dorsomesial face level; ischium usually with row of spinules on ventral margin. Ventral margins of dactyli of ambulatory legs with 6–8 corneous spines; carpi of P_2 with 1 spine on dorsal surface posteriorly. Posterior lobes of telson with simple lateral margins delimited by spine anteriorly, at least on one side. In life, chelae with short, light tan stripes, carpi and meri with brown stripes on white background.

DESCRIPTION. Shield approximately as long as broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, unarmed or with very small terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles one-half to two-thirds shield length, broad basally, corneae slightly dilated. Ocular acicles subrectangular, multispinose (3–5 marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

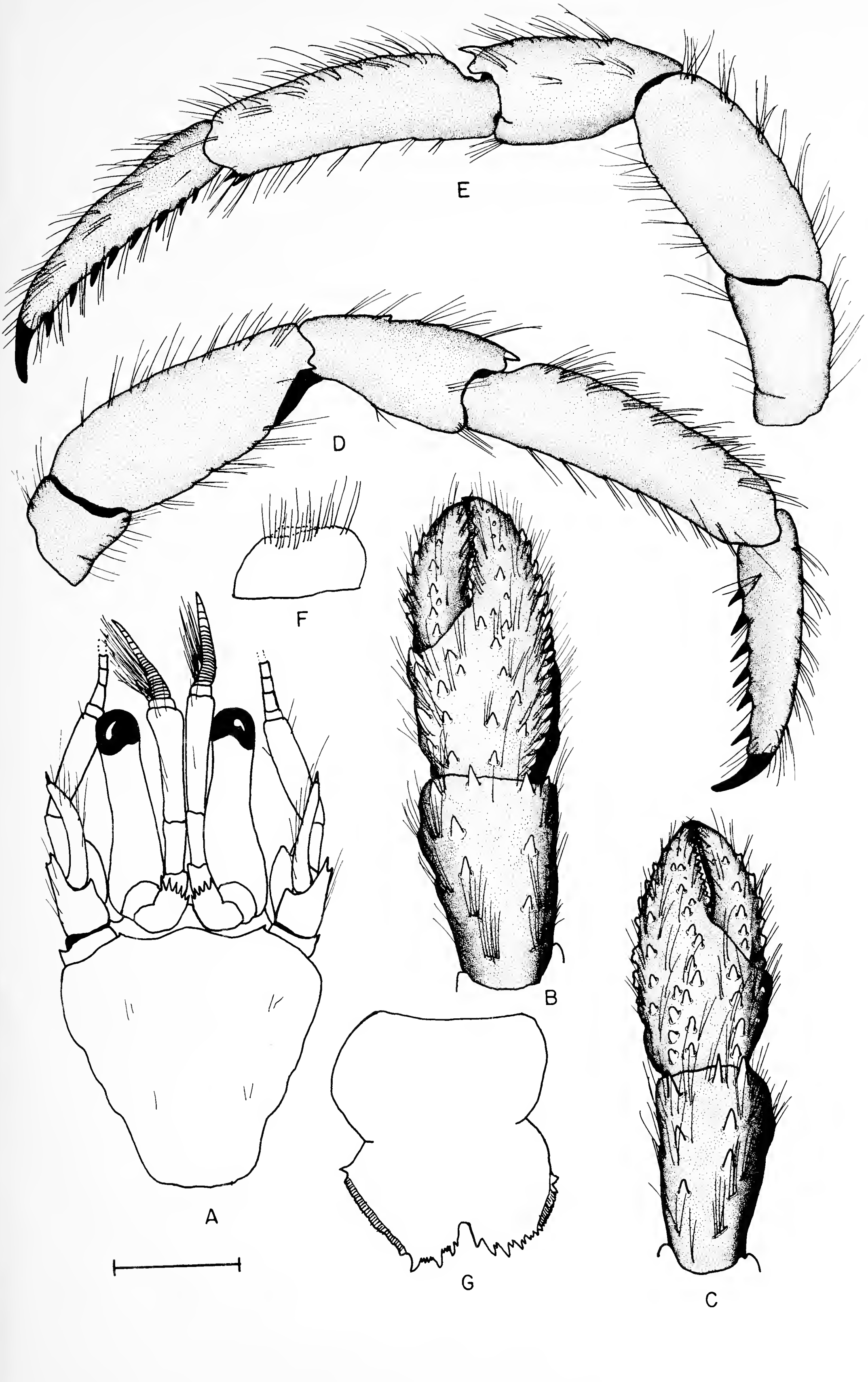
Antennular peduncles overreach ocular peduncles by approximately one-half length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered setae on dorsal and ventral margins. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral margin distally.

Antennal peduncle only slightly overreaching corneae. Fifth and fourth segments with few tufts of setae. Third segment with small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins occasionally with accessory small spine and with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 2 or 3 short setae or bristles every article.

Right cheliped with dactylus approximately as long as palm, only slightly overlapped by fixed finger and with slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth, interspersed with small calcareous teeth, in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half, rest of cutting edge with small calcareous teeth, terminating in calcareous tip. Dorsomesial margin of dactylus with row of small, acute spines, dorsal surface slightly elevated in midline and also armed with row of spines and tufts of long, stiff setae, dorsomesial margin and ventral surface with tufts of long, stiff setae. Palm slightly shorter than carpus; dorsomesial margin with row of spines, dorsal surface with irregular rows of small spines, stronger in females, and with numerous tufts of long, stiff setae, fixed finger with irregular row of spines in midline or adjacent to cutting edge, dorsolateral margin with row of small spines often strongest on fixed finger. Carpus slightly longer than merus; dorsomesial and dorsolateral margins each with row of spines (stronger in females), 1 spine on or near distal margin, dorsal surface unarmed but with numerous tufts of long setae, laterodistal margin often with small spine dorsally, lateral and mesial faces with scattered setae, ventrolateral margin with acute spine distally. Merus subtriangular, dorsal margin with few tufts of setae, ventromesial and ventrolateral margins unarmed or with 1 small spine on ventromesial margin and short row of small spines on ventrolateral margin in distal half. Ischium unarmed.

⟶

Figure 1. *Pagurus rhabdotus* paratype [AHF 6817 (LACM 68-407.1), Bahía Magdalena, west Baja California, Mexico]: **A**, shield and cephalic appendages; **B**, chela and carpus of right cheliped (dorsal view); **C**, chela and carpus of left cheliped (dorsal view); **D**, right 2nd pereopod (lateral view); **E**, left 3rd pereopod (lateral view); **F**, anterior lobe of sternite of 3rd pereopods; **G**, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).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C

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus one-fourth to one-third longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of stiff setae near cutting edge, second row of longer setae in midline accompanied by row of spines, and with row of spines on dorsomesial margin, mesial face and ventral surface also with tufts of long setae. Palm approximately two-thirds length of carpus; elevated in midline, and armed with irregular double row of spines, extending onto the fixed finger as single row, dorsolateral face strongly sloping ventrally, with row of spines and tufts of setae in ventral half and second row of spines and tufts of long setae marginally, dorsomesial face level, dorsomesial margin with row moderate to strong spines and tufts of setae, mesial face with low, sometimes spinulose protuberances and tufts of setae. Carpus usually equaling merus in length, dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, laterodistal margin usually with small spine, dorsal surface and mesial and lateral faces with scattered setae, ventrolateral margin with 1–3 low protuberances or small spines. Merus triangular, dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with row of spines (only on proximal half in large males), ventral surface with long setae. Ischium frequently with row of spinules on ventral margin.

Second and 3rd pereopods similar. Dactyli slightly less to slightly more than one-half length of propodi (often shortest on left 3rd), moderately broad, terminating in strong, curved corneous claw; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–8 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-third to one-half own length, dorsal surfaces with tufts of long, stiff setae, ventral surfaces each with pair of corneous spines at distal margin (2nd) and usually paired 1st, followed by row of 3–5 widely spaced corneous spines in distal half (3rd). Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces usually with 1 small spine proximally (2nd), or low protuberances (3rd), and with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins, ventral margins usually with 1 spine (2nd) and low, sometimes spinulose protuberances (2nd and 3rd) and tufts of long setae, ventrolateral margins each with acute spine distally. Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular, unarmed. Fourth pereopods with long dactyli, small preungual process at base of claw; propodal rasp of 4–6 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long, moderately dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with posterior lobes subquadrate, terminal margins slightly oblique, each armed with row of spines, 1 or 2 usually stronger; lateral margins with narrow plate delimited anteriorly by small spine, at least on one side.

COLOR. Antennal flagellum with 3 or 4 brown articles alternating with transparent article. Shield mottled tan and olive drab with reddish rostral region. Ocular peduncles brown on transparent background in median half and olive drab proximally; corneae brown with flecks of gold. Antennular peduncles with white chromatophores dorsally near distal margin of ultimate segment with olive drab on transparent background over all. Antennal peduncles olive drab. Chelipeds with brown patches laterally or mesially on dactyli and fixed fingers, palms with light tan short stripes; carpi and meri with brown longitudinal stripes on white background, ambulatory legs with white distally on dactyli and short, longitudinal brown stripes on white background proximally; propodi, carpi and meri with brown longitudinal stripes on white background (E. Ball field notes).

DISTRIBUTION. Outer coast of Baja California peninsula, Mexico; 2–20 m.

AFFINITIES. Among the Pacific *provenzanoi*-group species, *P. rhabdotus* is one of four species characterized by a delimiting lateral telsonal spine. Although these species are superficially quite similar, the level dorsomesial surface of the palm of the left chela immediately distinguishes *P. rhabdotus* from *Pagurus redondoensis* Wicksten, a species in which this surface is strongly sloped. *Pagurus vetaultae* Harvey and McLaughlin and *Pagurus nanodes,* n. sp., the other species of the quartet, also can usually be distinguished by the slope of this surface of the left chela; however, representatives of both of these species have been observed to have only a moderate slope that could result in a misidentification if this were the only character considered. *Pagurus rhabdotus* may also be distinguished from *P. redondoensis* and *P. vetaultae* by the presence of 1 or more posterior spines on the dorsal surfaces of the carpi of the first pair of ambulatory legs, and by the usually spinose ischium of the left cheliped; however, these characters will not always distinguish *P. rhabdotus* from *P. nanodes.* The longer antennal flagella with only short setae on the articles, the usually more numerous spines on the ventral margins of the dactyli of the ambulatory legs, and larger size at maturity aid in distinguishing *P. rhabdotus* from *P. nanodes* (also see affinities under the latter species). *Pagurus rhabdotus* is also closely allied to *P. lepidus* (Bouvier). Both are distinguished from other related species by the level dorsomesial face of the left chela. However, as previously indicated, the lateral telson plates are delimited anteriorly by a spine, at least on one side, in *P. rhabdotus.* No such spine is present in *P. lepidus.*

In life, the distinctive tan to brown stripes on the dorsal surfaces of the segments of the chelipeds serve to distinguish *P. rhabdotus* from *P. lepidus* with its generally greenish brown overall color set off by white spines often tinged with red-brown. However, a similar pattern of striping on the chelipeds is also seen in *P. vetaultae,* although the stripes in the latter species are darker, broader, and more diffuse. Differences in the color patterns of the ocular peduncles may aid in rapid field separation. In *P. rhabdotus* the ocular peduncles are brown medially on a transparent background and olive drab proximally, whereas those of *P. vetaultae* are opaque with flecks of red and a white ring at the base of the cornea. The proximal band of color on the dactyli of the ambulatory legs in *P. redondoensis* and *P. nanodes* will also distinguish these species from *P. rhabdotus,* in which longitudinal brown stripes overlie the basic white of these appendages.

ETYMOLOGY. From the Greek *rhabdotus* meaning striped.

REMARKS. *Pagurus rhabdotus* is superficially very similar to *P. lepidus* and has been mistakenly identified as the latter in earlier reports (Haig et al., 1970; Ball and Haig, 1974). Although several taxa had been recognized among the collections of the Allan Hancock Foundation, it was not until we were able to precisely define *P. lepidus* (Haig and McLaughlin, 1991) that correct species assignments could be made.

Pagurus virgulatus new species

Figure 2A–G

Pagurus sp. (*miamensis* group): Ball and Haig, 1974:102 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.5 mm), AHF 3516 (LACM 35-188.1). **Type locality.** Puerto Parker, Costa Rica, "Velero III" station 468-35, 9 m, February 9, 1935.

PARATYPES. Mexico: El Morro, Bahía de Acapulco, 2 ♂ (SL = 1.2, 1.7 mm), "Te Vega" station 18-21, 6–9 m, May 23, 1968, collector E. Ball, AHF 6821 (LACM 68-409.1). Costa Rica: Bahía Brasilito, 1 ovigerous ♀ (SL = 1.2 mm), "Te Vega" station 18-18, 4.5 m, May 13, 1968, collector E. Ball, AHF 6820 (LACM 68-410.1); Puerto Parker, 3 ♂, 1 ovigerous ♀ (SL = 1.2–2.1 mm), "Velero III" station 467-35, 3.6 m, February 9, 1935, USNM 244079, RMNH D 38110, NHRM 4180. Cocos Island: SW of Isla Pajara, Bahía Weston, 1 ♂ (SL = 1.7 mm), 9–15 m, April 27, 1988, LACM 88-23.1; Bajo Alcyone, 1 ♂ (SL = 1.3 mm), 35 m, March 27, 1989, collector K. Kaiser, LACM 89-179.1. Colombia: Off Isla Gorgona, 1 ♂ (SL = 1.5 mm), "Velero III" station 224-34, 18 m, February 12, 1934, MNHN. Ecuador: Atacames Reef, 2 ♂ (SL = 0.9, 1.2 mm), "Te Vega" station 18-8, 8 m, April 23, 1968, collectors M. Youngbluth and P. Smith, AHF 682 (LACM 68-411.1).

DIAGNOSIS. Shield longer than broad. Ocular peduncles three-fourths to five-sixths shield length; acicles multispinose. Articles of antennal flagella each with 1–3 short setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with 4 or 5 spines on dorsomesial margin. Left cheliped with dorsomesial face of palm strongly sloping; ischium with few spinules on ventral margin. Dactyli of ambulatory legs each with 6–9 corneous spines on ventral margins. Posterior lobes of telson with simple lateral margins, no delimiting spine anteriorly. In life, chelipeds with splotches or stripes of brown; ambulatory legs with longitudinal brown stripe on mesial and lateral faces of carpi and meri, short brown stripe dorsally on propodi and short dorsolateral and dorsoventral stripes on dactyli.

DESCRIPTION. Shield longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum rounded or obsolete, unarmed. Lateral projections subtriangular to broadly rounded, unarmed or with very small terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles three-fourths to five-sixths shield length, slightly broadened basally and moderately slender distally, cornea slightly dilated. Ocular acicles subrectangular, multispinose (3–5 widely spaced marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreach ocular peduncles by approximately one-eighth to one-fourth length of ultimate segment. Ultimate and penultimate segments with few scattered setae. Basal segment with 1 acute spine on dorsolateral margin distally.

Antennal peduncle only slightly overreaching corneae. Fifth and fourth segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally (small individuals), ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 1–3 short setae or bristles every article.

Right cheliped with dactylus approximately as long as palm, slightly overlapped by fixed finger. Hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth distally, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half, rest of cutting edge with small calcareous teeth, also terminating in corneous claw. Dorsomesial margin of dactylus with row of small acute or blunt spines, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long, stiff setae, dorsomesial margin and ventral surface with tufts of long, stiff setae. Palm slightly shorter than carpus; dorsomesial margin with row of spines,

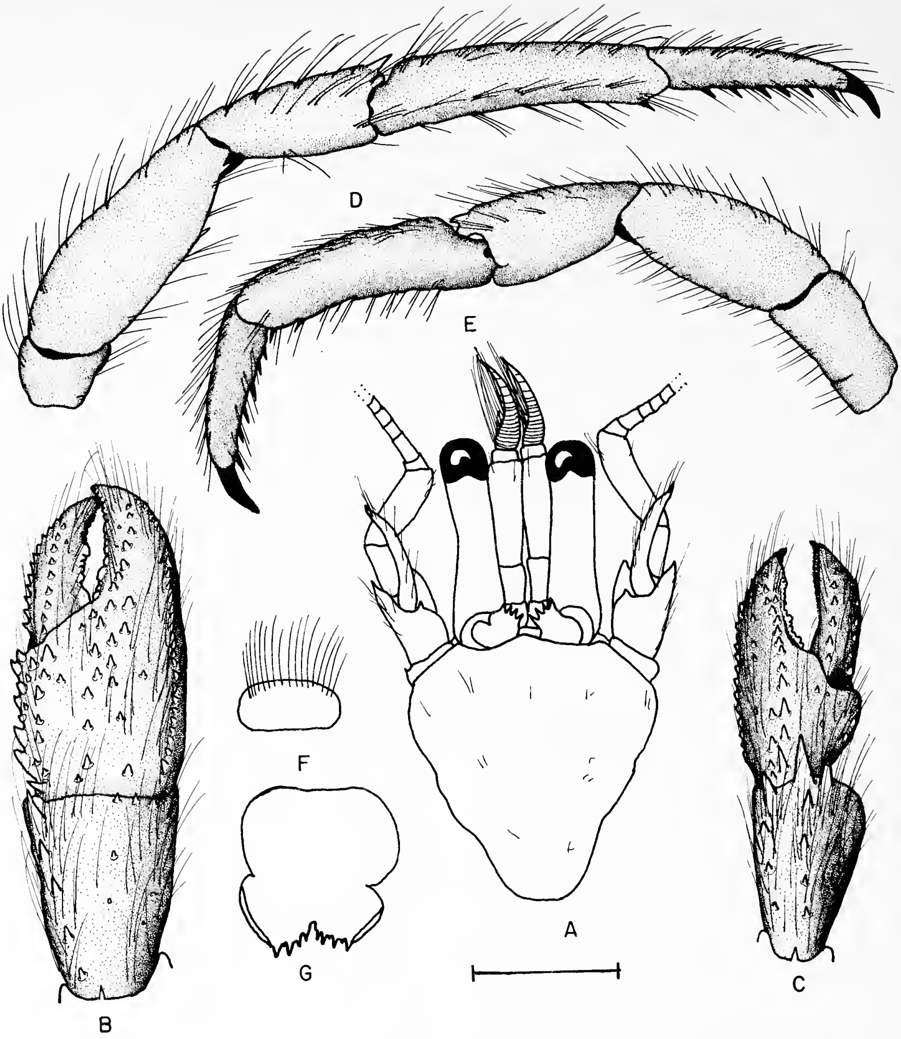


Figure 2. *Pagurus virgulatus* paratype [LACM 88-23.1, Bahía Weston, Cocos Island]: **A**, shield and cephalic appendages; **B**, chela and carpus of right cheliped (dorsal view); **C**, chela and carpus of left cheliped (dorsal view); **D**, right 2nd pereopod (lateral view); **E**, left 3rd pereopod (lateral view); **F**, anterior lobe of sternite of 3rd pereopods; **G**, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).

dorsal surface with several irregular rows of small spines and tufts of long setae, also with row of spines and few additional scattered spinules on fixed finger, dorsolateral margin with row of small spines extending length of fixed finger. Carpus slightly longer than merus; dorsomesial margin with row of 4 or 5 rather widely spaced spines strongest distally, 1–3 spines on or near distal margin and frequently additional row of spines laterad of midline, dorsal surface also with numerous tufts of long setae, dorsolateral margin not delimited, lateral and mesial faces with low protuberances and tufts of setae. Merus subtriangular, dorsal margin with few setae, ventromesial and ventrolateral margins unarmed or with 1–3 spines distally, distal margin sometimes with acute spine. Ischium unarmed or with small spine at ventrolateral distal angle.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus slightly longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of spines and stiff setae, mesial margin with row of low, spinulose protuberances and long setae, ventral surface also with tufts of long setae. Palm slightly more than half length of carpus; elevated in midline, often into prominent crest, and armed with irregular double row of spines, extending onto fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with longitudinal row of widely spaced small spines or only row of setae in ventral half, margin with row of spines and tufts of long setae, dorsomesial face also usually strongly sloping, armed with few scattered spines and tufts of long setae, dorsomesial margin not delimited. Carpus approximately equaling merus in length; dorsomesial and dorsolateral margins each with row of strong, acute spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, ventrolateral margin with 1 strong spine distally. Merus triangular, dorsal margin with row of long setae and often acute spine on distal margin, ventrolateral and ventromesial margins each with row of acute spines and long setae. Ischium with few minute spinules on ventral margin.

Second and 3rd pereopods similar. Dactyli one-half to two-thirds length of propodi, 3rd dactyl usually moderately broad, terminating in strong, curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–9 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-third to one-half own length, dorsal surfaces with tufts of long, stiff setae, ventral surfaces each with 1 or 2 corneous spines at distal margin (2nd) and 1 additional spine in distal third of segment (3rd). Carpi two-thirds to three-fourths length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with long setae on dorsal margins, ventromesial or ventrolateral (2nd) margin usually with 1 to several spines distally and tufts of long setae. Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subquadrate, unarmed. Fourth pereopods with moderately long dactyli, small preungual process at base of claw; propodal rasp of 4 or 5 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with tufts of long setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with subtriangular posterior lobes; terminal margins usually oblique, each armed with row of spines, 1 or 2 sometimes stronger; lateral margins with simple narrow plate, no anterior spine.

COLOR. Antennal flagellum banded with brown spots (2 or 3 articles) interspersed with white (1 or 2 articles). Shield off-white with few brown patches. Ocular peduncles off-white or white with hints of brown; corneae black or black with flecks of gold. Antennules white with hint of blue or uniformly off-white. Antennal peduncles off-white; antennal acicle with patches of brown. Chelipeds off-white with splotches (smaller individuals) or with brown stripes on white background. Ambulatory legs with short brown stripes on white background dorsally on propodi, carpi, and meri and long, longitudinal stripe on lateral and mesial faces; dactyli with short dorsolateral and ventrolateral stripes proximally (E. Ball field notes).

DISTRIBUTION. Acapulco, Mexico to Ecuador; Cocos Island; 5–40 m.

AFFINITIES. *Pagurus virgulatus* is most closely allied to *Pagurus arenisaxatilis* Harvey and McLaughlin, a species apparently endemic to the Gulf of California, Mexico. The two species are distinguished by the armature of the carpus of the right cheliped and ventral margins of the dactyli of the ambulatory legs, and by the setation of the antennal flagella. *Pagurus virgulatus* has only 4 or 5 rather widely spaced spines on the dorsomesial margin of the carpus of the right cheliped, whereas an irregular, often distally double row of 7–10 spines is present on this margin in *P. arenisaxatilis.* The ventral margins of the dactyli of the ambulatory legs are armed with 5–8 corneous spines, and the articles of the antennal flagella are provided with only 1–3 short setae or bristles in *P. virgulatus.* In *P. arenisaxatilis* the dactyli of the ambulatory legs are armed with 7–13 corneous spines and the articles of the antennal flagella have both long and short setae, at least in the proximal half. In living specimens, the color patterns of the two species provide reliable distinctions. Although these two species, like most others of the Pacific *provenzanoi* group, have striped ambulatory legs, the chelipeds of *P. virgulatus* are splotched with brown in small individuals or have brown stripes on a white background. The chelipeds of *P. arenisaxatilis* are generally solidly colored olive or tan, with the distal halves of the dactyli and fixed fingers white.

ETYMOLOGY. From the Latin *virgulatus,* meaning striped and referring to the color patterns of the chelipeds and ambulatory legs.

REMARKS. Ball and Haig (1974) referred to three undescribed species as *Pagurus* spp. (*miamensis* group) [*miamensis* being an earlier name for the *provenzanoi* group of *Pagurus* species; see McLaughlin, 1975]. Of these specimens, three lots from Mexico, Costa Rica, and Ecuador represent *P. virgulatus.*

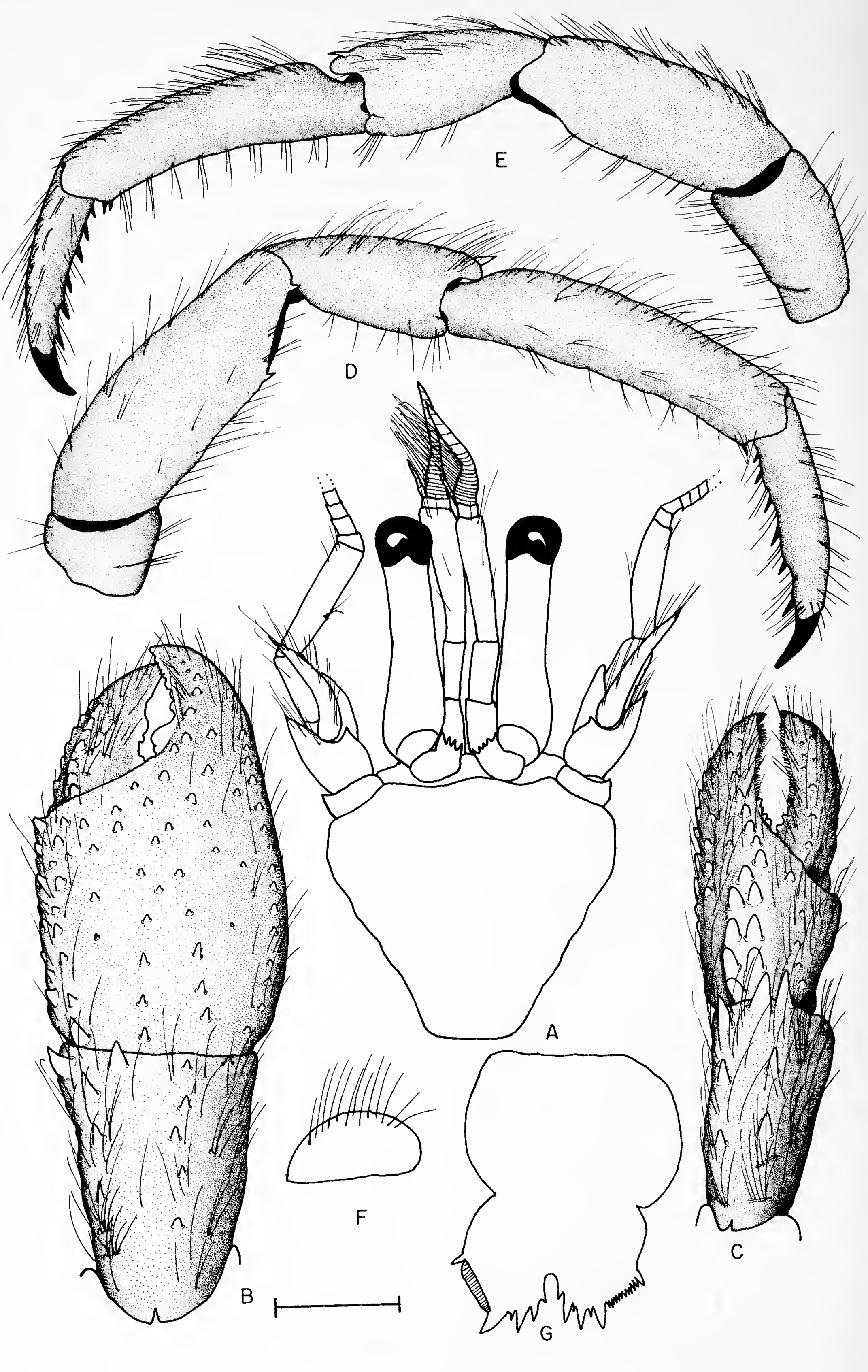
Pagurus nanodes new species

Figure 3A–G

Pagurus spp. (*miamensis* group): Ball and Haig, 1974:102 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.0 mm), AHF 681 (LACM 68-412.1). **Type locality.** Punta Paitilla, Panama, "Te Vega" station 18-14b, 1.8 m, May 6, 1968, collector E. Ball.

PARATYPES. Costa Rica: Bahía Brasilito, 3 ♂ (SL = 1.3–1.4 mm), "Te Vega" station 18-18, 4.5 m, May 13, 1968, collector E. Ball, AHF 6826 (LACM 68-413.1); near Puntarenas, 2 ♂ (SL = 0.9, 1.1 mm), "Te Vega" station 18-17c, intertidal, May 11, 1968, collectors L. Eickstaedt and E. Ball, AHF 6825 (LACM 68-414.1). Panama: Punta Paitilla, 4 ♂, 2 ovigerous ♀ (SL = 1.6–2.0 mm), "Te Vega" station 18-14b, 1.8 m, May 6, 1968, collector E. Ball, AHF 6822 (LACM 68-415.1); Isla Naos, 1 ovigerous ♀ (SL = 0.9 mm), "Te Vega" station 18-14a, 1.5–3 m, May 5, 1968, collector E. Ball, AHF 6824 (LACM 68-416.1); Isla Taboguilla, 1 ovigerous ♀ (SL = 1.8 mm), "Albatross," 1.8 m, October 31, 1904, USNM; W side Isla Taboguilla, 9 ♂, 4 ♀, 21 ovigerous ♀, 2 juveniles (SL = 1.0–1.8 mm), LGA station 57, 2 m, April 7, 1969, collectors L.G. Abele


E
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and A. Rodaniche, USNM 244089; same locality, 1 ovigerous ♀, 1 juvenile (SL = 0.8, 1.2 mm), LGA station 93, 2 m, April 7, 1969, collectors L.G. Abele and A. Rodaniche, USNM 244092; same locality, 4 ♂, 2 ovigerous ♀, 2 juveniles (SL = 0.9–1.8 mm), LGA station 59, 2 m, April 11, 1969, collectors L.G. Abele, A. Rodaniche, and J. Graham, USNM 244090; Taboga, 37 ♂, 6 ♀, 16 ovigerous ♀ (SL = 0.8–2.4 mm), intertidal, December 24, 1990, collector J. Crain, USNM; Isla Culebra, 1 ♂, 1 ovigerous ♀ (SL = 1.7, 2.2 mm), intertidal, December 20–21, 1990, collector J. Crain, USNM; Panama Bay, 12 ♂, 7 ♀, 5 ovigerous ♀ (SL = 0.7–1.2 mm), December 11, 1981, collector T. Spight, AHF 8112 (LACM 81-130.1), MNHN; Panama Bay, 5 ♂, 1 ♀ (SL = 1.2–1.7 mm), ? 1981, collector T. Spight, RMNH D 38108, NHRM 4178; Pacific Panama, 3 ♂ (SL = 1.7–2.2 mm), 1976, collector P. Abrams, AHF 7616 (LACM 76-627.1). Ecuador: Isla de Santa Clara, Gulf of Guayaquil, 2 ovigerous ♀ (SL = 1.4, 2.0 mm), "Te Vega" station 18-1, 7.5 m, April 6, 1968, collectors Ball, Yarnall, Youngbluth and Smith, AHF 6823 (LACM 68-417.1).

DIAGNOSIS. Shield longer than broad. Ocular peduncles one-half to three-fourths shield length; acicles multispinose. Articles of antennal flagella each with 2–4 short and usually 1 or 2 longer setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with row of widely spaced spines on dorsomesial margin. Left cheliped with dorsomesial face of palm moderately to strongly sloped; ischium unarmed. Dactyli of ambulatory legs each with 5–7 corneous spines on ventral margins. Posterior lobes of telson with simple to denticulate lateral plates delimited anteriorly by strong spine. In life, chelipeds with distally white or light orange dactyli and fixed fingers; ambulatory legs with proximal band of brown (dactyli), distal band of blue (propodi and meri), carpi brown or orange.

DESCRIPTION. Shield usually longer than broad, appreciably so in small individuals, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin roundly truncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, unarmed, or with very small terminal spinule. Dorsal surface of shield often with scattered tufts of setae.

Ocular peduncles one-half to three-fourths shield length, broad basally and tapering to base of slightly dilated corneae. Ocular acicles subrectangular, multispinose (3–6 marginal or submarginal spines); separated basally by one-half to entire basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreach ocular peduncles by one-fourth to one-half length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered setae on dorsal and ventral margins. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral margin.

Antennal peduncle overreaching corneae by one-fourth to one-half length of ultimate segment. Fifth and fourth segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral margin often with accessory spine, mesial margin with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment occasionally with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 2–4 short setae or bristles and often 1 or 2 longer setae every article.

Right cheliped exhibiting marked sexual dimorphism in large males. Dactylus shorter than to approximately as long as palm, overlapped by fixed finger. Slight to prominent hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth, interspersed with small calcareous teeth, in distal half or only calcareous teeth (large males), terminating in small corneous or calcareous claw. Cutting edge of fixed finger often with few calcareous teeth proximally and row of corneous teeth distally, terminating in corneous or calcareous tip. Dorsomesial margin of dactylus with row of small acute or blunt spines, dorsal surface slightly elevated in midline, sometimes forming prominent crest, and also armed with row of small spines and tufts of long, stiff setae, dorsomesial and ventromesial margins and ventral surface with tufts of long, stiff setae in large (>2.0 mm) males, but often with row of spinulose protuberances on ventromesial margin in small individuals. Palm equaling or somewhat shorter than carpus; dorsomesial margin with single or double row of spines, strongest in small specimens, dorsal surface with numerous tufts of long setae and small spines in irregular rows or scattered distally, row of small spines on fixed finger adjacent to cutting edge, dorsolateral margin with low protuberances proximally becoming row of small spines on fixed finger (large males) or row of strong spines (small males and females). Carpus slightly longer than merus, dorsomesial margin with row of rather widely spaced spines, and 1 or 2 stronger spines on or near distal margin, dorsal surface with row of spines

←

Figure 3. *Pagurus nanodes* paratype [AHF 7616 (LACM 76-627.1), Pacific Panama]: **A**, shield and cephalic appendages; **B**, chela and carpus of right cheliped (dorsal view); **C**, chela and carpus of left cheliped (dorsal view); **D**, right 2nd pereopod (lateral view); **E**, left 3rd pereopod (lateral view); **F**, anterior lobe of sternite of 3rd pereopods; **G**, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).

laterad of midline, decreasing in strength with increased size of individuals, and with numerous long setae, dorsolateral margin not clearly delimited, lateral and mesial faces with scattered setae, ventrolateral margin with acute spine distally. Merus subtriangular, dorsal margin with few tufts of setae, distal margin often with 1 spine, ventromesial margin unarmed or with 1 or 2 blunt spines, ventrolateral margin with 1–4 acute spines. Ischium unarmed.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus slightly longer than palm. Cutting edge often with few calcareous teeth proximally and row of corneous teeth distally, terminating in corneous claw, dorsal surface with row of stiff setae near cutting edge, second row of longer setae and row of small spines in midline, dorsomesial margin with row of low protuberances or small spines and tufts of long setae, ventral surface also with tufts of long setae. Palm approximately two-thirds length of carpus; slightly elevated in midline and armed with irregular double row of spines, extending onto fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with row of small spines in ventral half and second row of protuberances or spines and tufts of long setae marginally, dorsomesial face with moderate to strong slope, dorsomesial margin delimited by row of low, spinulose protuberances or moderate to strong spines (small individuals) and tufts of setae, mesial face with low protuberances and tufts of setae. Carpus usually equaling or slightly longer than merus; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, laterodistal margin usually with acute spine dorsally and 1 acute spine on ventrolateral margin distally. Merus triangular, dorsal margin with tufts of setae, distal margin often with 1 spine, ventrolateral margin with row of acute spines in distal half, ventromesial margin also with row of acute spines, ventral surface with long setae. Ischium unarmed.

Second and 3rd pereopods similar. Dactyli slightly less to slightly more than one-half length of propodi, moderately broad, terminating in strong, curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 5–7 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length, dorsal surfaces with tufts of long setae, ventral surfaces each with 1 or 2 corneous spines at distal margin (2nd) or paired 1st and usually 1 additional spine in distal third of segment (3rd). Carpi equaling or slightly shorter than meri; dorsodistal margins each with 1 spine, dorsal surfaces with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal and ventral margins, ventrolateral distal angle with acute spine and ventrolateral margin with acute spine distally (2nd) or unarmed (3rd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to semisubcircular, unarmed. Fourth pereopods with long dactyli, small preungual process at base of claw; propodal rasp of 4–6 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long, dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with posterior lobes subtriangular; terminal margins oblique, each armed with row of spines, 2–4 stronger; lateral margins with narrow, simple, or denticulate plate delimited by strong spine.

COLOR. Antennal flagellum with brown (or red) and white articles alternating (4 brown, 1 white). Shield white with hints of orange. Ocular peduncles with numerous small red chromatophores on off-white background; corneae black with patches of gold. Antennules off-white with brown stripe distally on ultimate and penultimate segments. Right cheliped with distal halves of dactylus and fixed finger white, palm mottled brown and white; carpus brown laterally and white, shading to orange mesially; merus brown with bright blue band at distal margin. Left cheliped with dactylus and fixed finger pale orange to white, palm mottled brown and white; carpus brown on mesial and lateral faces, orange grading to white dorsally; merus dark brown with bright blue band at distal margin. Ambulatory legs with dactyli pale orange in distal half and dark brown band proximally; propodi with bright blue band at distal margin, pale orange grading to white in following distal half, brown in proximal half; carpi brown; meri with bright blue band at distal margin, with orange in remaining distal half, proximal half white with hints of pale brown (E. Ball field notes).

DISTRIBUTION. Costa Rica to Ecuador; intertidal to 3.5 m.

AFFINITIES. *Pagurus nanodes* appears to be most closely related in morphology to *P. redondoensis* Wicksten and *P. vetaultae* Harvey and McLaughlin. In life it is readily distinguished from all other eastern Pacific *provenzanoi*-group representatives by its distinctive color patterns, most notably bands rather than longitudinal stripes of color on the propodi of the ambulatory legs and solidly colored (orange) carpi. In preserved material where color patterns have faded, it is best distinguished from both *P. redondoensis* and *P. vetaultae* by the fewer spines (5–7) on the ventral margins of the dactyli of the ambulatory legs. Specimens of *P. nanodes* in which the dorsomesial margin of the left chela exhibits only a moderate slope might be confused with specimens of *P. rhabdotus.* The short antennal flagella, with more setose articles, immediately distinguish *P. nanodes,* as does its extremely small size. Females of this species are ovigerous at shield lengths between 0.9 and 1.4 mm.

ETYMOLOGY. The specific name is from the Greek *nanodes,* meaning small or dwarfish.

REMARKS. Numerous specimens from Ecuador, Panama, and Costa Rica cited by Ball and Haig (1974) as *Pagurus* spp. (*miamensis* group), and some of the specimens from Panamanian *Pocillopora* habitats cited by Abele (1972) as an undescribed species of *Pagurus* have proved to be *P. nanodes.*

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A NEW GENUS AND SPECIES OF MIDDLE MIOCENE ENALIARCTINE PINNIPED (MAMMALIA, CARNIVORA, OTARIIDAE) FROM THE ASTORIA FORMATION IN COASTAL OREGON

LAWRENCE G. BARNES

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A NEW GENUS AND SPECIES OF MIDDLE MIOCENE ENALIARCTINE PINNIPED (MAMMALIA, CARNIVORA, OTARIIDAE) FROM THE ASTORIA FORMATION IN COASTAL OREGON

LAWRENCE G. BARNES[1]

ABSTRACT. A complete fossil pinniped cranium from the early Middle Miocene (*circa* 16 million years old) part of the Astoria Formation of Oregon, U.S.A., represents a new genus and species of primitive sea lion-like otariid, *Pacificotaria hadromma.* It belongs in the extinct Enaliarctinae, the most primitive subfamily of otariids, which now includes six eastern North Pacific species in four genera, dating back to latest Oligocene or earliest Miocene time (*circa* 24 to 25 Ma). Slightly smaller than some Recent fur seals, *Pacificotaria hadromma* differs from enaliarctines of the genera *Enaliarctos* Mitchell and Tedford, 1973, *Pteronarctos* Barnes, 1989, and *Pinnarctidion* Barnes, 1979, in its more protuberant and more anteriorly directed eyes that are positioned farther anteriorly on the cranium, larger anterior narial opening, exceptionally robust rostrum, vaulted palate, and straighter upper cheek tooth rows. *Pacificotaria* is closely related to but more primitive than *Pteronarctos,* and the two may have shared a relatively close common ancestry with *Enaliarctos. Pacificotaria* was not directly ancestral to fur seals and sea lions, although it has some characters that are apparently convergent with these later otariines. The holotype and only known specimen of *P. hadromma* was recovered from the same part of the Astoria Formation that has yielded another enaliarctine, *Pteronarctos piersoni* Barnes, 1990, and the large desmatophocine otariid, *Desmatophoca oregonensis* Condon, 1906. The presence of three otariid species in the same horizon of the Astoria Formation suggests significant niche partitioning and/or seasonal migration by these early Middle Miocene pinnipeds along the Oregon coast.

INTRODUCTION

Fossil pinnipeds of the family Otariidae have been found in deposits around the margins of the North Pacific Ocean, the most ancient ones having been found along the west coast of North America, principally in California and Oregon. Living otariids are relatively abundant and taxonomically diverse in the North Pacific. Most otariids of the world live in high latitudes or in the Arctic (walrus); however two species live on the equatorial Galapagos Islands, and the California sea lion (*Zalophus californianus* (Lesson, 1828)) and the South American sea lion (*Otaria byronia* (Blainville, 1820)) both range into warm latitudes. For a review of my classification of fossil and living otariid pinnipeds, the reader is referred to Barnes (1989).

Outcrops of Tertiary age marine sediments in Oregon and Washington have produced several important otariid fossils, the majority of which have been found along the Oregon coast in Lincoln County, Oregon (Ray, 1976). The history of such fossil pinniped discoveries in Oregon Middle Miocene deposits begins with the landmark publication of *Desmatophoca oregonensis* by Condon in 1906. After a considerable lapse of time, this was followed by the recent discoveries of diverse primitive otariids (Barnes, 1987, 1989, 1990) from late Early Miocene to early Middle Miocene age rocks referred to the Astoria Formation that are exposed in Lincoln County.

Three otariid species have now been reported from rocks of this formation that crop out in the coastal sea cliffs in Lincoln County. The holotype of *Desmatophoca oregonensis* Condon, 1906, was discovered from the early Middle Miocene part of the Astoria Formation. This pinniped was, for its time, a relatively large, highly evolved animal and is the type species of the genus *Desmatophoca* Condon, 1906, which is the type genus of the monotypic otariid subfamily Desmatophocinae. From approximately correlative parts of the same formation, in rocks about 16 million years (Ma) old, relatively high in the stratigraphic section, have been discovered a referred specimen of *Desmatophoca oregonensis* (see Barnes, 1987) and a primitive enaliarctine, *Pteronarctos piersoni* Barnes, 1990. From just above the base of the Astoria Formation near Newport, in older strata that are about 19 Ma old, has been described the late Early Miocene enaliarctine, *Pteronarctos goedertae* Barnes, 1989. Such discov-

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eries indicated taxonomic diversity and geologic and geographic range extensions of enaliarctines in the coastal Pacific Northwest and have fulfilled predictions made by Ray (1976) that the Oregon coast would provide significant new specimens. Prior to the discovery of *Pteronarctos goedertae,* the few known enaliarctines were from California, principally from the earliest Miocene age Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill in Kern County (Mitchell and Tedford, 1973; Barnes, 1979). The sequence of rocks at the latter locality produced the type materials of *Enaliarctos mealsi* Mitchell and Tedford, 1973, *E. mitchelli* Barnes, 1979, and *Pinnarctidion bishopi* Barnes, 1979.

The present article describes a new genus and species of Enaliarctinae based on a fossil cranium from coastal exposures of the Astoria Formation in Lincoln County. This new fossil is from the same relatively high stratigraphic level of the Astoria Formation (early Middle Miocene age, *circa* 16 Ma) that yielded *Pteronarctos piersoni* and *Desmatophoca oregonensis.* Because the new species is based on a virtually complete cranium, the characters used to diagnose it and all previously described enaliarctines, also described from crania, are directly comparable.

METHODS AND MATERIALS

The specimen described herein was discovered in an indurated calcareous sandstone concretion. Most of the matrix was removed from the specimen using rock-cutting saws and pneumatic chisels. Fine surface preparation was accomplished by removing the last remaining matrix from the bone using formic acid. When laboratory preparation revealed all of the critical structures in the left orbit, the matrix filling the right orbit was left in place.

Anatomical terminology used here is adapted from that of Howell (1929), Miller et al. (1964), Mitchell (1966, 1968), Hershkovitz (1971), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). The suture ages of the cranium, calculated following the methods of Sivertsen (1954), are relative ages and not necessarily the same as ages in years. To determine a suture age, the extent of ontogenetic closure of each of nine cranial sutures is subjectively graded on a scale of 1 to 4 (from open to completely closed), then the scores of these nine sutures are added together to yield a relative individual age. This method is useful for comparing the relative individual ages of specimens for which teeth have not been sectioned to reveal growth layers. Its use in fossil taxa assumes that the rate and pattern of suture closure has remained relatively uniform throughout the history of the Otariidae.

I have identified which cranial measurements in Table 1 are the same as those that were defined by Sivertsen (1954:18–20) by appending to them the numbers that were given them by Sivertsen. Other measurements in Table 1 are as defined by Barnes (1972:fig. 1; 1979:4–5). The facial angles were measured as explained by Repenning et al. (1971:2, fig. 1). The measurements of the crowns of the cheek teeth that are given in the description were made on the left side, although the right teeth provided virtually the same measurements. The transverse and anteroposterior measurements of the cheek tooth crowns are maximum dimensions across the crown at the cingulum. The crown heights were measured from the apex of the crown as preserved to a line that would intersect the margin of the enamel at the anterior and posterior ends of the labial cingulae.

Geologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979), following the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). Millions of years is abbreviated Ma. The acronyms for institutions housing specimens are as follows:

LACM—Natural History Museum of Los Angeles County, Los Angeles, California.
UCMP—University of California Museum of Paleontology, Berkeley, California.

In addition to the holotype of the new species and museum specimens of the Recent California sea lion (*Zalophus californianus* (Lesson, 1828)) and the northern sea lion (*Eumetopias jubatus* (Schreber, 1776)), type and other published specimens of the following enaliarctines were studied:

Enaliarctos mealsi Mitchell and Tedford, 1973—holotype cranium, LACM 4321; partial cranium, LACM (CIT) 5303; P^4, LACM 4364; M^1, UCMP 86211.
Enaliarctos mitchelli Barnes, 1979—holotype rostrum, UCMP 100391; paratype palate, UCMP 80943.
Enaliarctos sp.—canine crowns, LACM 30540, 72381.
Pteronarctos piersoni Barnes, 1990—holotype cranium, LACM 127972; paratype cranium, LACM 128002.
Pteronarctos goedertae Barnes, 1989—holotype cranium, LACM 123883.
Pinnarctidion bishopi Barnes, 1979—holotype cranium, UCMP 86334; natural endocranial cast, LACM (CIT) 5302.

The holotype cranium of *Pacificotaria hadromma,* new genus and species (LACM 127973), was coated prior to photography with a sublimate of ammonium chloride. My cranial restorations of the species are based entirely on the holotype. The right side of the specimen has been displaced posteriorly by postmortem diagenetic compression, as evidenced by the posteriorly twisted right glenoid fossa and concomitant posterior displacement of the right dental row, zygomatic arch, and right half of the basicranium. Therefore, the restorations (Figs. 2, 4, 6) are based principally on the anatomy of the less distorted left side. There has also been some dorsoventral compression of the cranium, so in the restored lateral view (Fig. 4), the cranium is shown 2 mm higher than the actual specimen at the posterior end of the cranium and 4 mm higher in the rostrum. I omitted the dentition on the right side in Figure 9a so that the shapes of the alveoli can be compared with those of other species. Anatomical abbreviations used in the illustrations are as follows:

ac—alisphenoid canal (posterior aperture)
at—auditory tube (= musculotubular canal, including Eustachian tube)
Bo—basioccipital
Bs—basisphenoid
cc—carotid canal
eam—external acoustic meatus
fh—hypoglossal foramen
fi—incisive foramen (= palatine fissure)
fio—infraorbital foramen
fl—lacrimal foramen

fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
flp—posterior lacerate foramen
fo—foramen ovale
fpal—palatine foramen
fpg—postglenoid foramen
Fr—frontal
fs—sphenopalatine foramen
fsm—stylomastoid foramen
g—glenoid fossa
hf—tympanohyal pit (= hyoid fossa)
Ju—jugal
mp—mastoid process
Mx—maxilla
Na—nasal
nf—nasolabialis fossa
Oc—occipital
occ—occipital condyle
Pa—parietal
Pal—palatine
Pmx—premaxilla
pp—paroccipital (= jugular) process
Ps—presphenoid
Pt—pterygoid
sop—supraorbital process
sp—fossa corresponding to pseudosylvian sulcus of brain
Sq—squamosal
tb—tympanic bulla

SYSTEMATICS

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Infraorder Arctoidea Flower, 1869
Parvorder Ursida Tedford, 1976
Family Otariidae Gill, 1866
Subfamily Enaliarctinae Mitchell and Tedford, 1973

TYPE GENUS. *Enaliarctos* Mitchell and Tedford, 1973.

INCLUDED GENERA. *Enaliarctos* Mitchell and Tedford, 1973; *Pteronarctos* Barnes, 1989; *Pacificotaria,* new genus; and *Pinnarctidion* Barnes, 1979.

DISCUSSION. The subfamily Enaliarctinae is paraphyletic (see also Repenning and Tedford, 1977: 76–77, fig. 6; Barnes, 1989:19, 1990:19; Berta, 1989), representing a basal group of primitive Otariidae from which several more derived lineages appear to have arisen. The subfamily diagnosis given in Barnes (1979) still pertains to all included genera.

Pacificotaria, new genus

DIAGNOSIS OF GENUS. A genus in the subfamily Enaliarctinae:

(1) differing from *Enaliarctos* by having skull with more nearly parallel cheek tooth rows; roots of P^2–M^1 more closely appressed; P^{2-3} with protocone and bilobed posterior roots; smaller and less sectorial P^4; protocone root of P^4 fused to posterolateral root; shallower embrasure pit for M_1 on palate between P^4 and M^1; larger and bilobed-rooted M^2; larger supraorbital process of frontal; more prominent anterolateral corner of braincase; shallower fossa on lateral side of braincase corresponding to pseudosylvian sulcus of brain; narrower squamosal fossa between braincase and zygomatic arch; incisive foramina (palatine fissures) entering external nares less vertically; smaller orbit; and different facial angle (138° in *P. hadromma versus* estimated 129° in *Enaliarctos mealsi*);

(2) differing from *Pteronarctos* by having cranium with wider rostrum that is expanded distally by protrusion of lateral corners around canine roots; anterior narial opening larger with wider and flatter ventral floor; prominent fossa on anterior surface of rostrum along maxillary-premaxillary suture dorsal to diastem between I^3 and canine; small eminence on narial border of premaxilla near junction with nasal bones; larger diameter I^3; P^2 with bilobed posterior root; protocone root of M^1 more posteriorly positioned relative to metacone root; nasolabialis fossa deeper and inclined more vertically; palatine grooves smaller; dorsal surface of rostrum more nearly parallel to palate; a transverse prominence between supraorbital processes rather than oblique crests extending from sagittal crest to each supraorbital process; orbit positioned more anteriorly and protruding more anterodorsally, causing anterior part of zygomatic arch to flare more prominently anterolaterally, to form a cup-like structure, and to depart from the cheek region more abruptly and more nearly horizontally, not smoothly sweeping posterolaterally; zygomatic process of jugal deeper dorsoventrally; palate more vaulted; cheek tooth row straighter; anteroventrally directed preglenoid process present at lateral portion of glenoid fossa; region of basicranium between glenoid fossa and internal naris more convex; pharyngeal tubercle of basioccipital larger and more convex; mastoid process more curved rather than essentially cuboid in shape, relatively larger and extended farther laterally, forming a more sigmoid crest joining with the paroccipital process; dorsal surface of cranium much more convoluted and rugose; and sagittal and nuchal crests larger; and

(3) differing from *Pinnarctidion* by having cranium with orbit directed more anteriorly, causing anterolateral border of orbit formed by zygomatic arch to flare more prominently anterolaterally; anterior part of zygomatic arch thicker; more highly vaulted palate; tapered (not dorsoventrally expanded) anterior end of zygomatic process of squamosal; anterior openings of optic foramina located relatively higher within interorbital septum; smaller pterygoid process of maxilla ventral to orbit, not formed into a shelf; cheek teeth more closely spaced; P^4 with protocone shelf more posteriorly located and extending more lingually; M^{1-2} larger; palatines ventral to internal choana forming an elongate

tube with rounded lateral edges; internal narial opening higher and narrower; strut formed by pterygoid spanning between palate and braincase longer, thicker, and not concave laterally; tympanic bulla not so inflated, especially in the lateral part; paroccipital process thinner, flatter dorsoventrally, and joined to mastoid process by thinner and narrower crest; and occipital condyles projecting more prominently from occipital shield.

TYPE AND ONLY INCLUDED SPECIES. *Pacificotaria hadromma,* new species, early Middle Miocene, Oregon.

ETYMOLOGY. The genus name is derived from Pacific, in reference to the Pacific Ocean distribution of this pinniped; plus *otaria,* from the generic name, *Otaria,* the type genus of the family Otariidae, ultimately from Greek, *otarion,* a little ear, in reference to the small external ear (pinna) of eared seals. The genus is feminine in gender, just as previous usages of the same root have been, for example, *Callotaria ursina cynocephala* Stejneger, 1936, *Otaria californiana* Lesson, 1828, and *Otaria japonica* Peters, 1866.

Pacificotaria hadromma, new species

Figures 1–6, 7a, 8a, 9a

DIAGNOSIS OF SPECIES. Because the genus is monotypic, the generic diagnosis serves for the species.

HOLOTYPE. LACM 127973, complete cranium with all teeth except left I^3 and right and left M^{1-2}, collected by Guy E. Pierson, 26 April 1983.

TYPE LOCALITY. LACM 4851, among loose boulders on Moolack Beach between the mouths of Schooner Creek and Moolack Creek, Lincoln County, Oregon. (Moolack is the locally used spelling for the names of both the beach and the creek, although both are shown as Moloch on the U.S. Geological Survey, Yaquina, Oregon, 15 minute topographic map, 1959 edition.)

FORMATION AND AGE. The strata that yielded the holotype of *Pacificotaria hadromma* are part of a stratigraphic section that has been referred to the Astoria Formation and are early Middle Miocene, approximately 16 Ma in age. They represent the Newportian Molluscan Stage and are correlated with the early part of the "Temblor" provisional provincial mega-invertebrate stage as characterized by Addicott (1972) on the basis of Californian fossils, with the Saucesian foraminiferal stage (Addicott, 1976; and see Moore, 1964:20–21), and with the Hemingfordian North American Mammal Age. The age, correlation, stratigraphic relationships, and other vertebrate fossils from this part of the Astoria Formation were discussed by Barnes (1990:3).

The holotype of *Pacificotaria hadromma* was found in a rounded, extremely hard, fine-grained gray concretion, typical of those that weather out of the upper part of the Astoria Formation that is exposed in the sea cliff at Moolack Beach from an easily recognizable concretionary horizon that has become known as the "Iron Mountain bed" (see Munthe and Coombs, 1979:78, 79; Armentrout, 1981:141 (note 29); Barnes, 1990:3). This is the same "Iron Mountain bed" that yielded the cranium of the dome-headed Hemingfordian chalicothere, *Tylocephalonyx* sp., described by Coombs (1979) and Munthe and Coombs (1979).

Pacificotaria hadromma is apparently the third otariid known from the "Iron Mountain bed", the probable source of the holotype and paratype of the enaliarctine, *Pteronarctos piersoni,* and of a partial cranium referred to the large desmatophocine, *Desmatophoca oregonensis* (see Barnes, 1987). All are from nodules that most probably were derived from the "Iron Mountain bed", and all were collected along the 1.5 km section of Moolack Beach extending northward from Schooner Point (located on the north side of the mouth of Schooner Creek) to the mouth of Moolack Creek (see Barnes, 1990).

The holotype and only known specimen of *Pteronarctos goedertae* is from a stratigraphically lower horizon, a bed close to the base of the Astoria Formation that is approximately 19 Ma old. It may be as much as 3 Ma older than the other otariids from the stratigraphically higher "Iron Mountain bed" (Barnes, 1990:1, 15).

ETYMOLOGY. The species name is derived from Greek; *hadros,* for well-developed or large, and *omma,* for eye; in reference to the protruding orbits of this pinniped.

DESCRIPTION AND COMPARISONS. The holotype cranium of *P. hadromma* is virtually complete, but postdepositional sediment compaction around the holotype (LACM 127973) has resulted in slight dorsoventral compression of the braincase and of the rostrum. The specimen has thus undergone breakage and outward displacement of the lateral surfaces of the rostrum, the braincase, and the orbital wall. Postdepositional distortion also has displaced the entire right side of the specimen posteriorly about 1 cm. A principal indicator of this is that the right glenoid fossa is canted posterolaterally (see Fig. 5), a feature uncommon for a pinniped and unknown for an enaliarctine. The left glenoid fossa is in the characteristic position, somewhat canted anterolaterally and normal to the tooth row. Therefore, the lateral edge of the right glenoid fossa is approximately 5 mm posterior of its original position on the cranium. Concomitant with this, there has been posterior displacement of the right dental row, the right zygomatic arch is swept posteriorly, and the right half of the basicranium is positioned farther posteriorly than the left. For the description and reconstructions, the left side of the holotype represents the true original morphology (see Methods and Materials). The cranium apparently also underwent preburial transport, separating it from the mandible and the rest of the skeleton and resulting in loss of some teeth prior to fossil-

Table 1. Measurements (in mm) of the holotype cranium, LACM 127973, of *Pacificotaria hadromma,* new genus and species (see Methods and Materials section for methods of measurements). All bilateral measurements were taken on the less distorted left side of the cranium.

Total length (condylobasal length) (0)*	212.3
Postpalatal length (palatal notch to basion)	105.4
Basion to anterior edge of zygomatic root (18)	151.2
Length of tooth row, C to M^2	68.9
Width of rostrum across canines (12)	54.6
Width of palate across anterior alveoli of P^4	47.1
Width between infraorbital foramina	50.0
Width across antorbital processes (5)	53.9
Width across greatest interorbital constriction (6)	40.8
Width across supraorbital processes (7)	40.7
Width across greatest intertemporal constriction	26.7
Width of braincase at anterior edge of glenoid fossa (8)	67.2
Zygomatic width (17)	126.1
Auditory width (19)	99.6
Mastoid width (20)	109.6
Paroccipital width	83.8
Greatest width across occipital condyles	50.0
Greatest width of anterior nares	29.7
Greatest height of anterior nares	28.6
Width of zygomatic root of maxilla (14)	13.0
Greatest width of foramen magnum	24.5
Greatest height of foramen magnum	15.7
Transverse diameter of infraorbital foramen	12.2

* Numbers in parentheses are measurements used by Sivertsen (1954).

Table 2. Degree of closure of sutures (1–4) and suture age of holotype cranium, LACM 127973, of *Pacificotaria hadromma,* new genus and species. Suture nomenclature, numbers, and methods follow Sivertsen (1954) (see Methods and Materials).

I. Occipito-parietal	4
II. Squamoso-parietal	3
III. Interparietal	4
IV. Interfrontal	3
V. Coronal	4
VI. Basioccipito-basisphenoid	3
VII. Maxillary	3
VIII. Basisphenoid-presphenoid	3
IX. Premaxillary-maxillary	3
Total (suture age)	30

ization. All teeth of the holotype remain in place, except for the left I^3 and the right and left M^{1-2}, which fell out of the cranium prior to final burial.

The holotype apparently represents a fully adult male (Group I of Sivertsen (1954)) based on the following observations: (1) the occipito-parietal, coronal, basioccipito-basisphenoid, jugal-maxillary, and anterior part of the premaxillary-maxillary sutures are obliterated by fusion, all other sutures are visible; (2) the cranium yields a suture age of 30 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in what would be the adult age class of Recent species; (3) as in most Recent adult male otariines (for example see Murie, 1874:pl. 77, figs. 12–21; Odell, 1981:fig. 4), a sagittal crest is present, the nuchal crest is prominent, the dorsal surface of the braincase is rugose, and cranial features are generally massive; and (4) all teeth are fully erupted, but not heavily worn, with only slight wear on the apices of the canines and on the protoconal shelves of P^{3-4}.

I have suggested (Barnes, 1979:16) that species of *Enaliarctos* were sexually dimorphic, with females having canines that are 20 to 32% smaller than those of males. The canines of the holotype of *P. hadromma* are nearly equal in size to the larger canines which I attributed to males of *Enaliarctos* sp. from near the type locality of *E. mealsi.* Additionally, the holotype cranium of *P. hadromma* is approximately the same size and has canines (or canine alveoli) equal in size to those of the holotype of *Pteronarctos goedertae* and of the holotype and paratype of *Pteronarctos piersoni,* all of which I interpreted as representing males (see Barnes, 1989, 1990). The holotype cranium, by this logic, is apparently the typical skull size for a mature male of the species. It has the same calculated suture age (see Table 2) as the paratype of *P. piersoni* (see Barnes, 1990:table 2), but on the latter a remnant of the basioccipito-basisphenoid suture and the maxillary-jugal suture remain unfused. The cranium of *Pacificotaria hadromma* is nearly identical in size and proportions (Table 1) to the two known crania of *Pteronarctos piersoni* but has a shorter and wider rostrum, more anteriorly placed and more protruding orbits, wider interorbital region, greater zygomatic width, and narrower occipital condyles (compare Table 1 with Barnes, 1990:table 1).

Unlike the condition in species of *Pteronarctos,* the rostrum does not taper anteriorly. Instead it is expanded anteriorly and the canine roots form prominent bulges in the cheek region. The anterior tip of the rostrum is slightly more broadly arcuate than it is in species of *Pteronarctos.* On both sides of the rostrum, the suture between the maxilla and premaxilla is clearly visible in its posterior part, but anteriorly, where it approaches the rostral extremity, it is fused and obliterated. On the anterior surface of the rostrum, along the premaxillary-maxillary suture between the locations of the roots of I^3 and the canine, is a distinct fossa. Such a fossa is not present in any previously described enaliarctine. In anterior view, the widest part of the external narial opening is about mid-height. The anterior narial opening is larger than that in *Pteronarctos piersoni* or in *P. goedertae* (Fig. 7). In contrast with *P. goedertae,* and more like the condition in *P. piersoni,* the anterior margin of each nasal bone is less concave, and the rostrum is deeper and its dor-

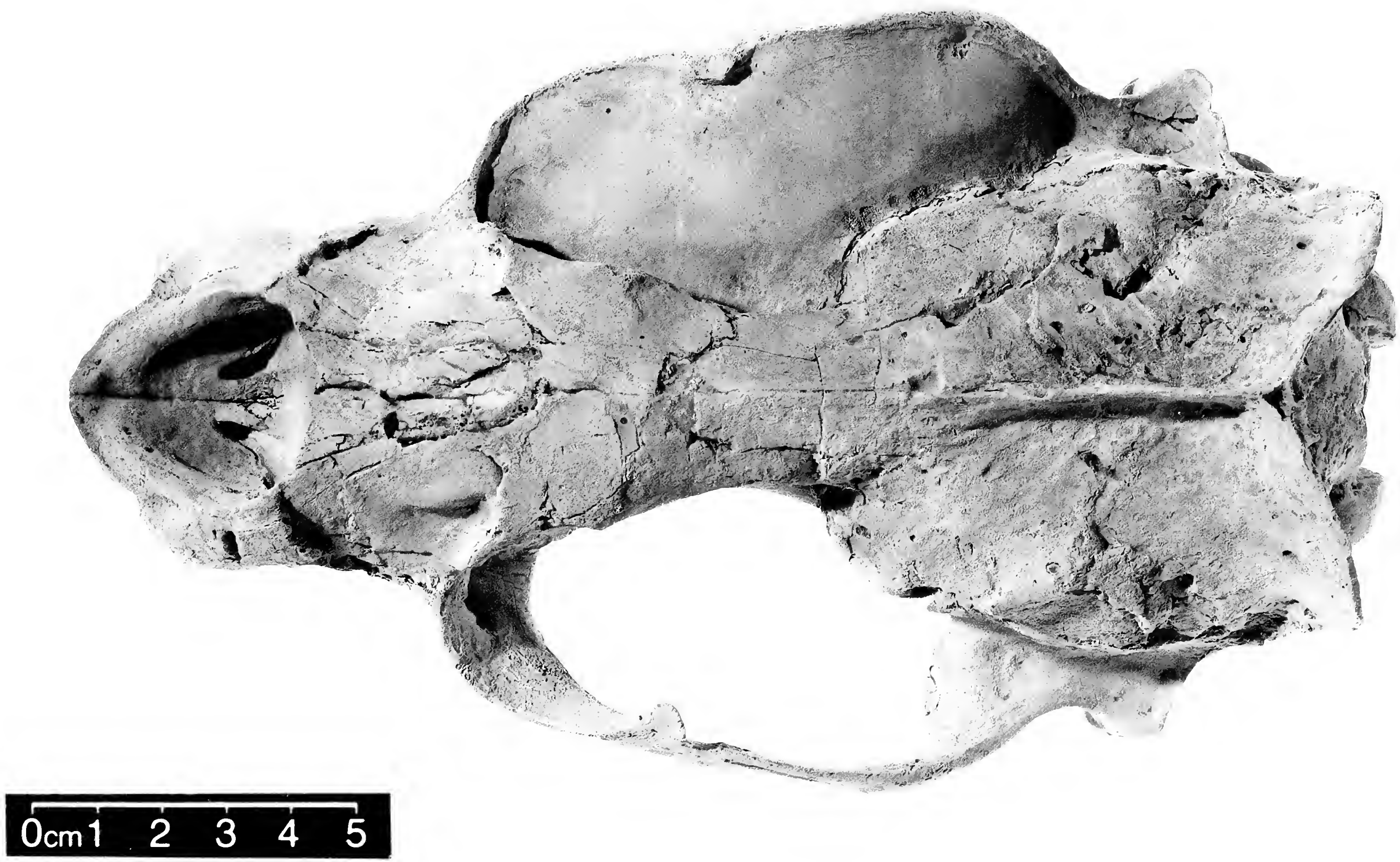


Figure 1. *Pacificotaria hadromma,* new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, dorsal view.

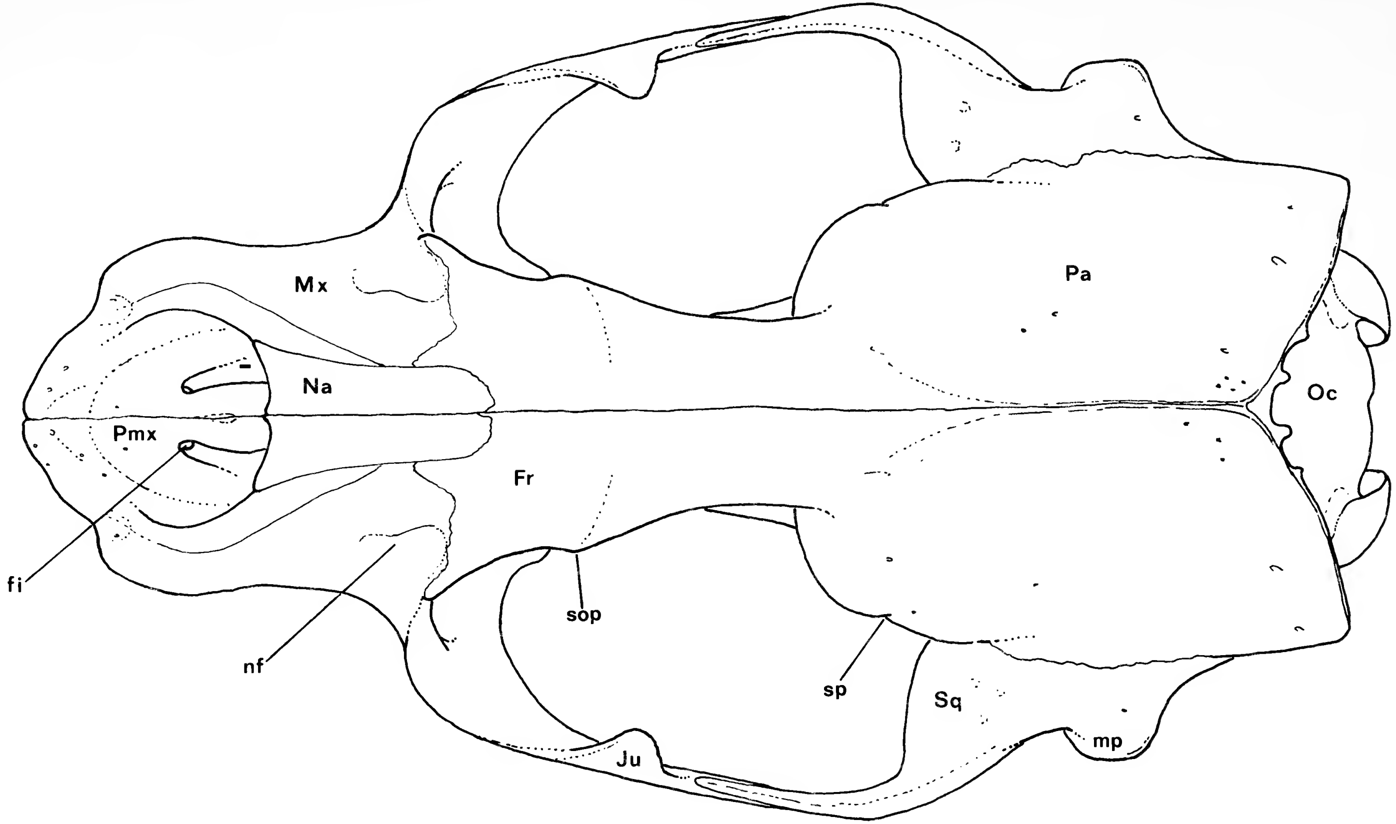


Figure 2. *Pacificotaria hadromma,* new genus and species, restoration of cranium based on holotype, dorsal view; for explanation of abbreviations see Methods and Materials.

Figure 3. *Pacificotaria hadromma*, new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, left lateral view.

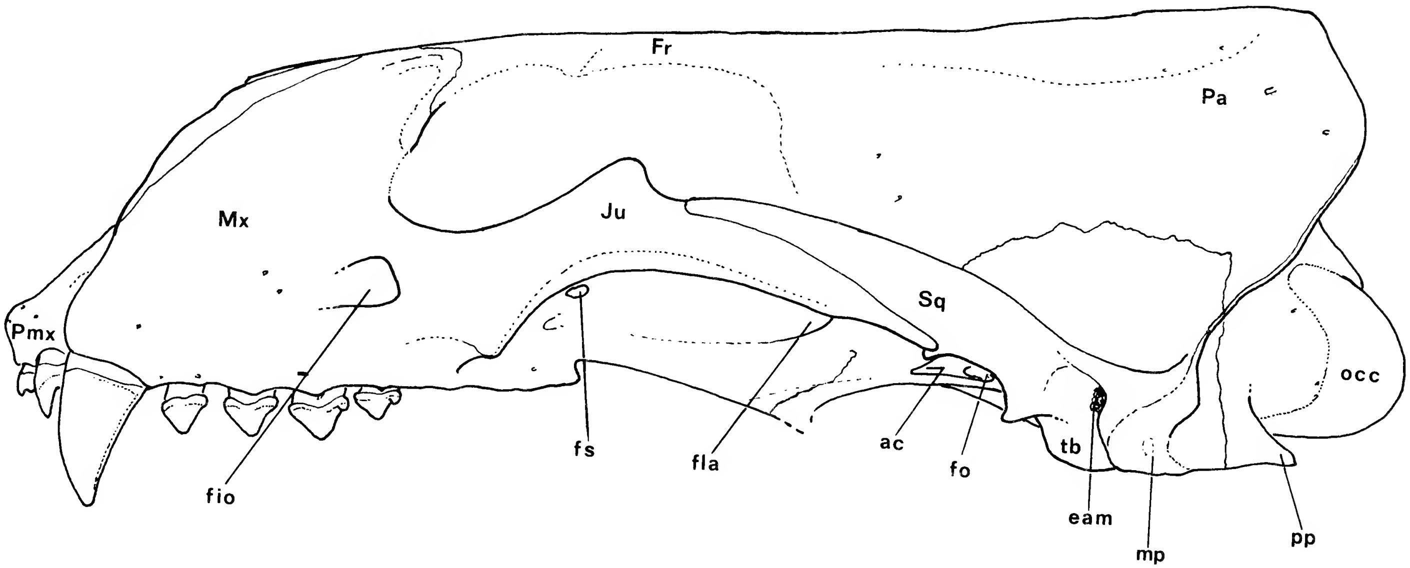


Figure 4. *Pacificotaria hadromma,* new genus and species, restoration of cranium based on holotype, left lateral view; I^3 is reversed from the right side, for explanation of abbreviations see Methods and Materials.

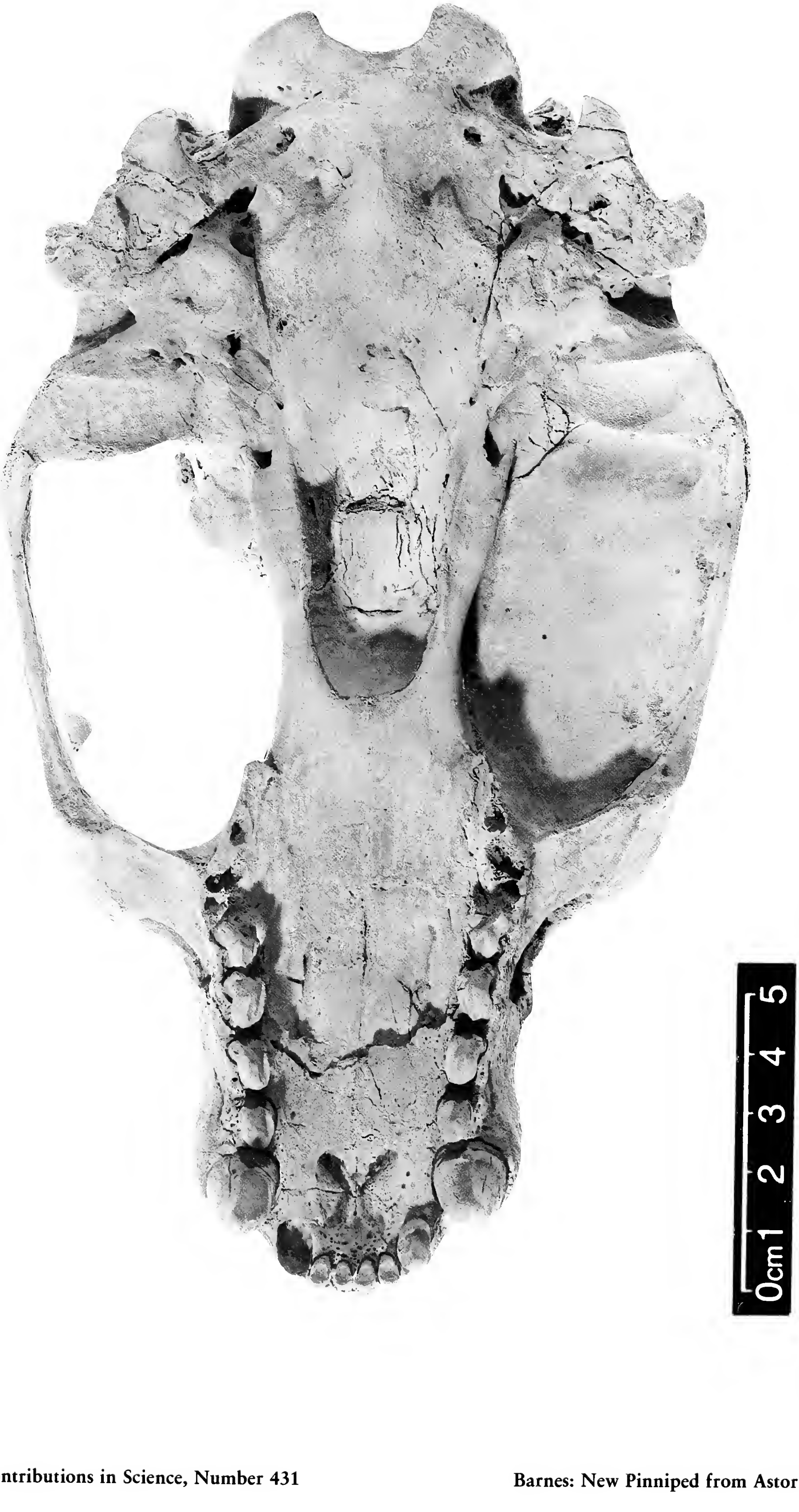


Figure 5. *Pacificotaria hadromma,* new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, ventral view.

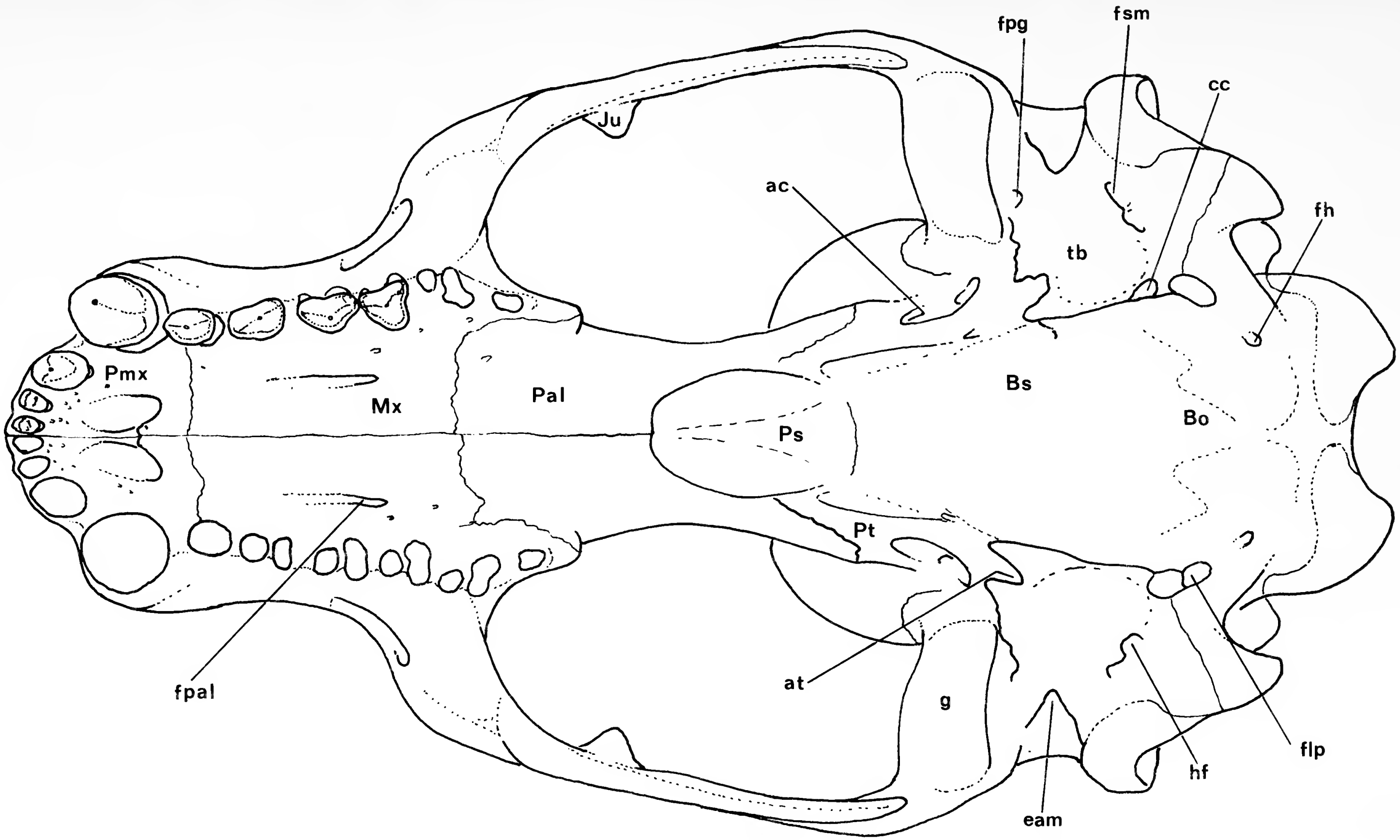


Figure 6. *Pacificotaria hadromma*, new genus and species, restoration of cranium based on holotype, ventral view; all of the right teeth are omitted to show pattern of alveoli, I^3 is reversed from the right side, for explanation of abbreviations see Methods and Materials.

sal surface is more arched. The nasolabialis fossa, anterior to the orbit, is more distinct than it is in any other known enaliarctine, has a sharp, slightly projecting dorsal margin, and is expanded vertically. As in *P. piersoni,* the ascending (nasal) process of the premaxilla terminates at approximately midlength on the nasal and does not extend as far posteriorly (Fig. 7) as it does in *P. goedertae.* A wide, tapered anterior process of the frontal extends along the margin of each nasal. From that point the maxillary-frontal suture trends laterally to reach the anterior margin of the orbit between the nasolabialis fossa and the small antorbital process.

In *Pacificotaria hadromma,* the transverse diameter of the infraorbital foramen is approximately 1.5 times that of the same foramen in *Pteronarctos piersoni,* nearly twice the diameter of the same foramen in *P. goedertae,* and larger than that in any other known enaliarctine. The zygomatic arch is more bowed dorsally and is deeper dorsoventrally in its anterior part than it is in either *P. piersoni* or *P. goedertae* (Fig. 8). It departs from the side of the rostrum at a more ventral location and more at right angles to the snout than in either species of *Pteronarctos* and makes a more prominent bend beneath the orbit. Around the orbit, the zygomatic arch is thicker than it is in either species of *Pteronarctos,* and it flares farther laterally. The relatively prominent postorbital process of the jugal is broad anteroposteriorly and curves dorsomedially. The jugal extends posteriorly ventral to the zygomatic process of the squamosal as an elongate, tapered splint that reaches the anterolateral corner of the glenoid fossa. The zygomatic process of the squamosal that extends dorsal to the jugal is likewise long and tapered and does not extend so far anteriorly as to reach the postorbital process of the jugal.

The orbit is virtually the same diameter as it is in all specimens of *Pteronarctos* but is approximately 75% of the diameter of that of the holotype of *Enaliarctos mealsi.* The smaller eye is significant because all these crania are essentially the same size. Compared with all other enaliarctines, the orbit of *Pacificotaria hadromma* protrudes more anterodorsally from the cranium. The sphenopalatine foramen is partly broken but appears to have been smaller than in either specimen of *Pteronarctos piersoni* and is located directly dorsal to the pterygoid process at the posterolateral corner of the palate. The bone at the anterior margin of each orbit is slightly crushed, and I cannot determine if there was a lacrimal foramen present as in *Pteronarctos goedertae.* A piece of bone has broken out of the medial wall of the left orbit. This does not appear to have been an orbital vacuity, and there are no vacuities elsewhere on the medial orbital wall. Likewise, there are no orbital vacuities in either species of *Pteronarctos.* As in *E. mealsi* and both species of *Pteronarctos,* the optic foramen is beneath the anterior margin of the braincase, relatively high within the orbit, and separated from the anterior lacerate foramen.

The interorbital region is wider than it is in species of *Pteronarctos* (Fig. 7), and instead of an oblique crest extending posteromedially from each supraorbital process and converging on the sagittal suture of the cranium, in *Pacificotaria hadromma* there is a transverse eminence spanning between the opposite supraorbital processes. This same eminence is found in *E. mealsi.* Also as in *E. mealsi* and *Pteronarctos goedertae,* the thin sagittal crest of *Pacificotaria hadromma,* which is as much as 10 mm high, extends from the braincase anteriorly as far as the posterior margin of the orbit. Although both known crania of *Pteronarctos piersoni* have a low sagittal crest on the braincase, in neither of them does the crest extend as far anteriorly as the interorbital area. Because the crania of all four species represent similarly aged males, these differences in the sagittal crest development probably represent diagnostic differences rather than those associated with ontogeny. The dorsal surface of the braincase is irregular, not as smooth as in *P. goedertae,* has a few small foramina, and is depressed posteriorly on either side of the sagittal crest.

The holotype of *Pacificotaria hadromma* has undergone breakage and some slight displacement of the braincase along the parietal-squamosal suture, and this suture can be traced on both sides and is shown in the restorations (Figs. 2, 4). The nuchal crest of *P. hadromma* is thick and posterodorsally directed as in *Pteronarctos piersoni,* not extended as far posteriorly over the occipital shield as in *P. goedertae.* The nuchal crest has an irregularly flattened posterior surface, and at its apex is a pair of small tubercles. Directly dorsal to the foramen magnum, which is horizontally expanded rather than circular, is a deep fossa in the supraoccipital.

As in *Pteronarctos piersoni,* the occipital condyles of *Pacificotaria hadromma* are larger and project farther posteriorly than they do in *Pteronarctos goedertae.* They are set off from the occipital shield more prominently, and they are thus visible extending beyond the nuchal crest in dorsal view (see Figs. 1, 2, 7). They are confluent ventrally with the basioccipital, diverge dorsally, and are separated ventrally by a prominent intercondylar notch.

Pacificotaria hadromma has a somewhat arched palate, unlike the flat palate typical of both species of *Pteronarctos.* All of the palatal sutures shown in Figure 6 are observable on the holotype; however, the locations of the fused pterygoid-palatine sutures are indicated by oblique, raised, and rugose ridges at the sites where such sutures would be expected. As is typical of enaliarctines, there are two palatine sulci that extend anteriorly from the large posterior palatine foramina, but these are shorter and shallower than in species of *Pteronarctos* or in *E. mitchelli.* Located at the posterior margin of the palate ventral to the orbit, the pterygoid process is prominent, similar to that of *Pter-*

onarctos goedertae but thicker, and larger than that in specimens of *P. piersoni* (Fig. 9). The bony palate is short as it is in *P. piersoni,* so that the internal narial opening is relatively farther anterior on the cranium than in *P. goedertae.* Concomitant with the shorter palate of *Pacificotaria hadromma,* there is a longer pterygoid-palatine strut.

The I^{1-2} are preserved on both sides of the holotype of *P. hadromma.* Each tooth has a transversely bifid crown, as is typical of the Otariinae, comprised of a principal transverse anterior cusp that is separated by a sulcus from a smaller posterior cusp. Despite considerable apical wear on the incisors, the anterior and small posterior cusps on the crowns are not obliterated.

The right I^3 is preserved, and as in *Pteronarctos goedertae,* it has a prominent, asymmetrically curved posterior cingulum that is continuous with a posterolateral cusp that is a remnant of such a cusp that is typical of ursids. The I^3 is nearly twice the diameter of the same tooth in *P. goedertae* and larger than the I^3 of *P. piersoni.*

The canines of *Pacificotaria hadromma* have a vertical posterior crista, continuous with a slight cingulum both laterally and medially. Their alveoli measure 12.5 mm transversely, and 13.5 mm anteroposteriorly. The canines are virtually the same size and have the same morphology as those of species of *Pteronarctos*; however, in *Pacificotaria hadromma* the canine crowns are nearly vertically oriented relative to the plane of the palate (see Fig. 8). In *Pteronarctos goedertae* the canine crowns are more procumbent.

In contrast to the condition in species of *Enaliarctos* and *Pteronarctos,* the cheek tooth row of *Pacificotaria hadromma* is less bowed laterally in the region of the P^4 and M^1. The locations, sizes, and shapes of the alveoli for P^{1-4} are very similar to those of both species of *Pteronarctos,* but the cheek tooth row is straighter. All four premolars are preserved in place on both sides of the holotype of *Pacificotaria hadromma.*

The P^1 has a root that is round in cross section. The crown (6 mm high, 5.5 mm transversely, 7.3 mm anteroposteriorly) is a simple cone, with a single central cusp bearing a crest on its anterior and posterior sides. The cingulum traverses the lingual side of the crown and extends around to the labial side both anteriorly and posteriorly.

The P^2 has two roots. The anterior one is round in cross section, as it is in species of *Pteronarctos,* but the posterior root is expanded transversely. As with P^1, the crown (6.6 mm high, 5.6 mm transversely, 8.9 mm anteroposteriorly) is a cone with anterior and posterior crests extending from the central cusp, but the axis of these crests is oblique to the sagittal plane of the cranium. The cingulum nearly encircles the crown and encompasses a posterolingual bulge of the crown that lies beneath the lingual bulge of the root. This posterolingual bulge appears to be a neomorph that is analogous to the protocone on P^4.

The P^3 has a root and crown pattern that are similar to those of the P^2. The anterior root is round in cross section, but the posterior root is larger and more transversely expanded. The crown (7.5 mm high, 6.1 mm transversely, 9.4 mm anteroposteriorly) is larger than that of P^2 and is aligned anteroposteriorly rather than obliquely, there is a slightly larger posterior cingular cusp, and the protocone is larger and more medially located.

The shape of the crown (5.0 mm high, 7.5 mm transversely, 9.1 mm anteroposteriorly) of the P^4 of *Pacificotaria hadromma* is nearly an equilateral triangle in occlusal view (Figs. 5, 6). The paracone is the major cusp and is broad anteroposteriorly and transversely compressed. It comprises the lateral part of the crown, and the small metacone lies directly posterior to it. A faint labial cingulum curves apically around both the anterior and posterior ends of the crown. The protocone shelf, larger than that on P^3, had a small cusp, which has become worn down flat on both the right and left teeth and is separated from the paracone by a trigon basin and bordered lingually by a cingulum. In comparison with the carnassial P^4 of *E. mealsi,* the P^4 of *P. hadromma* is much less sectorial, the metacone is much smaller and is located more anteriorly, and the protocone is located more posteriorly relative to the paracone. As in species of *Pteronarctos,* the anterior root above the paracone remains separate, and the posterior root above the metacone has merged with the medial one above the protocone to form a single, bilobed posterior root. The P^4 of *Pacificotaria hadromma* is very similar in shape to the P^4 of *Pteronarctos piersoni* and of *Pinnarctidion bishopi.* The P^4 of *Pacificotaria hadromma* differs from that of *Pteronarctos piersoni* by not having a slight inward bow on the labial side of the tooth and by not having such a deep notch in the posterior margin of the crown, posterior to the trigon basin.

As in *P. piersoni,* the M^1 of *Pacificotaria hadromma* had a single round anterior root and a distinctly bilobed posterior root. The bilobed elongation of the posterior root is oriented obliquely to the sagittal plane (Figs. 9a, b) and represents the two originally separate roots, one above the protocone and one above the metacone. *Pteronarctos goedertae* has a more derived condition with a single nearly round posterior root on M^1 (see Fig. 9c), which is elongate anteroposteriorly. The alveolus for M^2 of *Pacificotaria hadromma* is bilobed, as it is in both species of *Pteronarctos,* and larger than it is in species of *Enaliarctos.*

The construction of the glenoid fossa is intermediate between that of *E. mealsi* and that of species of *Pteronarctos.* In *E. mealsi,* the postglenoid process is wide, and for most of its width it projects anteroventrally beneath the fossa. In *Pacificotaria hadromma* it is narrower and does not extend so far anteroventrally (Fig. 5). In *Pteronarctos* it is smaller and projects less anteroventrally. *Enaliarctos mealsi* has a well developed preglenoid process, which in its lateral part projects ventrally. There is a similar but smaller preglenoid process in *Pacificotaria hadromma* (Fig. 5), but species of *Pteronarctos* lack the process. There is a large postglenoid foramen on the posterior side of each postglenoid process of *Pacificotaria hadromma.*

Because the holotype is the only documented specimen of the species, and because the matrix on the specimen is very indurated and difficult to remove, it was decided not to destroy one of the bullae in an attempt to remove the matrix from it. The auditory region, as in *Pteronarctos piersoni,* is positioned on the basicranium posterior to the postglenoid process, in a location that is typical of otariids and generalized fissipeds. This is in contrast to the relatively unusual condition in *P. goedertae,* in which the ear region extends more anteriorly on the basicranium, and the anterior part of the tympanic bulla and styliform process, ventral to the auditory tube, extend anteromedial to the postglenoid process.

In *P. goedertae,* the tympanic bullae are broad and most inflated in their centers. In contrast, the bullae of *Pacificotaria hadromma,* as in *Pteronarctos piersoni,* are relatively smaller, most inflated toward the basioccipital, and slope uniformly toward the external acoustic meatus. The anteromedial part of the bulla is retracted ventral to the auditory tube, and the opening of the tube is flanked on each side by a prominent styliform process of the bulla. There is a wider space between the mastoid and postglenoid processes in *Pacificotaria hadromma* than in specimens of *Pteronarctos,* and the inframeatal lip of the bulla is retracted ventral to the external acoustic meatus. A prominent ridge of bone spans between the mastoid process and the bulla, and immediately posterior to this is the stylomastoid foramen, which opens anteroventrolaterally toward the ridge. Posteromedial to the stylomastoid foramen is the hyoid fossa, which is at the posterolateral side of the bulla. As in all specimens of *Pteronarctos,* there is a prominent recess surrounding the stylomastoid foramen and the hyoid fossa, making them confluent. In *E. mealsi* there is no such recess, and the stylomastoid foramen and hyoid fossa are separate. In *Pacificotaria hadromma,* a strut of bone 7 mm wide separates the hyoid fossa from the posterior lacerate foramen. The posterior lacerate foramina are not symmetrical right to left and are irregularly shaped and elongate anteroposteriorly. At the posterior carotid foramen, the ventral part of the bulla is retracted so that the foramen opens ventral to a shelf of bone anterior to the posterior lacerate foramen.

As in all specimens of both species of *Pteronarctos,* the basisphenoid-presphenoid suture is open and has been offset by compression. Except for a short length on the left side, the basioccipital-basisphenoid suture is fused and obliterated on the holotype. The visible part of this suture is on the left margin of the basioccipital opposite the opening of the auditory tube. The basioccipital is relatively wide, expands posteriorly, and has a prominent tuberosity on each side, marking the insertions of the rectus capitis ventralis muscles. Each tuberosity extends posteriorly into the anterior part of a broad fossa that extends as far posterolaterally as the hypoglossal foramen. This foramen is small and its opening faces anterolaterally.

In *Pacificotaria hadromma* the mastoid process is thicker anteroposteriorly than it is in *Pteronarctos goedertae,* and the crest of bone that joins the mastoid process with the paroccipital process is also thicker, as in *P. piersoni.* In *Pacificotaria hadromma* the lateral margin of this crest is straighter between the two processes than it is in species of *Pteronarctos.* As in both species of *Pteronarctos,* the paroccipital process is relatively broad, and its laterally bowed external margin gives it the appearance of bending medially at the posterior end. The exoccipital-squamosal suture is visible as it extends straight across the lateral surface of the paroccipital process (Fig. 4), thence on the ventral surface of the process to the anterolateral side of the posterior lacerate foramen (Fig. 6).

DISCUSSION

MORPHOLOGICAL BASES FOR INTERPRETING RELATIONSHIPS

The holotype crania of the three enaliarctines known from the Astoria Formation, *Pteronarctos piersoni, Pteronarctos goedertae,* and *Pacificotaria hadromma,* all appear to represent adult males of similar size and age. Therefore, cranial differences between them that are on the same scale as those differentiating Recent otariine genera and species may be interpreted as being taxonomically significant. The characters differentiating the genera *Pacificotaria* and *Pteronarctos* are similar in kind and in magnitude to differences between Recent genera of fur seals and sea lions (see for example illustrations in Sivertsen, 1954; King, 1960; Ridgway and Harrison, 1981). The kinds and degrees of similarities and differences among the two species of *Pteronarctos,* as among those of *Enaliarctos,* are similar to those among species of the living polytypic genus of fur seals, *Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826 (see illustrations in King, 1954; Repenning et al., 1971; Bonner, 1981).

In the following discussion, selected characters of enaliarctines are concluded to be either plesiomorphic (primitive) or apomorphic (derived), and the polarities and occurrences of these characters among enaliarctines are shown in Table 3 and influenced the cladogram (Fig. 10) and the classification presented here. Following are explanations of the characters and my logic for determining their polarities in the enaliarctines.

Zygomatic Arch Relatively Straight. The primitive state in carnivorans is a laterally bowed and dorsally curved zygomatic arch. This is typical of virtually all fissipeds and of *Enaliarctos mealsi.* Various groups of derived otariids have a straighter

Table 3. **Some derived cranial characters of the Enaliarctinae and their polarity states in various species. All judgments are based solely on the comparative degrees of development of the character among the Enaliarctinae.**

	Enaliarctos mealsi	*Enaliarctos mitchelli*	*Pacificotaria hadromma*	*Pteronarctos piersoni*	*Pteronarctos goedertae*	*Pinnarctidion bishopi*
Zygomatic arch relatively straight	—*	+	—	o	+	+
Occipital condyles broadly joining occiput	—	?	—	—	+	+
Orbits enlarged	+	+	—	—	—	+
M^2 greatly reduced in size	+	+	—	—	—	+
Palate extended posteriorly beneath choana	+	+	—	—	o	+
Rostrum lengthened	—	—	—	+	+	—
Cheek tooth row nearly straight	—	—	+	o	o	+
P^4 protocone reduced and located posteriorly	—	—	+	+	+	+
P^3 with protocone and bilobed posterior root	—	—	+	+	+	+
Paroccipital process tabular, bent medially	—	?	+	+	+	+
All cheek teeth reduced in size	—	?	+	+	+	+
I^3 diameter increased	?	—	+	o	—	?
P^2 with protocone and bilobed posterior root	—	—	+	o	—	—
Rostrum expanded transversely at canines	?	—	+	—	—	?
Orbits protruding anterolaterally	—	—	+	—	—	—
Infraorbital foramen enlarged	o	—	+	+	—	—
Mastoid process expanded anteroposteriorly	—	?	+	+	o	o
Ascending process of premaxilla shortened	—	?	o	+	—	?
Preglenoid process lost	—	?	—	+	+	o
Nasolabialis fossa reduced, shallow	o	—	—	+	+	o
Anterior narial opening enlarged	—	+	+	—	—	—
Pterygoid process of palatine large	o	o	o	o	—	+
M^1 with single, round posterior root	—	—	—	—	+	—
Tympanic bulla extended anteriorly	—	—	—	—	+	—
Nuchal crest projected over occipital shield	—	?	—	—	+	—
Pterygoid strut expanded transversely	—	—	—	—	—	+
Zygomatic process of squamosal deep	—	—	—	—	—	+
Antorbital process present and large	—	—	—	—	—	+
Paroccipital-mastoid crest broad	—	?	o	o	o	+
Interorbital region narrow	o	+	—	o	o	+

* + = derived character present; — = derived character absent; o = derived character developed to an intermediate extent; ? = structure not preserved on available specimen(s) and therefore not determinable.

zygomatic arch, in some species virtually straight on the lateral side, and this derived condition is probably convergent in different lineages.

Occipital Condyles Broadly Joining Occiput. The primitive state in carnivorans is condyles that protrude prominently from the occipital shield and are set off from it by surrounding sulci. This is typical of many fissipeds and of *Enaliarctos mealsi, Pacificotaria hadromma, Pteronarctos piersoni,* and the living fur seals and sea lions (subfamily Otariinae). Various groups of derived otariids (e.g., *Pinnarctidion bishopi, Pteronarctos goedertae, Allodesmus kernensis* Kellogg, 1922, Odobeninae) have condyles that are more widely set, closer to the occipital shield, and without surrounding sulci. This derived condition is concluded to have evolved convergently in different lineages.

Orbits Enlarged. The plesiomorphic condition in carnivorans is orbits that are not appreciably enlarged, and this is typical of most fossil and living fissipeds. The development of large eyes in pinnipeds is associated with the ability to gather more light to aid in feeding at considerable depths (King, 1983:194, fig. 6.9; Mitchell, 1966:6). Living phocids and otariids have greatly enlarged orbits, as do certain fossil pinnipeds, especially the highly derived Allodesminae. Compared with most other pinnipeds, walruses do not have very large eyes, and this is undoubtedly correlated with the fact that they are not very deep divers. Paradoxically, among the enaliarctines, the orbits of the otherwise relatively primitive species, *Enaliarctos mealsi,* are approximately 25% greater in diameter than those of either species of *Pteronarctos* or of *Pacificotaria hadromma.* Eye enlargement is a derived condition that is shared by both species of *Enaliarctos* and undoubtedly evolved to varying degrees convergently in different lineages.

M^2 Greatly Reduced in Size. The primitive state in carnivorans is to have a three-rooted M^2 that is similar to but slightly smaller than the M^1. In generalized canids and primitive ursids the M^2 is usually more than ½ the size of the M^1. In some fossil and living pinnipeds the M^2 is reduced, and in many of these species it is absent on one or both sides (Barnes, 1972:49, 1989:11–12). Clearly, reduction and loss of this tooth in pinnipeds is a derived feature. Significantly, in both species of *Enaliarctos* the M^2 is especially tiny, even smaller than in the later and otherwise generally more highly derived enaliarctines. In the Imagotariinae and in *Pinnarctidion bishopi* the M^2 has three roots or a tri-lobed root, and this situation is more primitive than that in typical enaliarctines, which have a bilobed root on M^2. Reduction of the M^2 in *Enaliarctos* appears to represent a relatively early acquisition of this shared derived character. Reduction in size and loss of the M^2 is a derived character that can help to define certain species.

Palate Extended Posteriorly Ventral to Choana. In most generalized and primitive carnivorans, the posterior end of the palate, as marked by the anterior edge of the internal narial opening, is approximately at the level of the posterior side of the M^2. This condition is typical of many fissipeds (e.g., canids, felids, amphicynodontine ursids). The most extreme derived condition in pinnipeds is a long posteriorly extended palate, such as that of the living South American sea lion, *Otaria byronia,* and the living walrus, *Odobenus rosmarus* (Linnaeus, 1758), in which the palate extends as far posteriorly as the anterior edge of the glenoid fossae. The palate is posteriorly extended, but not to such an extreme, in the Australian sea lion, *Neophoca cinerea* (Péron, 1816). In most other living otariines, the position of the posterior margin of the palate is intermediate between the usual condition in fissipeds and that in *Otaria byronia.* Although most otariids have some degree of posterior extension of the palate, this is not strictly an aquatic adaptation, because most living ursines have the palate extended just as far posteriorly. Species of *Enaliarctos* have an intermediate condition, in which the palate is extended farther posteriorly than it is in *Pacificotaria hadromma* and species of *Pteronarctos,* which are otherwise relatively highly evolved enaliarctines. Posterior palatal extension is a derived character that is concluded to have evolved convergently in different lineages.

Rostrum Lengthened. Although the typically primitive mammalian condition is a long, rather slender snout, I believe that the primitive condition for the Enaliarctinae is a short, blunt, and small snout. This is the shape of the snout in the majority of known enaliarctines, in mustelids, in the canid *Cynodesmus* Scott, 1893, in the primitive ursid *Cephalogale* Jourdan, 1862, in *Potamotherium* Geoffroy, 1833, etc. Among the known enaliarctines, only the species of *Pteronarctos* have an elongate rostrum, a shared derived character, and I consider this elongation to be a secondary derived character in the group.

Cheek Tooth Row Nearly Straight. The generalized and primitive condition among carnivorans is a cheek tooth row that is bowed laterally, particularly at the P^4 and M^1, and curved medially at the M^2. This is exemplified by virtually all generalized carnivorans. The tooth row is bowed laterally in both species of *Enaliarctos* but is straight or nearly so in virtually all of the later groups of pinnipeds, especially in those that have a homodont dentition, and a straight tooth row and homodonty are concomitant in highly evolved otariids. Among the Enaliarctinae, *Pacificotaria hadromma* and *Pinnarctidion bishopi* have the straightest cheek tooth rows, and species of *Pteronarctos* have rows that are slightly bowed, intermediate between the former and *Enaliarctos* spp. A straight cheek tooth row is a derived character that is concluded to have evolved convergently in different lineages of otariids, and among enaliarctines a tooth row that only bows slightly laterally is the most highly evolved state.

P^4 Protocone Reduced and Located Posteriorly. The generalized and primitive condition among carnivorans is a P^4 on which the protocone is located at the anterolingual side of the crown. This condition exists in miacids, felids, hyaenids, canids, mustelids, and in the amphicynodontine ursid genus *Cephalogale.* The protocone is similarly anteriorly located in *Enaliarctos mealsi,* and I conclude that this location of the protocone is the primitive state for the Enaliarctinae. However, the protocone (or the root above it) is located more posteriorly, approximately centered on the medial side of the tooth, in all of the other species of enaliarctines. This medial location is also enhanced by reduction of the talon, which serves to make the crown of the tooth a more nearly equilateral triangle. The protocone on the P^4 of *P. hadromma* is reduced, the paracone having become the principal cusp, thus creating a crown form that is somewhat like that of the P^3. Such protocone reduction is a derived character and is consistent with previous observations (see Barnes, 1990:14) that the derived enaliarctines were in the process of achieving homodonty. Therefore, among the enaliarctines, a protocone positioned medial to the mid-part of the P^4 is concluded to be a shared derived character of all taxa except species of *Enaliarctos.*

P^{2-3} with Protocone and Bilobed Posterior Root. Generalized and primitive carnivorans have a transversely compressed crown and two approximately equal-sized roots on the P^{2-3}. This condition exists in miacids, felids, canids, mustelids, and the amphicynodontine ursids of the genera *Cephalogale* and *Pachycynodon* Schlosser, 1887; and among the enaliarctines, this condition exists in both species of *Enaliarctos.* In all other enaliarctines, the posterior root of P^3 is bilobed, and the holotype of *Pacificotaria hadromma* demonstrates that the medial lobe of this root is associated with a posterolingual expansion of the P^3 crown. I interpret this expansion as an incipient protocone, a newly evolving apomorphic character, not a remnant of a previously three-rooted condition. (Note that this contradicts my earlier statement (Barnes, 1989:12) that the bilobed posterior root on P^3 of *Pteronarctos goedertae* is a remnant of a previously three-rooted condition.) The P^2 of *Pacificotaria hadromma* also has a bilobed posterior root and an incipient protocone that are slightly less developed than those on the P^3. I interpret these changes to the P^{2-3} as resulting from a molarization process that was spreading from the carnassials to the more anterior premolars (see following discussion under "Dentition of *Pacificotaria Hadromma*").

Paroccipital Process Tabular and Bent Medially. In primitive carnivorans, the paroccipital process is usually relatively small, tapered, and ventrally directed. This primitive carnivoran condition exists in *Enaliarctos mealsi.* In derived otariids such as Odobeninae, Otariinae, and Imagotariinae, the paroccipital process is short and blunt, and this is a commonly encountered derived character state amongst various taxa. However, another derived character state exists in which the paroccipital process is elongated and extended posteriorly. This condition exists in both species of *Pteronarctos, Pacificotaria hadromma, Pinnarctidion bishopi,* the Allodesminae, and the Desmatophocinae. The shared derived condition among all enaliarctines except species of *Enaliarctos* is a process that is dorsoventrally flattened and curved posteromedially.

All Cheek Teeth Reduced in Size. In primitive and generalized fissiped carnivorans the carnassials and the cheek teeth on either side of them are relatively large. In *Enaliarctos mealsi* the P^2 through M^1 are still relatively large, even though the P^1 and M^2 are reduced in size. In the later enaliarctines, the P^2 through M^1 are reduced in size, resulting in more uniformly sized cheek teeth. This is one aspect of increasing homodonty and is the derived condition in the Enaliarctinae.

I^3 Diameter Increased. The primitive condition among carnivorans (Miacidae, Canidae, etc.) is to have an I^3 that is not appreciably larger than the medial incisors. In various derived members of the Felidae, Ursidae, etc., the I^3 is greatly enlarged, and this is the derived condition. Among the Otariidae, the I^3 is moderately enlarged in *Desmatophoca oregonensis,* much enlarged in the aberrant dusignathine *Gomphotaria pugnax* Barnes and Raschke, 1991, and enlarged and caniniform in the Allodesminae. Among the Enaliarctinae, the most primitive known condition is present in *Enaliarctos mitchelli* and *Pteronarctos goedertae,* in which the alveolus of I^3 is slightly greater in diameter than those of the medial incisors. In contrast, in *Pteronarctos piersoni* the I^3 diameter is twice that of the I^{1-2}, and in *Pacificotaria hadromma* it is nearly three times the I^{1-2} diameter. The latter represents the most highly derived state of I^3 among known enaliarctines.

Rostrum Expanded Transversely at Canines. Such primitive and generalized carnivorans as species of the Miacidae and Canidae have relatively uniformly tapering rostra. This primitive condition is also present in the oldest and most primitive enaliarctines (both species of *Enaliarctos*), as well as in both species of *Pteronarctos.* In *Pacificotaria hadromma,* the distal end of the rostrum is expanded transversely, and the maxillae flare around the large roots of the canines. This species is the only known enaliarctine that has such a distally expanded snout, and this apomorphic character is similar to the condition in living species of the fur seal genus *Arctocephalus,* especially in the South African and Tasmanian fur seals (*Arctocephalus pusillus* (Schreber, 1776); see Repenning et al., 1971:pl. 3; Bonner, 1981:fig. 8).

Orbits Protruding Anterolaterally. In generalized carnivorans and in species of *Enaliarctos,* the part of the zygomatic arch that curves around the anterolateral side of the eye sweeps uniformly posterolaterally from the side of the cranium. This is the primitive condition. In *Pacificotaria hadromma* the orbit protrudes farther anterolaterally, causing the zygomatic arch to depart from the cheek more nearly at right angles. This is the apomorphic condition.

Infraorbital Foramen Enlarged. Generalized mammals and primitive carnivorans have a relatively small infraorbital foramen, and highly evolved pinnipeds, such as Recent walruses and otariines, have a large foramen, which is the apomorphic condition. Among the Enaliarctinae, the foramen is smallest in *Enaliarctos mitchelli, Pinnarctidion bishopi,* and *Pteronarctos goedertae,* largest in *Pteronarctos piersoni* and *Pacificotaria hadromma,* and intermediate in size in *Enaliarctos mealsi.* Because the foramen is large in one species but not the other of both *Enaliarctos* and *Pteronarctos,* and because it appears in different genera, I conclude that it is a convergently acquired derived character in different enaliarctine lineages. It is diagnostic for certain species, however.

Mastoid Process Expanded Anteroposteriorly. Generalized arctoid carnivores have a relatively small and rounded or crescentic mastoid process. In the Otariinae and Odobeninae the mastoid process is enlarged, protrudes ventrally, and is expanded anteroposteriorly to form a broad crescent. In the Allodesminae and Desmatophocinae the mastoid process is expanded anteroposteriorly and is nearly cubic in shape when viewed laterally. These various ways in which the mastoid process is enlarged are derived character states. Among the Enaliarctinae, *Enaliarctos mealsi* has a relatively small, vertically oriented crescentic mastoid process, which is probably the primitive character state for the subfamily. In both *Pacificotaria hadromma* and *Pteronarctos piersoni* the mastoid process is expanded anteroposteriorly, forming a broad crescent that is approximately as wide as it is high. In *Pteronarctos goedertae* and *Pinnarctidion bishopi* the process is a broad crescent but is not so expanded anteroposteriorly, and in this aspect it is intermediate between the two other conditions. Because the large mastoid appears in one species but not the other of *Pteronarctos,* and because it appears in different genera, I conclude that it is a convergently acquired derived character that is diagnostic for certain species.

Ascending Process of Premaxilla Shortened. In generalized mammals and in mammal-like reptiles, the premaxilla has a short ascending process; it does not touch the frontal, and it intersects the lateral edge of the nasal at an anterior location. In this situation, the maxilla contacts most of the lateral edge of the nasal between the frontal and the premaxilla. In generalized carnivorans, the premaxilla has an elongate, narrow ascending process that extends posteriorly along the lateral margin of the nasal. The frontal also has an anterior extension along the lateral side of the nasal. These two processes approach one another, although they do not make contact, excluding the maxilla from much of its previous contact with the nasal. In the Recent Ursidae, these two processes meet, thereby excluding the maxilla from any contact with the lateral margin of the nasal. This character state is derived for the Ursidae among the Carnivora.

All specimens of *Enaliarctos mealsi* and *E. mitchelli* either do not have the structure in question preserved or the premaxillary sutures are obliterated due to fusion, so that the relationships between the bones are not clear. A primitive enaliarctine skull, LACM 128004, as yet unidentified, from the latest Oligocene or earliest Miocene part of the Pysht Formation in Washington, has the tips of the processes of the premaxilla and frontal just barely touching. The same condition exists in *Pteronarctos goedertae,* and I consider that this is the primitive condition for the Enaliarctinae (see Barnes, 1990:13). In the Otariinae, the Allodesminae, and *Pteronarctos piersoni* the premaxilla is shorter, it does not touch the frontal, and the maxilla makes extensive contact with the nasal, and I conclude that this is a derived character state for the Otariidae, that it is a reversal back to the primitive mammalian condition, and that it has evolved in various lineages of the Otariidae. The condition in *Pacificotaria hadromma* is intermediate between the long ascending process of the premaxilla that reaches the frontal and the highly derived condition of the short ascending process such as is present in the Allodesminae.

Preglenoid Process Lost. In carnivorans with a large preglenoid process, the process is typically on the lateral side of the anterior margin of the glenoid fossa. This structure helps hold the mandibular condyle in the squamosal. It is present to some extent in most fissiped carnivorans and is greatly developed in some. The most primitive otariid, *Enaliarctos mealsi,* has a moderate sized preglenoid process on the lateral side of the glenoid fossa, and this process is developed almost exactly as in a Recent lion. In various derived lineages of otariids, e.g., *Allodesmus kernensis,* living Otariinae, and both species of *Pteronarctos,* the anterior margin of the glenoid fossa has a straight border that lacks a preglenoid process. I conclude that the loss of the process is therefore a convergent derived character in different lineages of the Otariidae, and it is a diagnostic derived character for some species.

Nasolabialis Fossa Reduced, Shallow. All enaliarctines have this fossa on the lateral side of the maxilla, high on the cheek, immediately anterior to the orbit. Its presence is a defining character of the subfamily. The fossa is virtually universally absent in all of the other (derived) subfamilies, and I consider that its loss is a derived character. Among species of the Enaliarctinae, the fossa ranges from deep (*Enaliarctos mitchelli, Pacificotaria hadromma*), to intermediate (*E. mealsi, Pinnarctidion bishopi*), to shallow (both species of *Pteronarctos*). The shallow fossa is diagnostic for *Pteronarctos,* but because it is shallow or lost in a variety of groups, this is a convergent derived character state.

Anterior Narial Opening Enlarged. In primitive mammals and in generalized carnivorans such as the Miacidae, Canidae, Ursidae, etc., the anterior naris is relatively small, and the premaxillae bordering it taper anteromedially. Nearly the same condition exists in living Otariinae, *Desmatophoca, Enaliarctos mealsi,* and both species of *Pteronarctos,* and I conclude that it is primitive for the Otariidae. In some otariids, however, the narial opening is enlarged. In *Enaliarctos mitchelli* it is highly vaulted and the premaxillary margins are thin and anteriorly directed. In *Pacificotaria hadromma* the narial opening is expanded transversely and the nasal bones are shorter, exposing more of the floor of the narial opening in dorsal view. A similar convergence is represented by the enlarged naris of the Recent gray seal, *Halichoerus grypus* (Fabricius, 1791), which is a member of the family Phocidae. Such enlargements of the narial openings are autapomorphies because they appear in different lineages and are structured in different ways.

Pterygoid Process of Palatine Large. Generalized carnivorans and primitive enaliarctines have a small process. The derived character in otariids is an enlarged shelf, and among enaliarctines it is an autapomorphy of *Pinnarctidion bishopi.*

M^1 with Single Round Posterior Root. The primitive condition for carnivorans is three roots on the M^1. The most primitive condition known in the Enaliarctinae is two roots, the posterior one being bilobed and the result of fusion of the original posterior root and the medial one over the protocone. In *Pteronarctos goedertae,* the posterior root is further reduced to a single round root, and this is an autapomorphy for the species.

Tympanic Bulla Extended Anteriorly. In most carnivorans and in all but one species of enaliarctines the tympanic bulla extends anteriorly to approximately the level of the postglenoid process. This is the primitive condition. *Pteronarctos goedertae* has a derived character state in which the bulla projects medial to the glenoid fossa as far anteriorly as the center of the glenoid fossa, and this is an autapomorphy that helps define the species.

Nuchal Crest Projected over Occipital Shield.

Typically in primitive carnivorans and in enaliarctines the nuchal crest projects posterodorsally, and this is the primitive condition. In *Pteronarctos goedertae* the crest projects more directly posteriorly and hangs prominently over the occipital shield. This is an autapomorphy that helps define the species.

Pterygoid Strut Expanded Transversely. In primitive carnivorans and generalized arctoids the strut of pterygoid that spans between the palate and the basicranium is elongate anteroposteriorly and narrow transversely. I conclude that this is the primitive character state, and it is present in the Otariinae and in most enaliarctines. Among the known enaliarctines, however, it is transversely broad and contains a fossa on its lateral side in *Pinnarctidion bishopi.* I view this expansion as a unique derived character in this species.

Zygomatic Process of Squamosal Deep. In most otariids, including all enaliarctines except for *Pinnarctidion bishopi,* the zygomatic process of the squamosal is elongate, relatively narrow, and tapered anteriorly. This is considered to be the primitive character state for the Otariidae. In *Pinnarctidion bishopi* the zygomatic process is deep dorsoventrally at its anterior extremity, and this is a unique derived character of the species.

Antorbital Process Present and Large. The only enaliarctine that has such a process is *Pinnarctidion bishopi.* Because this process is not present in primitive carnivorans or primitive enaliarctines, it is regarded as a unique derived character of *P. bishopi.*

Paroccipital-mastoid Crest Broad. As in generalized carnivorans, the mastoid and paroccipital processes of *Enaliarctos mealsi* are separate. This is the primitive condition. In other enaliarctines, the two processes are joined to varying degrees by a shelf of bone between them, and this shelf is broad and forms a crest in *Pinnarctidion bishopi.* The presence of a crest is the derived condition.

Interorbital Region Narrow. Generalized carnivorans have a broad interorbital region, which is defined as that part of the cranium across the dorsal surfaces of the frontal bones between the orbits. The interorbital breadth is enhanced by the presence a broad, triangular supraorbital process of the frontal, which has a ridge extending posteroventrally from it that demarcates the posterior margin of the orbit. This is the primitive condition for the Carnivora. In most pinnipeds, the interorbital region is variably narrow, and this is commonly associated with enlargement of the orbits and reduction or loss of the supraorbital process of the frontal. The primitive condition for the Otariidae and the Enaliarctinae appears to be a moderately broad interorbital region with very small but broadly triangular supraorbital processes, such as exists in *Pacificotaria hadromma.* The most derived state of this character among the enaliarctines exists in *Enaliarctos mitchelli* and *Pinnarctidion bishopi,* in which the interorbital region is very narrow, virtually parallel sided, and merges with the narrow intertemporal region. In other enaliarctines, for example in both species of *Pteronarctos* and in *Enaliarctos mealsi,* the degree of constriction of the interorbital region is intermediate.

COMPARISONS WITH *PTERONARCTOS*

Among the known Enaliarctinae, *Pacificotaria* and *Pteronarctos* are the two most closely related genera; they have similar dentitions and basicrania, and it is primarily in the rostrum, anterior narial aperture, palate, orbit, and interorbital region that they differ. Both species of *Pteronarctos* differ from *Pacificotaria hadromma* by having a gracile and tapered rostrum, flat palate, small anterior naris, slender interorbital region, and non-protruding, laterally directed orbit, which is positioned farther posteriorly on the cranium. These characters, among others, serve to unite *Pteronarctos goedertae* and *P. piersoni* in one genus.

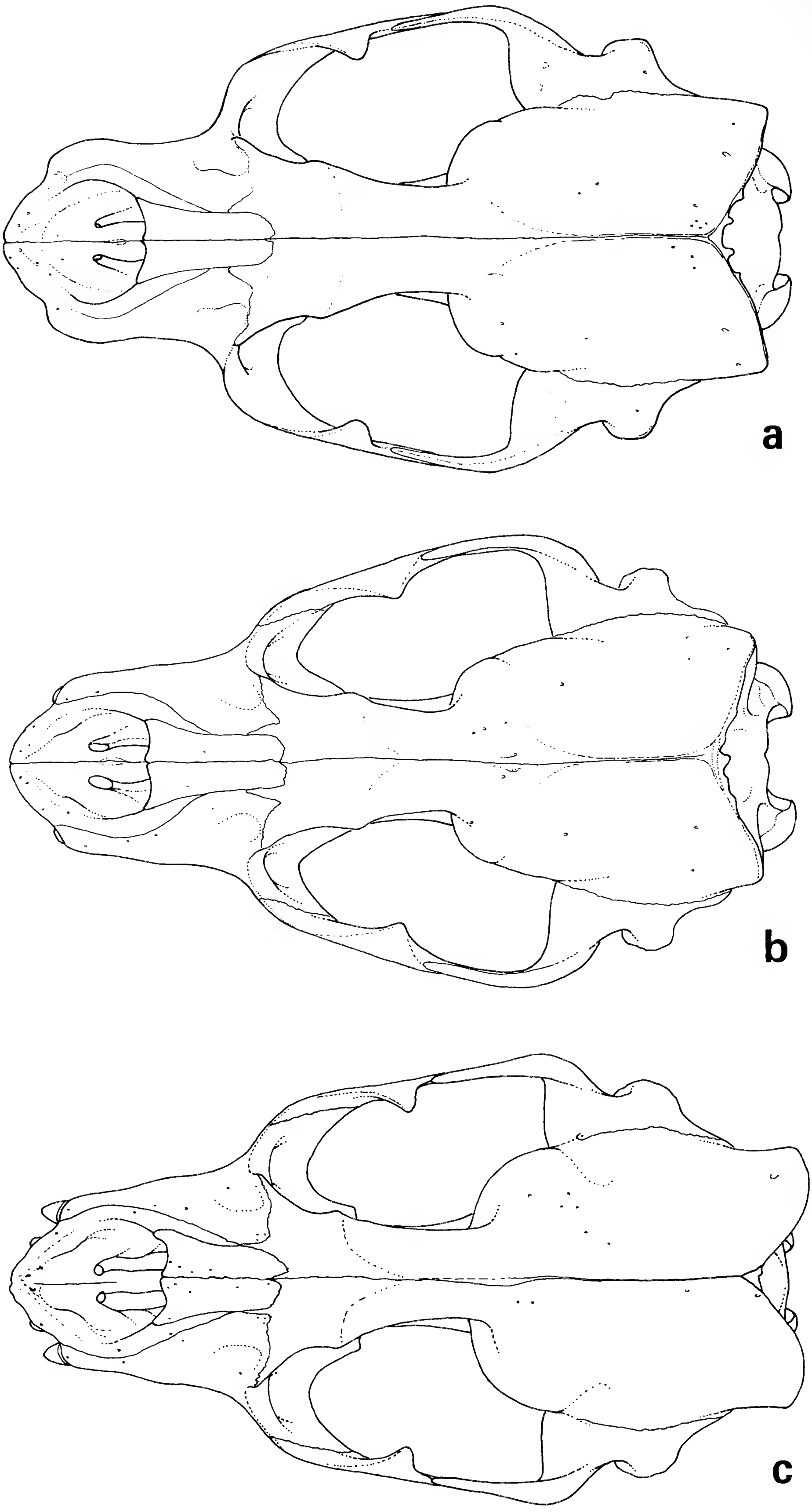
Autapomorphies of *Pacificotaria hadromma* in comparison with both species of *Pteronarctos* include rostrum shorter and transversely expanded distally around enlarged canine roots, enlarged anterior narial opening, larger infraorbital foramen, reduced P^4 crown size, vaulted palate, protuberant eyes positioned relatively farther anteriorly on the cranium, and bilobed posterior root on P^2. These characters, among others, are diagnostic for the genus *Pacificotaria.*

Pacificotaria hadromma differs from *Pteronarctos piersoni,* in addition to the characters that distinguish the two genera, in the following ways: a larger pterygoid process of the palate ventral to the orbit, mastoid-paroccipital crest larger and more sigmoid in shape, and an extension of the sagittal crest farther anteriorly onto the intertemporal part of the cranium.

Pacificotaria hadromma also shares a significant number of plesiomorphic cranial characters with *Pteronarctos piersoni,* which is the more primitive of the two species of *Pteronarctos.* These characters are interpreted to be primitive because they are present in generalized arctoid carnivores and *Enaliarctos mealsi* and/or are absent in the derived Otariidae. They include, but are not limited to deep nasolabialis fossa on the cheek, zygomatic arch curved dorsally, rostrum deep dorsoventrally, canine crown vertically oriented, palate short, bulla not extended appreciably anterior to glenoid fossa, tympanic bulla small and inflated mostly at the medial side so that it extends noticeably ventral to the level of the basioccipital, posterior root of M^1 distinctly bilobed, and occipital condyles projecting prominently from the occipital shield. These several characters shared between *Pteronarctos piersoni* and *Pacificotaria hadromma* indicate that the two species are probably close to the divergence between the two lineages that produced the two genera.

COMPARISONS WITH *ENALIARCTOS*

Although *Enaliarctos mealsi* is, on the whole, the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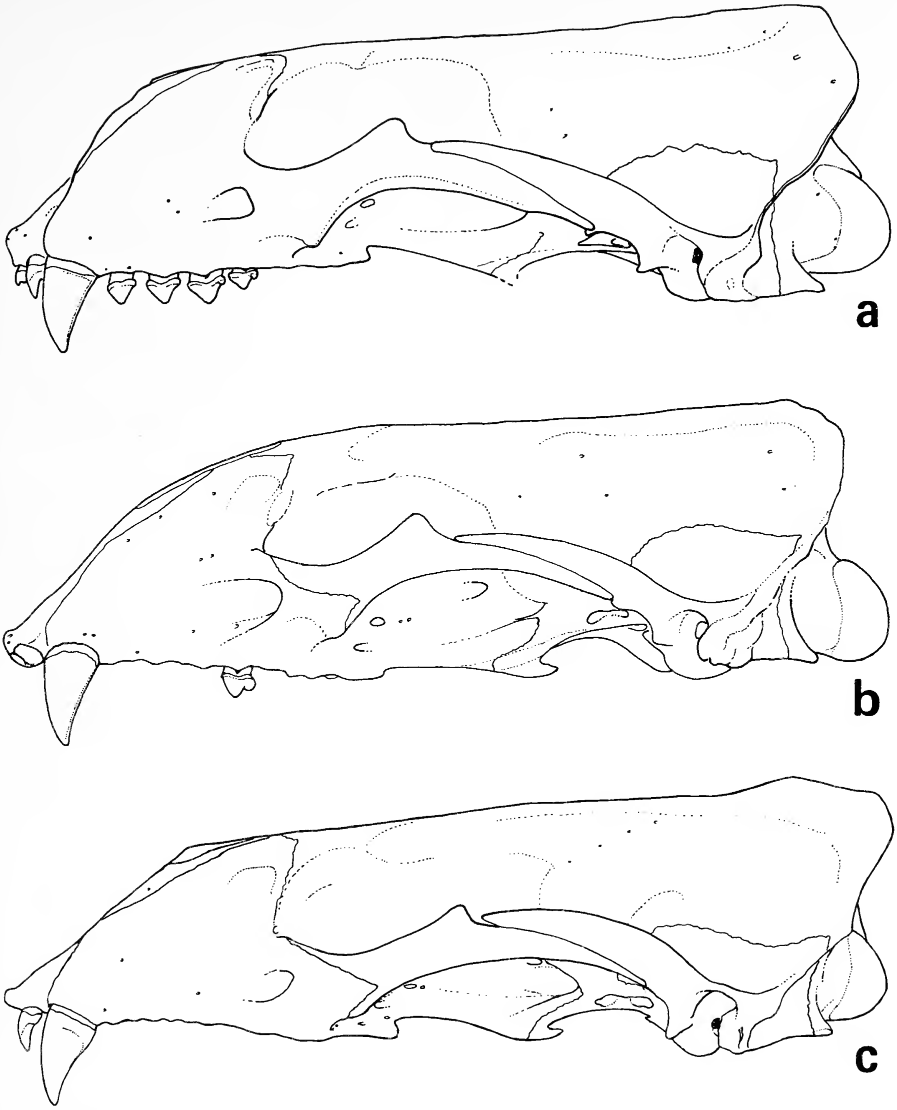

Figure 8. Comparative lateral views of crania of Enaliarctinae from the Astoria Formation: **a,** *Pacificotaria hadromma,* new genus and species; **b,** *Pteronarctos piersoni* Barnes, 1990; **c,** *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; b after Barnes, 1990:fig. 11a; c after Barnes, 1990:fig. 11b).

most primitive species of otariid pinniped yet described, *Pacificotaria hadromma* (as are both species of *Pteronarctos,* see Barnes, 1989:15, 1990:19) is more primitive than *E. mealsi* in the following ways: posterior extension of the palate ventral to the choana shorter, posterior lacerate foramen smaller, and M^2 alveolus larger. Until and unless evolutionary reversals of these characters are indicated in the fossil record of enaliarctines, and for the sake of parsimony, the presence of these primitive characters in *Pacificotaria hadromma* excludes any known species of *Enaliarctos* from consideration as an ancestor of *P. hadromma.*

The generally primitive nature of *P. hadromma* is demonstrated by the plesiomorphies that it shares with *Enaliarctos mealsi.* These include the presence of a preglenoid process on the anterolateral border of the glenoid fossa, the bilobed posterior root on M^1, vertically oriented upper canines, narrow zygomatic process of the squamosal, and narrow pterygoid strut between the palate and the basicranium.

Most of the ways in which *Pacificotaria had-*

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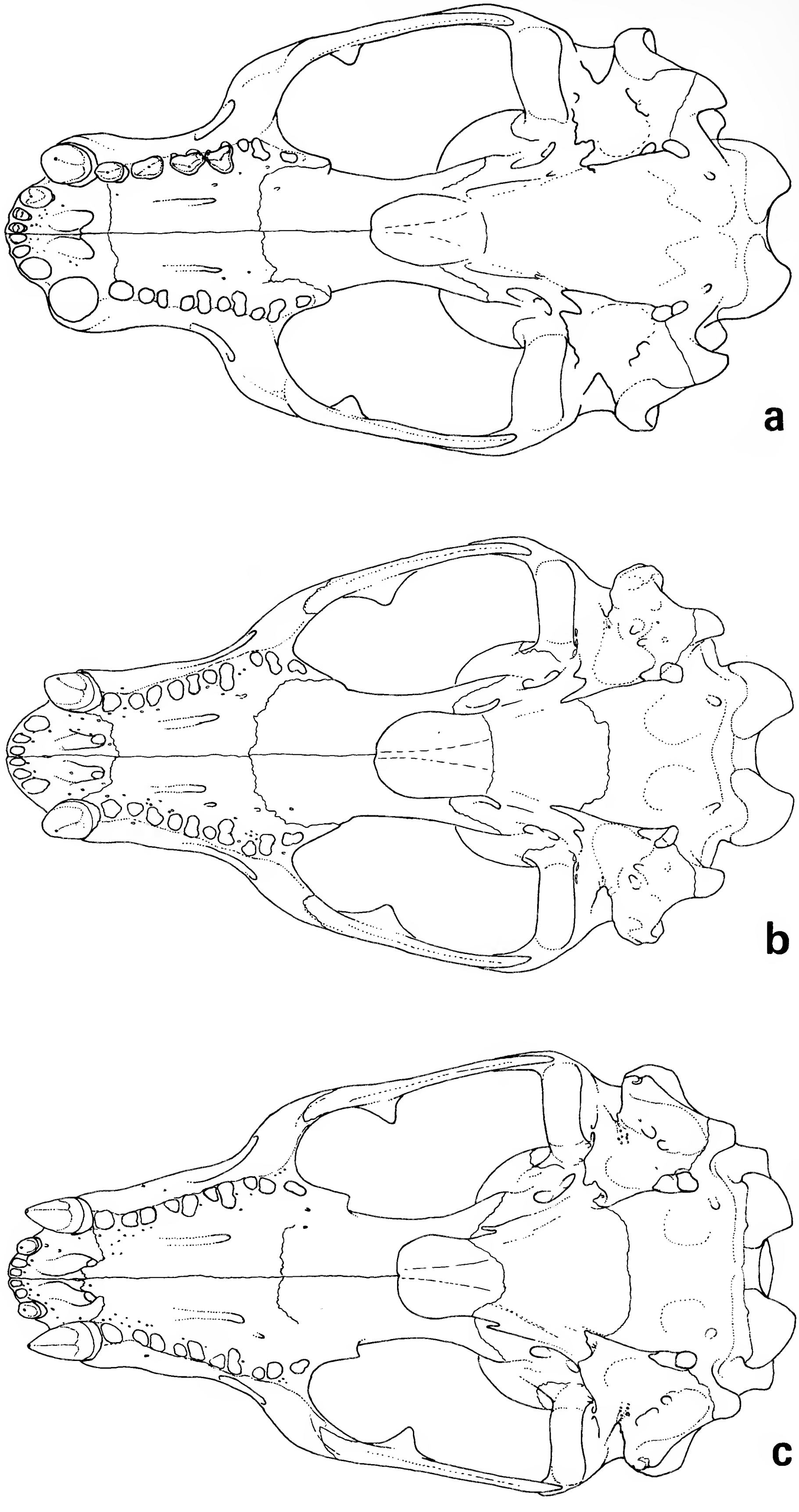
Figure 7. Comparative dorsal views of crania of Enaliarctinae from the Astoria Formation: **a,** *Pacificotaria hadromma,* new genus and species; **b,** *Pteronarctos piersoni* Barnes, 1990; **c,** *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; b after Barnes, 1990:fig. 3; c after Barnes, 1989:fig. 2).


a
b
c

romma differs from species of *Enaliarctos*, however, are in its apomorphic characters. In *P. hadromma* the rostrum is wider, the canines larger, the mastoid-paroccipital crest larger, and the cheek tooth row straighter and more nearly homodont. All of these are apomorphies of *P. hadromma* based on comparisons with primitive carnivorans, and, therefore, are also apomorphies in relation to *Enaliarctos mealsi*. Therefore, as I have also concluded previously for *Pteronarctos* (see Barnes, 1989: fig. 9; 1990:19), and for similar reasons, although *Pacificotaria* may share a relatively close common ancestry with *Enaliarctos*, each has a suite of autapomorphies that excludes either taxon from being an ancestor of the other.

COMPARISONS WITH AND RELATIONSHIPS TO SELECTED OTHER OTARIID GROUPS

I have previously suggested that *Pteronarctos* might be near the ancestry of modern fur seals and sea lions of the subfamily Otariinae (Barnes, 1989, 1990). Although in its overall cranial proportions and morphology, its enlarged orbits, and transversely bifid I$^{1-2}$ crowns, *Pacificotaria hadromma* resembles the generalized Otariinae such as *Pithanotaria starri* Kellogg, 1925, and Recent fur seals of the genera *Arctocephalus* and *Callorhinus* Gray, 1859, its cranial details indicate that it is a highly evolved enaliarctine with unique derived characters that would exclude it from the ancestry of the Otariinae. Such derived characters, not present in the primitive or generalized Otariinae include a vaulted palate, transversely expanded rostrum, enlarged canines, greatly enlarged anterior narial opening, protruding and anterodorsally directed orbits, and protocone and transversely expanded posterior root on the P$^{2-3}$.

Neotherium mirum Kellogg, 1931, a small Middle Miocene pinniped from the Sharktooth Hill Bonebed in California, has been classified as a primitive imagotariine (Repenning and Tedford, 1977; Barnes, 1989). The definitive cranial fossils that demonstrate its distinction from *Pacificotaria hadromma* remain to be published; however, I have previously (Barnes, 1989:13–14) listed cranial features that distinguish *N. mirum* from *Pteronarctos goedertae*. I have also assigned *Prototaria primigena* Takeyama and Ozawa, 1984, a Middle Miocene pinniped from Japan, to the Imagotariinae, suggesting that it is close to or congeneric with *Neotherium mirum*. The same distinctions that separate *Pteronarctos goedertae* and *Prototaria primigena* also apply to *Pacificotaria hadromma* and, in fact, many of these characters may serve to distinguish the Enaliarctinae from the Imagotariinae.

DENTITION OF *PACIFICOTARIA HADROMMA*

The dentition of the holotype of *Pacificotaria hadromma* is the most complete of any enaliarctine specimen that has yet been described. Although only the I^{3}, canine, and P^{4} are known for species of *Pteronarctos*, the sizes, shapes, and distribution of alveoli of the available specimens indicate that the dentitions of species of *Pteronarctos* and of *Pacificotaria hadromma* were probably quite similar.

The I$^{1-2}$ of *Pacificotaria hadromma* are the first such teeth documented among the enaliarctines. As in the later Otariinae, the crowns of these teeth are transversely bifid. Because I$^{1-2}$ with bifid crowns are present in the Enaliarctinae and Otariinae, the character is probably primitive for the Otariidae. The medial incisors are lost from most fossil pinniped crania in museum collections, and these teeth are worn flat on the holotype of *Imagotaria downsi* Mitchell, 1968, and are not preserved on published fossils of the Dusignathinae and Allodesminae.

Pacificotaria hadromma has bilobed posterior roots on P$^{2-3}$, and these teeth have posterolingually expanded crowns. The bilobed posterior root and posterolingual protuberance are more developed on the P^{3} than on the P^{2}. These are derived characters because they are absent in *Enaliarctos mealsi* (as well as *E. mitchelli*, based on the alveolar shapes) and absent in generalized or primitive carnivorans, animals in which the P$^{2-3}$ have a transversely compressed crown and a posterior root that is circular in cross section, much like the anterior root of each tooth. It appears that the condition of the P$^{2-3}$ of *Pacificotaria hadromma* has arisen through a process of molarization (as defined by Hershkovitz, 1971:99), with the result that these medial premolars have acquired structures that are neomorphs. These structures are analogous to the protocone and the root above it on the P^{4} of generalized carnivorans and of species of *Enaliarctos*.

This molarization of the medial premolars of *P. hadromma* accompanies degeneration (as per the definition of Hershkovitz, 1971:99) of the P^{4}, its paracone becoming the principal cusp, with the result that the P^{4} is more like the P^{3}. This results in a gradational transition from the P^{4} to the P$^{3-2}$ and creates a near homodont condition. This type of near homodonty in *Pacificotaria hadromma*, however, is the opposite of that that more typically evolved in most otariid groups (subfamilies Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusignathinae, and Odobeninae). In the typical homodonty seen in these groups, the P^{4} and molars become progressively premolariform through degeneration (see Barnes, 1989:11–12). In

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Figure 9. Comparative ventral views of crania of Enaliarctinae from the Astoria Formation: **a,** *Pacificotaria hadromma*, new genus and species; **b,** *Pteronarctos piersoni* Barnes, 1990; **c,** *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; b after Barnes, 1990:fig. 9; c after Barnes, 1989:fig. 6).

this process, the posterior and medial roots of the P^4 and M^1 unite, forming one bilobed root, which then becomes round in cross section. Ultimately each tooth from P^2 through M^2 becomes premolariform and has but one single root and a crown that approaches the form of a single-cusped cone resembling that of the P^1.

CLASSIFICATION

The following classification, showing the position of *Pacificotaria* within the subfamily Enaliarctinae, is modified from Barnes (1990:19). The genus *Enaliarctos* is listed first because it has the greatest number of primitive characters. Overall, *Pacificotaria hadromma* is more primitive than either species of *Pteronarctos.*

Family Otariidae Gill, 1866
  Subfamily Enaliarctinae Mitchell and Tedford, 1973
    Enaliarctos Mitchell and Tedford, 1973
      Enaliarctos mealsi Mitchell and Tedford, 1973
      Enaliarctos mitchelli Barnes, 1979
    Pacificotaria, new genus
      Pacificotaria hadromma, new species
    Pteronarctos Barnes, 1989
      Pteronarctos piersoni Barnes, 1990
      Pteronarctos goedertae Barnes, 1989
    Pinnarctidion Barnes, 1979
      Pinnarctidion bishopi Barnes, 1979

INFERENCES ABOUT APPEARANCE, BIOLOGY, AND BEHAVIOR OF *PACIFICOTARIA HADROMMA*

The sagittal crest, prominent nuchal crest, rugose dorsal cranial surface, proportionally large canines, and general massiveness of structure of the cranium are secondary male sex characters and indicate that the holotype of *P. hadromma* is from a male. Sexual dimorphism is present in adult males of all living otariids, and there is indication that it existed in virtually all fossil species for which we thus far have informative material (see Mitchell, 1966; Barnes, 1972, 1979, 1989; Repenning and Tedford, 1977). (For examples of male cranial secondary sex characteristics in Recent Otariinae see Murie, 1874:pl. 77, figs. 12–21 (partly reproduced with modifications by Scheffer, 1958:pl. 1); and Odell, 1981:fig. 4.)

The presence of male secondary sex characteristics in the holotype of *P. hadromma* implies that the species was sexually dimorphic both in anatomy and in size. Sexual dimorphism among living otariids is related to complex breeding behavior and rookery utilization, and this type of life history may also include long periods of pelagic existence (see Bartholomew, 1970). If *Pacificotaria hadromma* was like living otariines, it may have formed harems, bred in rookeries, and spent long periods feeding at sea.

Considering that the holotype of *Pacificotaria hadromma* probably is a male, then based on comparative cranial lengths, the body size of the animal in life probably would have been slightly smaller than that of the Recent northern fur seal, *Callorhinus ursinus* (Linnaeus, 1758). The snout of *P. hadromma* is proportionally about as short as that of some Recent species of *Arctocephalus* (for example, *A. galapagoensis* (Heller, 1904), *A. australis* (Zimmerman, 1783), *A. forsteri* (Lesson, 1828)). The snout is relatively wide, however, and the fleshy nose (rhinarium) was probably wide and somewhat flat, possibly like that of the gray seal, *Halichoerus grypus* (see King, 1983:photo on p. 78). The forehead was relatively flat (accentuated by the sagittal crest being low and located posteriorly), and the orbits were relatively protuberant and anterodorsally directed.

The dentition and cranial proportions of *Pacificotaria hadromma* are similar to those of *Pteronarctos piersoni* and, like that species, *Pacificotaria hadromma* may have been able to catch and eat squid or crustaceans, but the major part of its diet, like that of most of the Recent Otariinae, probably was fish (see Barnes, 1990:15). I have previously commented on the possible environmental conditions at the time and place of fossilization of *Pteronarctos piersoni* and on the associated marine and terrestrial vertebrates (see Barnes, 1990:15). The same conditions would also apply to *Pacificotaria hadromma.*

The same strata that yielded the holotype of *Pacificotaria hadromma* also produced the type material of another enaliarctine, *Pteronarctos piersoni* Barnes, 1990, and a referred specimen of the large desmatophocine otariid, *Desmatophoca oregonensis* Condon, 1906. Thus, otariids representing at least three species in as many genera of otariid pinnipeds are found in this same stratigraphic interval of the Astoria Formation: *Pacificotaria hadromma, Pteronarctos piersoni,* and *Desmatophoca oregonensis.*

CONCLUSIONS

Rocks assigned to the Astoria Formation exposed in Lincoln County on the Oregon coast have yielded an important new primitive pinniped, *Pacificotaria hadromma,* new genus and species, belonging to the extinct subfamily Enaliarctinae of the carnivoran family Otariidae. The holotype of this species is a complete cranium from a relatively high stratigraphic level in the Astoria Formation, of early Middle Miocene age, *circa* 16 Ma. It is the fourth named species of otariid pinniped described from the Astoria Formation in coastal Oregon, three of which have been reported from the same stratigraphic interval in the formation: *Pacificotaria hadromma, Pteronarctos piersoni,* and *Desmatophoca oregonensis.* Such diversity among apparently sympatric early Middle Miocene pinnipeds indicates significant niche partitioning and/or seasonal migration of their populations at that time along the Oregon coast.

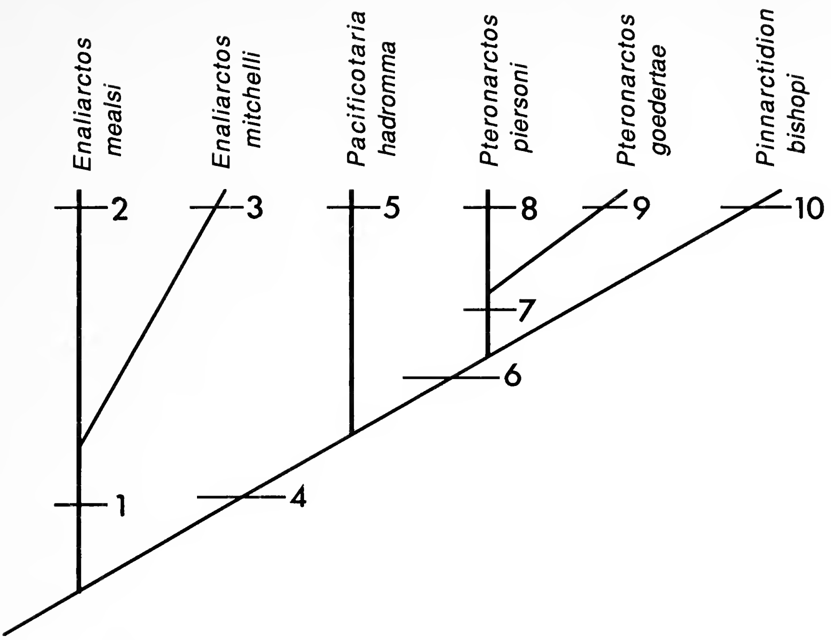

Figure 10. Cladogram showing relationships of enaliarctine species. Suites of derived characters uniting clades, discussed in the text and with their occurrences shown in Table 3, are as follows: 1) orbits enlarged, M^2 greatly reduced in size, palate extended posteriorly beneath choana; 2) infraorbital foramen moderately enlarged, nasolabialis fossa reduced and shallow; 3) zygomatic arch relatively straight, anterior narial opening enlarged, interorbital region narrow; 4) P^4 protocone reduced and located posteriorly, P^3 with protocone and bilobed posterior root, paroccipital process tabular and bent medially, all cheek teeth reduced in size; 5) cheek tooth row nearly straight, I^3 diameter increased, P^2 with protocone and bilobed posterior root, rostrum expanded transversely at canines, orbits protruding anterolaterally, infraorbital foramen enlarged, mastoid process expanded anteroposteriorly, anterior narial opening enlarged; 6) palate relatively flat; 7) rostrum lengthened, preglenoid process lost, nasolabialis fossa reduced and shallow; 8) infraorbital foramen enlarged, mastoid process expanded anteroposteriorly, ascending process of premaxilla shortened; 9) zygomatic arch relatively straight, occipital condyles broadly joining occiput, M^1 with single round posterior root, tympanic bulla extended anteriorly, nuchal crest projected over occipital shield; 10) zygomatic arch relatively straight, occipital condyles broadly joining occiput, orbits enlarged, M^2 greatly reduced in size, palate extended posteriorly beneath choana, cheek tooth row nearly straight, pterygoid process of palatine large, pterygoid strut expanded transversely, zygomatic process of squamosal deep, antorbital process present and large, paroccipital-mastoid crest broad, interorbital region narrow.

Pacificotaria hadromma is approximately the same size as species of *Enaliarctos* and *Pteronarctos,* and its unique suite of derived characters includes protuberant and anterodorsally directed orbits that are positioned relatively far anteriorly on the cranium, a large anterior narial opening, an exceptionally wide rostrum, a vaulted palate, molarized P^{2-3}, and nearly straight upper cheek tooth rows. *Pacificotaria hadromma* is otherwise a relatively generalized, primitive otariid, and although it has some characters that are convergent with some of the later members of the subfamily Otariinae (fur seals and sea lions), its derived characters show that it was not directly involved in the ancestry of these later otariid groups. It is in most characters more primitive than *Pteronarctos,* the most closely related genus, and has similar dental and basicranial characters. *Pacificotaria* may have a close common ancestry with *Pteronarctos* as well as with *Enaliarctos* and may represent a side branch of evolution within the subfamily Enaliarctinae.

The subfamily Enaliarctinae, as presently constituted, is a paraphyletic group, the most primitive subfamily of Otariidae. *Enaliarctos mealsi,* the most primitive enaliarctine, is paraphyletic, being defined only by primitive characters or by derived characters that occur elsewhere in the group as convergences. Enaliarctines include the geologically oldest known pinnipeds in the world, of which *E. mealsi,* of latest Oligocene to earliest Miocene age (*circa* 24 to 23 Ma), is still the oldest known species. Description of *Pacificotaria hadromma* demonstrates additional diversity of taxa in the subfamily Enaliarctinae, which now includes two species in the genus *Enaliarctos,* one in *Pacificotaria,* two in *Pteronarctos,* and one in *Pinnarctidion.*

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DECAPOD CRUSTACEAN LARVAE COLLECTED OFF NORTHERN CHILE DURING AN EL NIÑO EVENT (FEBRUARY–MARCH, 1983)

PEDRO BÁEZ R. AND JOEL W. MARTIN

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DECAPOD CRUSTACEAN LARVAE COLLECTED OFF NORTHERN CHILE DURING AN EL NIÑO EVENT (FEBRUARY–MARCH, 1983)

PEDRO BÁEZ R.[1,2] AND JOEL W. MARTIN[2]

ABSTRACT. Decapod crustacean larvae were sorted from plankton samples collected between Arica (18° 30′ S, 70° 20′ W) and Huasco (28° 30′ S, 71° 15′ W), a distance of about 1,050 km along the northern coast of Chile, from February 19 to March 28, 1983, during this century's strongest recorded El Niño event. The samples were taken from 11 east–west transects extending from near the coast (5 km offshore) to approximately 200 km offshore, each with 4 stations approximately 65 km apart. Larvae (nauplius, protozoea, zoea, or megalopa) from 22 species (17 genera, 15 families) were collected; most larvae were zoeae. Of the zoeal larvae, 1.8% were Dendrobranchiata and 98.2% were Pleocyemata. Among the Pleocyemata, the Brachyura were most abundant (88.0%), followed distantly by Anomura (9.9%), Caridea (1.8%), and Thalassinidea (0.2%). Grapsid and pagurid larvae were most numerous within the Brachyura and Anomura (respectively) and were the dominant taxa at coastal stations. The number of species found (22) is far fewer than the normal stock of 139 species (94 genera, 38 families) of decapod crustaceans recorded as adults for this area of northern Chile, although the lack of earlier sampling efforts precludes comparison with decapod larval fauna of non-El Niño years. Protozoeae and zoeae of oceanic species of the genera *Xiphopenaeus* (Penaeidae) and *Sicyonia* (Sicyoniidae), not previously recorded from Chilean waters, were also found. The presence of larvae of these tropical oceanic genera, and the high ratio in which other tropical families and species appeared, may be due to the effects of the strong El Niño event.

INTRODUCTION

Despite the importance of decapod crustaceans to Chile's economy, there are relatively few publications on Chilean marine decapods, especially the larval stages. Most studies dealing with the decapod fauna of the southeastern Pacific have focused on the biology of adults, and often these studies have been restricted to intertidal and shallow water species or are based on few specimens. Most of our knowledge concerning larval development of Chilean decapods is based on descriptions of the same species from other geographic areas. Studies of larval abundance in Chilean waters have been particularly limited geographically (e.g., Palma, 1976, 1980; Palma et al., 1976). Complete larval histories are known for very few species of decapods (see Quintana, 1981), and there have been few examinations of other faunal components of the Chilean plankton (e.g., Antezana, 1970, 1981; Fagetti, 1972) or of Chilean zooplankton community structure (see Fagetti and Fischer, 1964).

Even if the collecting deficit is overlooked, there is indeed a real pattern of lower diversity and lower endemism in the southeastern Pacific as compared to, for example, the western coast of North America (see Wicksten, 1989). Among the hypotheses proposed to explain this low diversity are certain faunistic extinctions in the eastern Pacific (Reaka and Manning, 1987) and the reduced oxygen concentration of waters over the continental slope of Peru and Chile (Rowe and Haedrich, 1979; Wicksten, 1989). Natural disturbances of the ecological conditions of the southern hemisphere have not been seriously considered as causes of the reduced diversity in this area.

The oceanic-atmospheric phenomenon known as El Niño Southern Oscillation (ENSO) is the planet's largest weather system. It introduces often dramatic change to the ecological and faunal conditions of the entire eastern Pacific (e.g., see Canby, 1984; Taft, 1985; Schoener and Fluharty, 1985, and articles in Oceanus 27(2), 1984). Distributions of benthic and pelagic Crustacea are undoubtedly affected by these very rapid and dynamic changes (Arntz and Valdivia, 1985a).

The 1982–1983 El Niño event was unprecedented in strength and impact (Canby, 1984). In Chile, the effects were felt as far south as Concep-

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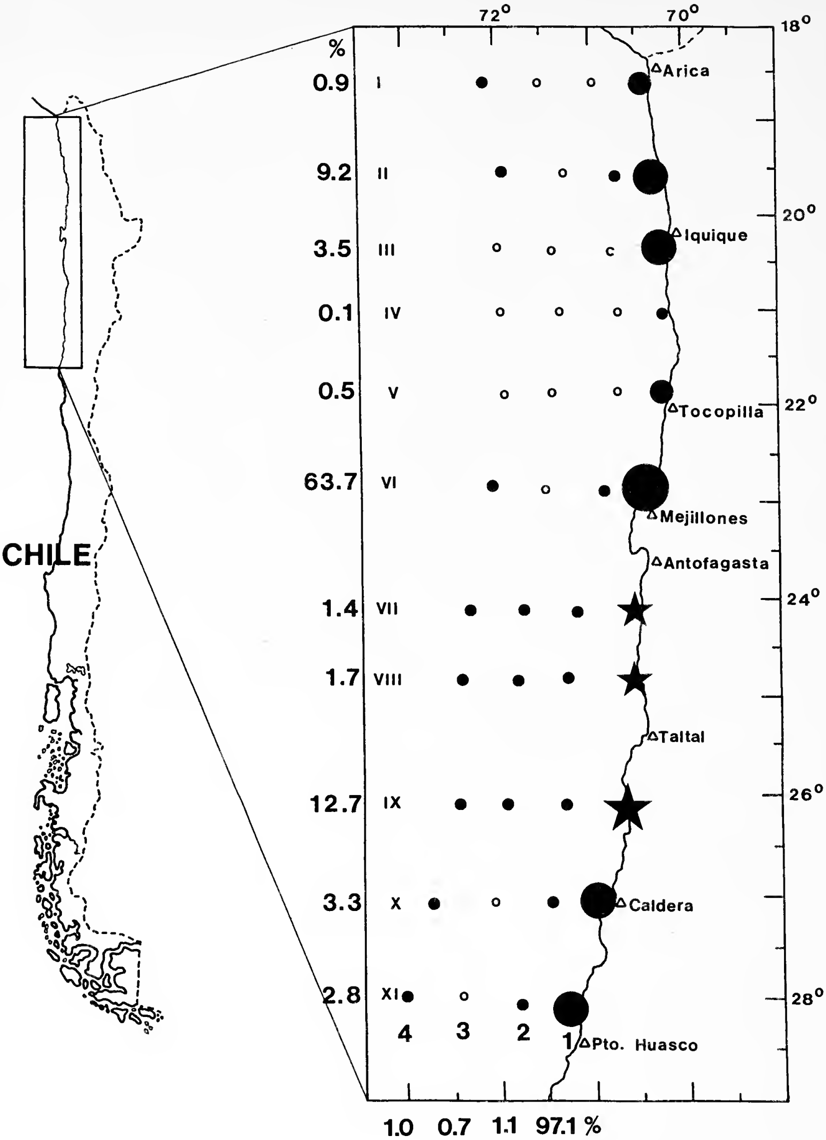

Figure 1. Area of northern Chile covered by cruise Sela I of the Chilean R/V *Itzumi* during the 1982–1983 El Niño event (February–March, 1983). Roman numerals = transect numbers; arabic numerals 1–4 (near bottom of figure) = stations (1 = coastal, 4 = oceanic). Numbers to left of transects are percentages of the total abundance of that transect (stations combined); numbers at bottom of figure are percentage totals by station. Legend for individual station symbols: open circle = 0–0.09% of total abundance; small dot = 0.1–0.4%; medium small dot = 0.5–0.9%; small star = 1.0–1.9%; medium large dot = 2–10%; large star = more than 10%; large dot = more than 50% (transect VI, station 1).

ción (36° 40′ S) (Gallardo, 1985). Among the observations stemming from a 1983 Ecuadorian workshop were positive (Arntz, 1984) and negative (Tsukayama and Santander, 1987) effects on the Peruvian ecosystem, including reduction of biomass of invertebrates from the continental shelf of Peru, species immigrations, increases in the distributions of some benthic invertebrates of the shelf and in their production, and expanded migration in coastal waters of tropical invertebrates. Most crabs diminished along the southern littoral zone of Peru, but in the north there was a strong increase in shrimp production and an invasion of portunid crabs (Arntz and Valdivia, 1985b). Similar distributional anomalies (i.e., increases as well as decreases in abundance) were reported recently by Lavaniegos-Espejo and Lara-Lara (1990) for zooplankton in the Gulf of California.

The Instituto de Fomento Pesquero (IFOP) organized a national workshop on El Niño that was held in Santiago, Chile, in November, 1984 (Investigación Pesquera, Chile, 1985). The plankton composition during El Niño 1982–1983 was reported in two papers, IFOP (1984) and Rojas and Orellana

(1984). Both papers focused on the biomass and abundance of zooplankton and on qualitative composition of the zooplankton exploited for economic purposes. The present paper draws from data collected by both studies. Additionally, Mendez (1987) presented an overview of the effects on Chile's fisheries, noting that ENSO 1982–1983 was detected in Chile about August–September, 1982, reaching its greatest intensity during February, 1983. The effects on Chilean decapod resources were reviewed by Mendez (1987), who noted that crab production increased during 1982–1983 by a remarkable 463% over previous years, constituting 9,142 tons (about 11%) of the yearly total of some 40,000 tons of commercially harvested crustaceans (two species of galatheids, *Pleuroncodes monodon* and *Cervimunida johni,* together constituted about 43%, while the "camaron nylon," *Heterocarpus reedi,* accounted for another 16%). Mendez (1987) noted the scarcity of information on the distribution of planktonic organisms during non-ENSO years that would allow comparisons of ENSO and non-ENSO zooplankton composition.

In this paper we document the distribution of the Chilean larval decapod fauna during the strong ENSO event of 1982–1983. These data will provide a backdrop for future comparisons with zooplankton composition and distribution patterns during ENSO's of varying magnitudes and will serve as a reference point for comparing the composition of the southeastern Pacific plankton in non-ENSO years.

MATERIALS

Forty-four plankton samples were collected by the Chilean R/V *Itzumi* (Cruise Sela I), along 11 parallel east–west transects (4 stations each) between 18° 38′ 00″ S and 28° 04′ 00″ S from near the coast (5 km offshore) to about 200 km west, from 19 February to 28 March, 1983 (Fig. 1). The 11 parallel transects were approximately 105 km apart (on average), spanning a distance of approximately 1,050 km along the northern coast of Chile, with the 4 stations per transect approximately 65 km apart (Fig. 1). The total study area was therefore approximately 210,000 km^2. Samples, taken while the ship was stationary, were collected with a cylindric-conic net type WP-2 (UNESCO, 1968) with an internal mouth diameter of 57 cm, a total length of 261 cm, and a mesh size of 300 μm. At each station the net was deployed with 100 m of line, but the actual depth reached by the net (estimated by depth recorder) varied from close to 100 m (98.8 m, Station 10.1) to almost 74 m (Station 6.1). The amount of water filtered was estimated using a flow-meter placed at the net mouth, following the methods of Smith and Richardson (1979). The average amount of water filtered was 0.36 ± 0.09 m^3 per vertical meter of water (IFOP, 1984). Additional details on collecting techniques and cruise data are available in the technical reports of the IFOP (1984), in Rojas and Orellana (1984), and from the senior author. Specimens were preserved in 5% formalin prepared with seawater. After removal of fish larvae (Rojas and Orellana, 1984) each sample was split and quartered using a Folsom apparatus. Decapod larvae were removed from two of the 25% aliquots, and quantitative estimates were calculated

Table 1. Summary of decapod crustacean families, and numbers of genera and species, reported as adults from the area of study.

Families[1]	No. of genera[2]	No. of species[2]
Suborder Dendrobranchiata		
*Penaeidae	3 (2)†	3 (2)†
*Sicyonidae	0 (1)†	0 (1)†
*Sergestidae	1 (1)	1 (1)
Suborder Pleocyemata		
Infraorder Caridea		
*Oplophoridae	4 (1)	7 (1)
Pasiphaeidae	1	1
Rhynchocinetidae	1	1
Palaemonidae	1	1
*Alpheidae	3 (1)	4 (1)
Hippolytidae	3	3
Pandalidae	1	1
*Crangonidae	2 (1)	2 (1)
Glyphocrangonidae	1	2
Infraorder Astacidea		
Nephropidae	1	1
Infraorder Thalassinidea		
*Callianassidae	1 (1)	1 (1)
Infraorder Palinura		
Polychelidae	1	2
Infraorder Anomura		
Coenobitidae	1	1
Diogenidae	1	2
Lithodidae	5	9
*Paguridae	1 (1)	4 (2)
Parapaguridae	1	3
Chirostylidae	1	1
*Galatheidae	2 (1)	9 (1)
*Porcellanidae	5 (1)	14 (1)
Albuneidae	2	2
*Hippidae	1 (1)	2 (1)
Infraorder Brachyura		
Homolodromiidae	1	1
Calappidae	2	2
Leucosiidae	1	1
Majidae	10	11
Hymenosomatidae	1	1
*Atelecyclidae	3 (1)	5 (1)
*Cancridae	1 (1)	4 (2)
Corystidae	3	3
Portunidae	4	4
Platyxanthidae	1	2
*Xanthidae	10 (1)	10 (1)
*Grapsidae	9 (2)	10 (5)
Pinnotheridae	4	5
Ocypodidae	2	5
Total 39 (15)	96 (17)	141 (22)

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[1] * = Collected as larvae during 1983 El Niño event.

[2] Numbers in parentheses are totals collected during El Niño. † = Not previously recorded.

Table 2. Families, genera, and species of decapod larvae collected, larval stage collected, and distribution by transect and station, 1983 El Niño event. Larvae listed under genus only possibly do not belong to same species.

Taxon	Larval stage	Transect and station
Suborder Dendrobranchiata		
Family Penaeidae		
Xiphopenaeus	Protozoea	9.4
Penaeus	Protozoea I	6.2, 6.4, 8.2
	Protozoea II	11.1
	Mysis I	1.4, 9.1
Family Sicyoniidae		
Sicyonia	Zoea, final stages	3.1, 3.4
Family Sergestidae		
Sergestes + *Sergia* (indistinguish.)	Protozoea I	11.1
	Protozoea II	10.4
	Protozoea III	6.2, 6.4, 8.3, 8.4
	Zoea I	1.4, 2.6, 3.2, 6.2, 7.1
	Zoea II	7.4
	Post larva	2.4, 5.1, 5.3, 6.4, 7.2, 7.4, 8.1, 9.2, 9.3, 9.4, 10.3, 10.4, 11.2
Suborder Pleocyemata		
Infraorder Caridae		
Family Oplophoridae		
Acanthephyra	Zoea, final stages	3.1, 6.1
Family Alpheidae		
genus indet.	Zoea, final stage	6.1
Family Crangonidae		
genus indet.	Zoea, int. stages	3.1, 5.1, 6.1, 8.1, 8.4, 9.1, 10.1, 10.2, 10.4, 11.1, 11.2, 11.4
Infraorder Thalassinidae		
Family Callianassidae		
Callianassa	Zoea, final stages	5.1, 6.1, 9.1, 11.1
Infraorder Anomura		
Family Paguridae		
genus indet.		
sp. "A"	Zoea I	6.1, 9.1
	Zoea II	2.1, 6.1, 8.1, 8.3
sp. "B"	Zoea II	3.1, 4.1, 5.1, 6.1, 7.1, 8.1, 9.1, 10.1, 11.1
	Zoea III	11.1
	Megalopa	1.1, 2.1, 4.1, 7.1, 10.1
Family Galatheidae		
Pleuroncodes	Zoea I	6.1, 11.1
	Zoea II	3.1, 11.1
Family Porcellanidae		
genus indet.	Zoea I	11.1
	Zoea III	9.1, 11.1
Family Hippidae		
genus indet.	Zoea I	1.1, 2.1, 3.1, 6.1, 7.3
	Zoea II	11.1
	Zoea III	7.3, 8.1, 9.1
	Zoea IV	4.1

Table 2. Continued.

Taxon	Larval stage	Transect and station
Infraorder Brachyura		
Family Atelecyclidae		
genus indet.	Zoea I	2.1, 3.1
	Zoea II	2.1, 3.1, 6.1
	Zoea III	11.2
Family Cancridae		
Cancer sp. "A"	Zoea I	1.1, 1.2, 2.1, 5.1, 11.1
	Zoea II	1.1, 8.1, 11.1
	Zoea III	3.1, 11.1
C. edwardsii	Zoea I	3.1, 6.1, 9.1, 11.1
	Zoea II	2.1, 6.1, 10.2
	Zoea III	2.3, 7.1, 7.3, 10.1, 10.2, 11.1
	Zoea IV	7.3, 8.2, 9.4
	Zoea V	2.1, 2.2
Family Xanthidae		
Homalaspis plana	Zoea I	3.1, 8.1
	Zoea III	3.1, 8.1
	Zoea IV	3.1, 8.1
Family Grapsidae		
Cyclograpsus punctatus	Zoea I	2.1, 6.1, 9.1
	Zoea II	2.1, 6.1, 8.1, 9.1
	Zoea III	2.1, 6.1, 6.2, 9.1, 9.2, 10.1, 10.2
	Zoea IV	2.1, 7.2
	Zoea V	2.2
genus indet.		
sp. "A"	Zoea I	3.1
	Zoea II	3.1
	Zoea III	3.1, 5.1
sp. "B"	Zoea I	1.1
	Zoea II	3.1
sp. "C"	Zoea II	3.1, 4.1, 6.1, 11.1
sp. "D"	Zoea I	6.1
	Zoea II	6.1

Table 3. Abundance of decapod crustacean larvae per 1,000 m^3 by transect and station, 1983 El Niño event.

Transects	Stations[1]				Average per station	Total per transect	%
	1	2	3	4			
1	2,467 (0.8)	129 (0)	—	232 (0.1)	707.0	2,828	0.9
2	27,627 (9.0)	266 (0.1)	149 (0)	240 (0.1)	7,070.5	28,282	9.2
3	10,471 (3.4)	122 (0)	—	129 (0)	2,680.5	10,722	3.5
4	391 (0.1)	—	—	—	97.8	391	0.1
5	1,517 (0.5)	—	128 (0)	—	411.2	1,645	0.5
6	193,823 (63.4)	448 (0.1)	—	344 (0.1)	48,653.8	194,615	63.7
7	3,322 (1.1)	246 (0.1)	442 (0.1)	251 (0.1)	1,065.3	4,261	1.4
8	3,474 (1.1)	268 (0.1)	1,032 (0.3)	381 (0.1)	1,288.8	5,155	1.7
9	37,628 (12.3)	264 (0.1)	286 (0.1)	543 (0.2)	9,678.3	38,721	12.7
10	8,028 (2.6)	1,255 (0.4)	141 (0)	835 (0.3)	2,564.8	10,259	3.3
11	8,099 (2.6)	387 (0.1)	—	230 (0.1)	2,179.0	8,716	2.8
Total	296,847	3,385	2,178	3,185	6,945.3	305,595	100.0
%	97.1	1.1	0.7	1.0		100.0	

[1] Number (%).

Table 4. Abundance of decapod larvae (per 1,000 m^3) by family, 1982–1983 El Niño event.

	Stations[1]								
Categories	1.1	1.2	1.4	2.1	2.2	2.3	2.4	3.1	3.2
Suborder Dendrobranchiata									
Family Penaeidae	—	—	116 (9.0)	—	—	—	—	—	—
Family Sicyoniidae	—	—	—	—	—	—	—	209 (61.8)	—
Family Sergestidae	—	—	116 (2.9)	—	—	—	240 (6.1)	—	122 (3.1)
Suborder Pleocyemata									
Family Oplophoridae	—	—	—	—	—	—	—	314 (68.1)	—
Family Alpheidae	—	—	—	—	—	—	—	—	—
Family Crangonidae	—	—	—	—	—	—	—	105 (2.2)	—
Family Callianassidae	—	—	—	—	—	—	—	—	—
Family Paguridae	176 (0.7)	—	—	533 (2.0)	—	—	—	314 (1.2)	—
Family Galatheidae	—	—	—	—	—	—	—	105 (5.9)	—
Family Porcellanidae	—	—	—	—	—	—	—	—	—
Family Hippidae	176 (12.8)	—	—	107 (7.8)	—	—	—	105 (7.6)	—
Family Atelecyclidae	—	—	—	107 (9.1)	—	—	—	209 (17.7)	—
Family Cancridae	1,586 (12.2)	129 (0.1)	—	533 (4.1)	133 (1.0)	149 (1.1)	—	314 (2.4)	—
Family Xanthidae	—	—	—	—	—	—	—	419 (28.0)	—
Family Grapsidae	529 (0.2)	—	—	26,347 (10.6)	133 (<0.1)	—	—	8,377 (3.4)	—
Total	2,467	129	232	27,627	266	149	240	10,471	122
%	0.8	<0.1	0.1	9.0	0.1	<0.1	0.1	3.4	<0.1

	Stations								
Categories	3.4	4.1	5.1	5.3	6.1	6.2	6.4	7.1	7.2
Suborder Dendrobranchiata									
Family Penaeidae	—	—	—	—	—	112 (8.6)	115 (8.9)	—	—
Family Sicyoniidae	129 (38.2)	—	—	—	—	—	—	—	—
Family Sergestidae	—	—	89 (2.2)	128 (3.2)	—	224 (5.7)	229 (5.8)	138 (3.5)	123 (3.1)
Suborder Pleocyemata									
Family Oplophoridae	—	—	—	—	147 (31.9)	—	—	—	—
Family Alpheidae	—	—	—	—	147 (100.0)	—	—	—	—
Family Crangonidae	—	—	89 (1.9)	—	294 (6.2)	—	—	—	—
Family Callianassidae	—	—	89 (11.3)	—	441 (56.1)	—	—	—	—
Family Paguridae	—	195 (0.7)	357 (1.4)	—	17,206 (67.3)	—	—	969 (3.8)	—
Family Galatheidae	—	—	—	—	—	—	—	—	—
Family Porcellanidae	—	—	—	—	—	—	—	—	—
Family Hippidae	—	98 (7.1)	—	—	294 (21.3)	—	—	—	—
Family Atelecyclidae	—	—	—	—	735 (62.3)	—	—	—	—
Family Cancridae	—	—	89 (0.7)	—	5,294 (40.6)	—	—	277 (2.1)	—
Family Xanthidae	—	—	—	—	—	—	—	—	—
Family Grapsidae	98 (<0.1)	—	804 (0.3)	—	169,265 (68.1)	112 (<0.1)	—	1,938 (0.8)	123 (<0.1)
Total	129	391	1,517	128	193,823	448	344	3,322	246
%	<0.1	0.1	0.5	<0.1	63.4	0.1	0.1	1.1	0.1

[1] Numbers in parentheses are percentage contributions of a station (totaled vertically) and family (horizontal) to the total catch of 305,595 larvae.

by taking the average of these two subsamples and multiplying that figure by 4. Specimens of species well represented in each sample were dissected to confirm identification. Larval nomenclature follows that of Williamson (1982). A checklist (not included in this paper) of 139 species of decapod crustaceans reported from the area of study (northern Chile) was prepared using both the published literature and unpublished data of P. Báez R. Space limitations do not allow us to list all 139 species reported to occur in northern Chile or consulted references, many of which report single species descriptions or range extensions. A summary of the families and the number of genera and species per family is presented in Table 1. Many of the more important references consulted for compiling the faunal list are in Retamal (1981) and Wicksten (1989); special mention should be made of the extensive compilations of Chilean decapods by Holthuis (1952, macrurans), Haig (1955, anomurans), and Garth (1957, brachyurans). Identification of the 22 species represented by larvae (Table 2) was accomplished using published literature on the larval development of northern Chilean decapod species where possible. Those species for which larval stages have not been described, or that were new for the area, were identified from literature describing related taxa from other geographic areas. Important references used as starting points to identify larvae to a particular developmental stage or to higher taxonomic levels (e.g., superfamily or family) include the works of Williamson (1957a, b, 1960, 1982), Bourdillon-Casanova (1960), Gurney (1939, 1942), Hart (1971), Rice (1980), and Boschi (1981). For the classification of the decapod families we have followed Bowman and Abele (1982).

RESULTS

Few nauplii, megalopae, or protozoeae were found. Most larvae were zoeae (Table 1). Twenty-two species of decapods were identifiable in the collections,

Table 4. **Continued.**

Categories	Stations								
	7.3	7.4	8.1	8.2	8.3	8.4	9.1	9.2	9.3
Suborder Dendrobranchiata									
Family Penaeidae	—	—	—	134 (10.3)	—	127 (9.8)	316 (24.4)	—	—
Family Sicyoniidae	—	—	—	—	—	—	—	—	—
Family Sergestidae	—	251 (6.3)	120 (3.0)	—	387 (9.8)	127 (3.2)	—	132 (3.3)	286 (7.2)
Suborder Pleocyemata									
Family Oplophoridae	—	—	—	—	—	—	—	—	—
Family Alpheidae	—	—	—	—	—	—	—	—	—
Family Crangonidae	—	—	599 (12.6)	—	—	127 (2.7)	791 (16.6)	—	—
Family Callianassidae	—	—	—	—	—	—	158 (20.1)	—	—
Family Paguridae	—	—	838 (3.3)	—	—	—	4,427 (17.3)	—	—
Family Galatheidae	—	—	120 (6.7)	—	—	—	—	—	—
Family Porcellanidae	—	—	—	—	—	—	316 (31.6)	—	—
Family Hippidae	221 (16.0)	—	120 (8.7)	—	—	—	158 (11.5)	—	—
Family Atelecyclidae	—	—	—	—	—	—	—	—	—
Family Cancridae	221 (1.7)	—	120 (0.9)	134 (1.0)	—	—	1,107 (8.5)	—	—
Family Xanthidae	—	—	1,078 (72.0)	—	—	—	—	—	—
Family Grapsidae	—	—	479 (0.2)	—	645 (0.2)	—	30,355 (12.2)	132 (<0.1)	—
Total	442	251	3,474	268	1,032	381	37,628	264	286
%	0.1	0.1	1.1	0.1	0.3	0.1	12.3	0.1	0.1

Categories	Stations								Total	%
	9.4	10.1	10.2	10.3	10.4	11.1	11.2	11.4		
Suborder Dendrobranchiata										
Family Penaeidae	136 (10.5)	141 (10.9)	—	—	—	98 (7.6)	—	—	1,295	0.4
Family Sicyoniidae	—	—	—	—	—	—	—	—	338	0.1
Family Sergestidae	136 (3.4)	—	—	141 (3.6)	716 (18.1)	—	129 (3.3)	115 (2.9)	3,949	1.3
Suborder Pleocyemata										
Family Oplophoridae	—	—	—	—	—	—	—	—	461	0.1
Family Alpheidae	—	—	—	—	—	—	—	—	147	0
Family Crangonidae	—	704 (14.8)	314 (6.6)	—	119 (2.5)	1,366 (28.7)	129 (2.7)	115 (2.4)	4,752	1.6
Family Callianassidae	—	—	—	—	—	98 (12.5)	—	—	786	0.3
Family Paguridae	—	563 (2.2)	—	—	—	—	—	—	25,578	8.4
Family Galatheidae	—	—	—	—	—	1,561 (87.4)	—	—	1,786	0.6
Family Porcellanidae	—	—	—	—	—	683 (68.4)	—	—	999	0.3
Family Hippidae	—	—	—	—	—	98 (7.1)	—	—	1,377	0.4
Family Atelecyclidae	—	—	—	—	—	—	129 (10.4)	—	1,180	0.4
Family Cancridae	271 (2.1)	282 (2.2)	627 (4.8)	—	—	1,756 (13.5)	—	—	13,022	4.3
Family Xanthidae	—	—	—	—	—	—	—	—	1,497	0.5
Family Grapsidae	—	6,338 (2.5)	314 (0.1)	—	—	2,439 (1.0)	—	—	248,428	81.3
Total	543	8,028	1,255	141	835	8,099	387	230	305,595	100.0
%	0.2	2.6	0.4	<0.1	0.3	2.6	0.1	0.1		99.5

although several could be assigned only to family or genus with any certainty (Table 1). The few nauplii were not recorded numerically because of difficulties in identification. The greatest abundance of zoeae and megalopae occurred in transect 6, north of Mejillones, where the number of larvae constituted 63.7% of the total study collection (Table 3, Fig. 1). Transect 9, between Taltal and Caldera, and transect 2, to the north of Iquique, followed in abundance with 12.7% and 9.2%, respectively. In all other transects the abundance was relatively low, ranging from 3.5% (transect 3) to near 0.1% (transect 4) of the total catch. There was a steady decrease in the number of larvae from transect 9 southward, but there were no other obvious latitudinal patterns of abundance. Coastal stations had by far the greatest density, accounting for 97.1% of the total number of larvae collected. At the most offshore stations (Station 4 of each transect) the combined abundance reached only about 1%. Nine offshore stations (Stations 1.3, 3.3, 4.2, 4.3, 4.4, 5.2, 5.4, 6.3, and 11.3) did not yield any larvae, and on transect 4, near Punta Patache, only the coastal station yielded any specimens. The average abundance per station was 6,945 larvae per 1,000 m^3, but the range was great, from 193,823 (transect 6, Station 1) to zero larvae (9 stations). The lowest station average for any transect was 98 larvae (per 1,000 m^3) per station along transect 4. By transect, the average abundance was 27,781 larvae per 1,000 m^3, ranging from 194,615 (transect 6) to 391 (transect 4) larvae per 1,000 m^3.

Taxonomic diversity also decreased markedly from coastal to more oceanic stations (Table 4); all families were represented in at least 1 coastal station whereas only 5 families (penaeids, sicyoniids, sergestids, crangonids, and cancrids) were found in Station 4 samples combined for all 11 transects.

Little insight on the significance of larval distributions is possible without information on adults. A total of 139 species belonging to 38 families is known from this area of northern Chile. Of those 38 families, 2 (Penaeidae and Sergestidae) are in the Dendrobranchiata and the remaining 36 are in the Pleocyemata, distributed taxonomically as follows: Caridea (9 families, 22 species), Astacidea (1 family, 1 species), Thalassinidea (1 family, 1 species), Palinura (1 family, 2 species), Anomura (10 families, 47 species), Brachyura (14 families, 64 species) (summarized in Table 1).

In rather sharp contrast, only 22 species (17 genera, 15 families) were found as larvae. Thus larvae were found for only 15.8% of the total species pool and 39.5% of the available families. Among collected larvae, dendrobranchiates constituted only 1.8% of the total number of larvae and were represented by 3 families and 4 species; the additional (third) family, not previously recorded from off Chile, was the Sicyoniidae (larvae of *Sicyonia* sp.). Among the Pleocyemata larvae, which accounted for 98.2% of the total larvae collected, there were 12 families and 18 species, distributed as follows: Caridea (3 families, 3 species), Thalassinidea (1 family, 1 species), Anomura (4 families, 5 species), Brachyura (4 families, 9 species). The number of Pleocyemata species is about 14% of the number of adult species (16% of the genera and 37% of the families) reported for the study area. The finding of larvae of two previously unreported dendrobranchiate genera, *Xiphopenaeus* and *Sicyonia*, raises the number of species reported from northern Chile to 141 (96 genera, 39 families).

Among the Pleocyemata, brachyuran larvae were most abundant (88.0% of the total yield), followed distantly by anomurans (9.9%), carideans (1.8%), and thalassinideans (0.2%). Brachyuran and anomuran larvae were the most abundant taxa at coastal stations, with most belonging to species common in the study area as adults. Crabs of the family Grapsidae were by far the most abundant, accounting for 81.3% of all larvae collected. The most numerous anomurans were pagurids (8.4% of the total), while the most numerous of the shrimp families was the Crangonidae (1.6%); the lowest abundance was in the snapping shrimp family Alpheidae (less than 0.1%). For some taxa a wide sequence of larval stages was found (*Sergestes* + *Sergia* [inseparable], Crangonidae, Hippidae; Table 2), and for some of the brachyuran species almost the entire sequence of larval stages was collected. For some genera and families, the same stages were found over a wide range of stations (genera *Sergestes* + *Sergia*, *Cancer*, and *Cyclograpsus* and families Crangonidae, Paguridae, and Hippidae). For a few species, most notably the brachyurans *Cyclograpsus punctatus* and "Grapsidae species A," different stages of the larval sequence (zoea I, II, and III) were found at a single station.

DISCUSSION

The large difference between the number of decapod species collected as larvae (22) and the number in the species list for this region of northern Chile (139) could be the result of several factors. It is probable that a significant factor was the strong ENSO event of 1983, displacing normally occurring plankton to the south and introducing the typically tropical genera *Xiphopenaeus* and *Sicyonia*. However, the results of the ENSO event cannot be clearly separated from a variety of other factors. Because the samples were taken during a relatively short (2 month) period, it is probable that larvae of some species were not in the plankton during that time of the year. For example, in a study of similar duration, larval stages of only 43 species of crabs (many not identifiable to species) were found in extensive plankton tows taken during July, 1976, in the northern Gulf of Mexico (Truesdale and Andryszak, 1983). The species pool for crabs of this area is about 100 (Felder, 1973; Powers, 1977), so that only about 43% of the species were represented (or captured) as larvae during that time of year. Even under non-ENSO conditions, it is unlikely that more thorough plankton sampling would yield larvae of all species in a given geographic area, as evidenced by the 2-year study of Sandifer (1973) in Chesapeake Bay. Sandifer's study, with plankton tows made at variable depths and salinities in all seasons, yielded only 37 species of decapods in an area of rather high adult decapod diversity (over 300 species; Williams, 1984). Patchiness of plankton and the fact that some of the decapods in the species list are restricted to deep waters also must be considered.

With the above caveats taken into consideration, it is not possible to say to what extent the 1982–1983 ENSO event affected abundance and distribution of decapod larvae off the coast of northern Chile. However, McGowan (1984) noted that one salient feature associated with all ENSO events in California was a "vast reduction in macrozooplankton abundance and, nearshore, the widespread occurrence of some nekton, normally found to the south, off central Mexico"; McGowan's observations were based on one of the few long-term data bases, the time series of zooplankton, temperature, salinity, and oxygen readings from 1949 through 1969 in southern California (McGowan, 1984). Miller et al. (1985) estimated that in 1983 the zooplankton off the coast of Oregon, an area even more distant from the equatorial Pacific than is our study area, was "about 30% of that in non-El Niño years," and Soto (1985) noted that the general faunal diversity, including decapods, in waters off northern Chile decreased significantly during the event. That only 22 species, 2 of which belonged to tropical genera normally not found in Chilean waters, were found as larvae off the coast of northern Chile, with over 80% of the total catch accounted for by a single family (Grapsidae), is consistent with the above observed patterns of response to ENSO in the zooplankton community. The actual effect on the decapod plankton may have been more severe than our figures indicate. It is probable that some families and genera recorded by us as present off Chile are in fact represented by tropical or subtropical species, and not the species normally found here as adults.

The overall picture of faunal response to the 1982–1983 ENSO is complex and unclear. In most areas, the local commercial fauna was greatly altered, with entire fisheries collapsing and with virtually all important decapods disappearing. In other areas, there were increases in faunal diversity, albeit mostly because of the arrival of tropical or subtropical species. Off the coast of Peru, there were enormous increases in swimming crabs of the genus *Euphyplax,* octopi, scallops, polychaete and nemertean worms, rays, and bottom feeding fish, at least partly as a result of changes in oxygen content (Arntz, 1984). Concerning the zooplankton, there were mixed results during 1983–1984 (i.e., increases and decreases in zooplankton biomass) even within relatively small geographic areas, such as the Gulf of California. There, Lavaniegos-Espejo and Lara-Lara (1990) reported a drop in the zooplankton biomass in the spring of 1984 in the southern Gulf (compared with earlier years) but increases in the biomass in more northern stations in the Gulf.

Because some other faunal components of the planktonic and midwater environments depend heavily upon crustaceans as food (e.g., see Smith, 1985), it is possible that furthering our understanding of planktonic Crustacea during an ENSO event will enhance our understanding of the more general effects on coastal faunas. At the very least, it is necessary that sampling be conducted off Peru and Chile in non-ENSO years for comparisons with data of the present study and to establish "normal" patterns of decapod larval abundance and distribution.

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PACIFIC SLOPE CRETACEOUS BIVALVES OF THE GENUS *CALVA*

L. R. SAUL[1] AND W. P. POPENOE[2]

CONTENTS

ABSTRACT. *Calva* is the common, venerid bivalve genus of shallow water North American Pacific Slope Cretaceous deposits. Sixteen species placed in four subgenera range in age from Albian through latest Maastrichtian. Six species (*Calva heliaca,* new species, Cenomanian; *C. regina* Popenoe, 1937, Turonian; *C. campanae,* new species, late early to late Campanian; *C. peninsularis* (Anderson and Hanna, 1935), latest Campanian–early Maastrichtian; *C. varians* (Gabb, 1864), mid and late Maastrichtian; and *C. baptisia,* new species, latest Maastrichtian) constitute the typical subgenus and give it an age range of Cenomanian through Maastrichtian. Seven species (*Calva byblidis,* new species, early Albian; *C. nitida* (Gabb, 1864), late Albian-Cenomanian; *C. spissa,* new species, Turonian; *C. taffi* (Anderson, 1958), Coniacian-Santonian–earliest Campanian; *C. buttensis* (Anderson, 1958), early Campanian; *C. bowersiana*

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(Cooper, 1894), late early–late Campanian; and *C. crassa,* new species, early Maastrichtian) constitute the new subgenus *Egelicalva,* giving it an age range of Albian through early Maastrichtian. *Calva elderi,* new species, Coniacian, and *C. haggarti,* new species, Campanian, constitute the new subgenus *Microcalva,* and *Calva marina,* new species, late Campanian–early Maastrichtian, is type species of the new subgenus *Penecallista.*

Although there is no obvious directional change in the external morphologic features studied, there is evidence of a trend in hinge morphology in the evolutionary lineages of *Calva* that is apparently traceable through the Late Cretaceous.

The restricted age ranges of species in these lineages makes them useful in dating deposits of Late Cretaceous age. In addition, the typical subgenus has a more southern distribution than the subgenus *Egelicalva,* suggesting that changes in their distributions through the Late Cretaceous may aid in climatic reconstructions.

INTRODUCTION

Venerid bivalves, especially of the genus *Calva,* are a common constituent of shallow water Late Cretaceous marine faunas of the Pacific Slope from Alaska south to Baja California. Two species of *Calva, Meretrix nitida* Gabb, 1864, and *Venus varians* Gabb, 1864, were among the earliest described bivalves of Cretaceous age from California. However, these and other species of *Calva* have been imprecisely diagnosed and their geologic occurrences incorrectly recognized, in part because several species are quite similar and easily confused. With careful discrimination the species can be useful in dating beds of Late Cretaceous age. Most species of *Calva* from northeast Pacific Slope deposits appear allocatable to two lineages or subgenera. Geographic occurrences of these two subgenera, *Calva* and *Egelicalva,* suggest that the typical lineage was more thermophilic than the other.

Popenoe (1937) proposed the genus *Calva* to include several Pacific Slope Cretaceous venerid species of medium to large size. He designated as type species *Calva regina* Popenoe, 1937, of Turonian age, and referred *Meretrix nitida* var. *major* Packard, 1922 = *Cucullaea bowersiana* Cooper, 1894, to *Calva.* He also tentatively included two much-cited species described by Gabb in 1864, *Venus varians* and *Meretrix nitida,* although at that time (1937) neither the morphology nor stratigraphic occurrence of either species was clearly understood. Gabb (1864) cited the two species as occurring together at four California localities: Cow Creek, Shasta County; Orestimba Canyon, Stanislaus County; Chico Creek, Butte County; and Division A at Martinez, Contra Costa County, and the two species have continued to be jointly cited from numerous Cretaceous localities by many workers up to the present. Gabb did not designate type specimens or type localities and gave no explanation for placing *V. varians* and *M. nitida* in different genera. He provided no description of the hinge of either species.

Whiteaves (1879) originally identified specimens that should probably be referred to *Calva* from several localities in the Nanaimo Basin deposits, British Columbia, as *Cytherea* (*Caryatis*) *plana* Sowerby, 1812, a species of late Albian age described from the Upper Greensand of Blackdown, Devon, England, but in 1903 he referred them to *Meretrix nitida* Gabb, 1864, a species of latest Albian and Cenomanian age. Whiteaves' material is presently only partially available, but his *Cytherea* (*C.*) *plana* and *M. nitida* are *Calva.* Some of his figured specimens have been misplaced, and the horizon and locality for a number of his specimens are imprecise.

The first step toward discriminating between Gabb's species and assigning them to an appropriate genus was made by Stewart (1930) who figured one of Gabb's original specimens of *Venus varians* and designated ANSP 4383 as lectotype. He figured two of Gabb's specimens of *Meretrix nitida* but designated neither as lectotype. He considered that *V. varians* and *M. nitida* might be conspecific but noticed subtle shape differences between specimens of the two separate lots. He partially exposed hinges of both species, showing that anterior lateral teeth are present in both, and, therefore, referred both species to *Aphrodina* Conrad, 1869. He considered the type locality of both to be Martinez, Contra Costa County, California, but commented that the striking differences in preservation might indicate that more than one stratum and perhaps more than one locality was included under the name "Martinez." He dated the Cretaceous fauna from "Martinez" as Cenomanian or earlier, an age appropriate to *M. nitida,* but not for *V. varians,* which is now known to be of Maastrichtian age.

Popenoe (1937, p. 395) indicated that *Venus varians, Meretrix nitida, M. nitida* var. *major* Packard, and *C. regina* Popenoe differ from *Aphrodina* in having posterior lateral teeth. At this time, he also tentatively assigned *Meretrix umzambiensis* Woods, 1906, from the Late Cretaceous of Pondoland, South Africa, to *Calva,* being unaware that *M. umzambiensis* had been designated type species of *Trigonocallista* Rennie, 1930 (p. 177). Upon discovering Rennie's designation, Popenoe sent specimens of *Calva* to Rennie at Rhodes University College, Grahamstown, South Africa. Rennie opined that *T. umzambiensis* was congeneric with the California specimens, and Popenoe (1940) placed *Calva* in the synonymy of *Trigonocallista.* Casey (1952, p. 172), however, recognized both genera because *Calva* was described as having smooth sided anterior lateral teeth, whereas *Trigonocallista* has striated anterior lateral teeth. He considered them both to be dosiniopsids.

Anderson (1958, p. 138) provided two new names for species of *Calva* collected at Chico Creek and figured by Taff et al. (1940): *Trigonocallista taffi* Anderson for *T. nitida* (Gabb) (Taff et al., 1940, pl. 2, figs. 3–4) and *T. buttensis* Anderson for *T. varians* (Gabb) (Taff et al., 1940, pl. 2, figs. 10–11).

Seven of the 15 species referable to *Calva* s.l. that are present in northeast Pacific Slope Cretaceous beds were named prior to this study. To these are added nine new species, giving the genus a time range in this region of Albian through Maastrichtian. In the past generic and specific relations have been obscured by incomplete knowledge of morphology of some species, careless identification of many specimens, and resultant confusion of the stratigraphic occurrences of species. This paper summarizes the species comprising *Calva* and their morphologic, geographic, and stratigraphic distinctness. This work was begun by W. P. Popenoe who gave a paper on *Calva* at the 1963 Cordillerian Section of the Geological Society of America (Popenoe, 1964, p. 219) and has been completed by L. R. Saul.

SOURCES OF MATERIAL STUDIED

During the years that he studied the Late Cretaceous molluscan faunas from the Pacific Slope of North America, Popenoe amassed collections that were carefully located geographically and stratigraphically, many of which contained specimens of the venerid bivalve *Calva*. Figure 1 indicates areas from which such specimens have been collected, and localities are keyed to it by a bracketed number. A framework for the study of this group is provided by several important sections. The Cretaceous sections at the northern end of the Sacramento Valley in the vicinity of Ono [9] and east of Redding [8], Shasta Co., comprising the Budden Canyon and the Redding Formations, have provided venerids of Albian through Santonian age. Outcrops of the Chico Formation, especially along Chico Creek [11], have provided venerids of Santonian through early Campanian age. The Santa Ana Mountains [26] section in Orange Co., comprising the Ladd and Williams Formations, has yielded venerids of Turonian and late Campanian age. In the Simi Hills [24] of Los Angeles and Ventura Cos., the Chatsworth Formation has yielded venerids of mid-Campanian through early Maastrichtian age. Although megafossils are sparse in much of the thick Great Valley Series cropping out along the western border of the San Joaquin–Sacramento Valleys, the region has provided venerids of Albian through late Maastrichtian age. North and south of Lake Nacimiento [21] in San Luis Obispo Co., outcrops of the El Piojo Formation have yielded late to latest Maastrichtian venerids.

Other areas from which important collections have been made include the Nanaimo Basin [1–3] in southern British Columbia and San Juan Co., Washington; the Hudspeth Formation in Wheeler and Grant Cos. [4], Oregon; the Hornbrook Formation in Jackson Co. [6], Oregon and Siskiyou Co. [7], California; the Jalama Formation in western Santa Barbara Co. [22], California; the Point Loma Formation of the Rosario Group in San Diego Co. [28], California; and the Rosario Formation in northern Baja California, Mexico [29].

Type specimens of the named taxa were borrowed. If preservation of the specimen was adequate and permission was granted by the loaning institution, matrix was removed so that the hinge teeth could be seen. New collections from type localities of described species have made possible assessments of the range of variation in these species. Although the type localities of species described by Gabb and Cooper lack precision, comparison of type material with large collections from the vicinity of the "type locality" has made it possible to assign these species to descrete horizons. Taxa included in *Calva*, especially *Venus varians* and *Meretrix nitida*, have been reported from many localities; reassessment of reported identifications has been effected by examining the specimens upon which the reports were based and/or by studying larger, better located collections from the area.

Calvas most commonly occur in sandstone deposits. Where specimens are not obviously displaced downslope, the conditions appear to have been normal marine and sublittoral, near or below wave base. *Calva* is commonly part of a fairly diverse molluscan assemblage that lived off-shore from communities dominated by *Cymbophora* and in slightly coarser substrate than those in which *Crassatella* was most abundant. Although common in many collections, *Calva* does not usually constitute more than a third of recovered specimens. In comparison to some thinner shelled bivalves in the same deposits, specimens of *Calva*, which are relatively robust, probably have a better recovery rate from hard matrix and are therefore disproportionally abundant in museum collections. Although all *Calva* have a well-developed pallial sinus and were doubtless infaunal filter-feeders, shell morphology and the typically disarticulated preservation of shells indicate that *Calva* was probably a shallow burrower.

DISTRIBUTION

In addition to the four Pacific Slope species, *Venus varians, Meretrix nitida, Cucullaea bowersiana,* and *Calva regina,* Popenoe (1937, p. 395) suggested that *Meretrix umzambiensis* from South Africa, *Cytherea subrotunda* Sowerby and *Cytherea caperata* Sowerby from England, *Dosiniopsis nebrascensis* (Meek and Hayden, 1856) from the Western Interior, and *Callista pseudoplana* Yabe and Nagao, 1925, from Hokkaido, Japan, might be referred to *Calva.* The generic placement of *M.*

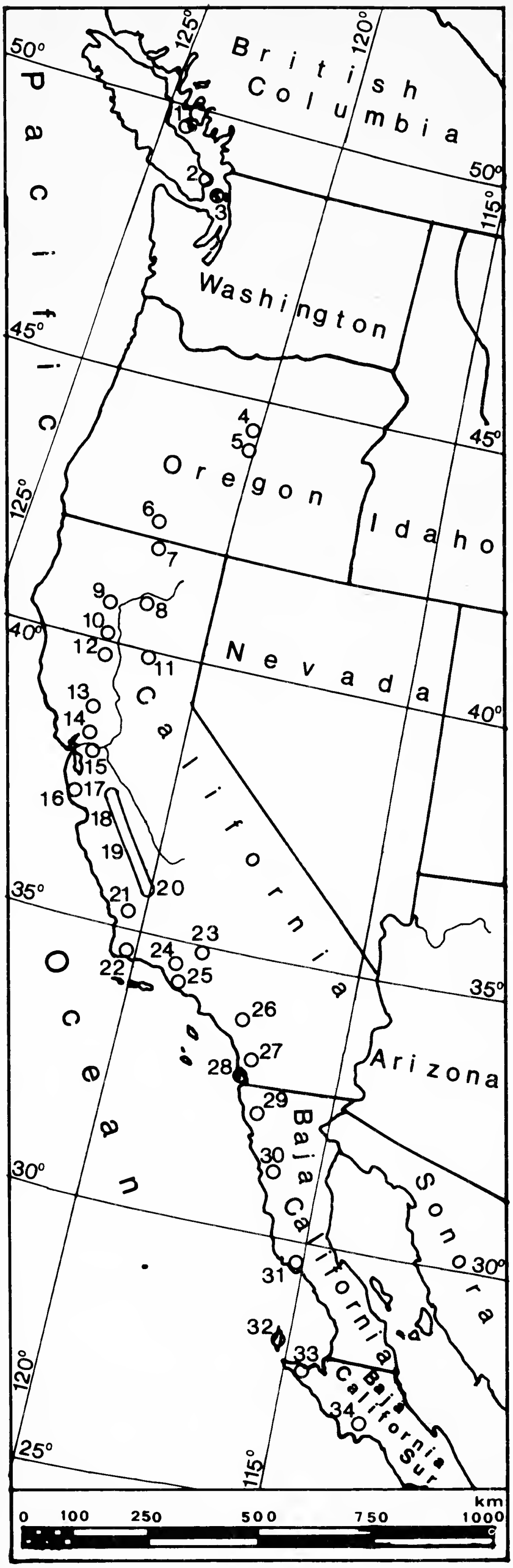


Figure 1. Index map to geographic occurrences of *Calva* spp. Localities are grouped into 33 areas that are numbered from north to south: 1—Denman Island, Hornby Island, and Texada Island, British Columbia. 2—Departure Bay and Nanaimo, Vancouver Island, British Columbia. 3—Sucia Island, San Juan Co., Washington. 4—Dayville, Grant Co., and Rock Creek, Wheeler Co., Oregon. 5—Andy Bernard Ranch and Suplee, Crook Co., Oregon. 6—Ashland Creek and Jacksonville, Jackson Co., Oregon. 7—Rancheria Gulch and Young Ranch, Siskiyou Co., California. 8—Clover Creek, Cow Creek, Dry Creek, Oak Run, Price Hollow, Redding, and Stinking Creek, Shasta Co., California. 9—North Fork of Cottonwood Creek, Ono, and Texas Springs, Shasta Co., California. 10—Elder Creek, Tehama Co., California. 11—Butte Creek, Chico Creek, and Pentz, Butte Co., California. 12—Stony Creek, Glenn Co., California. 13—Antelope Creek, Peterson Ranch, and Sites, Colusa Co., and Thompson Creek, Yolo Co., California. 14—Benicia and Glenn Cove, Solano Co., California. 15—Curry Canyon, Deer Valley, and Martinez, Contra Costa Co., and Pleasanton area, Alameda Co., California. 16—Bolsa Point, San Mateo Co., California. 17—Garzas Creek, Orestimba Creek, and Salado Creek, Stanislaus Co., California. 18—Laguna Seca, Los Baños Creek, Pacheco Pass, and Ortigalita Creek, Merced Co., California. 19—Coalinga, Cooper Canyon, Los Gatos Creek, Fresno Co., California. 20—Garza Peak, McClure Ridge, north of Sunflower Valley, Kings Co., California. 21—Cantinas Creek, Dip Creek, Lake Nacimiento, San Luis Obispo Co., California. 22—Jalama Creek, Sisquoc River, Hurricane Deck Quadrangle, Santa Barbara Co., California. 23—Warm Springs Mountain, Los Angeles Co., California. 24—Bell Canyon, Simi Hills, Ventura Co., and Dayton Canyon, Los Angeles Co., California. 25—Santa Monica Mts., Los Angeles Co., California. 26—Baker and Black Star Canyons, Bee Canyon, Holz Ranch, Pankratz Ranch, Wildcat and White Canyons, and Williams Canyon, Santa Ana Mts., Orange Co., California. 27—Carlsbad area, San Diego Co., California. 28—La Jolla and Point Loma, San Diego Co., California. 29—Punta Banda, Baja California, Mexico. 30—San Antonio del Mar, Baja California, Mexico. 31—Vicinity of El Rosario and Arroyo Santa Catarina, Baja California, Mexico. 32—Cedros Island, Baja California, Mexico. 33—Northwest Vizcaíno Peninsula, Baja California Sur, Mexico. 34—Vizcaíno Peninsula inland from Punta Abreojos, Baja California Sur, Mexico. Place names mentioned in text listed alphabetically and assigned to a numbered area: 5—Andy Bernard Ranch; 13—Antelope Creek; 15—Arroyo del Valle; 31—Arroyo Santa Catarina; 6—Ashland Creek; 26—Baker Canyon; 26—Bee Canyon; 24—Bell Canyon; 14—Benicia; 26—Black Star Canyon; 16—Bolsa Point; 11—Butte Creek; 21—Cantinas Creek; 27—Carlsbad; 32—Cedros Island; 11—Chico Creek; 8—Clover Creek; 19—Coalinga; 19—Cooper Canyon; 8—Cow Creek; 15—Curry Canyon; 24—Dayton Canyon; 4—Dayville; 15—Deer Valley; 1—Denman Island; 2—Departure Bay; 17, 18, 19, 20—Diablo Range; 21—Dip Creek; 8—Dry Creek; 10—Elder Creek; 31—El Rosario; 20—Garza Peak; 17—Garzas Creek; 14—Glenn Cove; 26—Holz Ranch; 1—Hornby Island; 22—Jalama Creek; 6—Jacksonville; 18—Laguna Seca; 28—La Jolla; 21—Lake Nacimiento; 18—Los Baños Creek; 19—Los Gatos Creek; 15—Martinez; 20—McClure Ridge; 2—Nanaimo; 15—Niles Canyon; 9—North Fork of Cottonwood Creek; 8—Oak Run; 9—Ono; 17—Orestimba Creek; 18—Ortigalita Creek; 18—Pacheco Pass; 26—Pankratz Ranch; 21—Pebblestone Shut-In; 11—Pentz; 13—Peterson Ranch; 15—Pleasanton area; 28—Point

umzambiensis has already been mentioned. Casey (1952) considered *Cytherea subrotunda* to be a typical *Calva* and designated *Cytherea caperata* as the type species of *Chimela,* a new subgenus of *Calva.* Speden (1970) consigned *Dosiniopsis nebrascensis* to the synonomy of *D. deweyi* (Meek and Hayden, 1856) and considered the species appropriately placed in *Dosiniopsis,* thereby extending the range of *Dosiniopsis* back into the Late Cretaceous. Nagao and Otatume (1963) placed *Callista pseudoplana* Yabe and Nagao, 1925, in *Aphrodina.* Hayami (1975, p. 145) questionably refered *Dosiniopsis* (?) cf. *D.* (?) *caperata* (Sowerby) of Yabe and Nagao, 1925, from the Cape Khoi beds (Cenomanian–Turonian) in the Aleksandrovsk area, Sakhalin Island, Russia, to *Calva* sp. In contrast, *Trigonocallista ornata* Ichikawa and Maeda, 1963, from the Izumi Group (Campanian) in the Hiketa area, Tokushima Prefecture, Japan, has the striated nymph of a *Trigonocallista.* Only species from the Pacific Slope can with certainty be assigned to *Calva.*

The genus *Calva* persisted along the Pacific Slope of North America from Albian through Maastrichtian but does not appear to have been common elsewhere. Figure 2 plots chronologic ranges of the studied species. *Calva* has been recognized from Alaska south to the Vizcaíno Peninsula [34], Baja California Sur, Mexico. Only a few Alaskan specimens, mainly from the Campanian Chignik Formation west of Chignik Bay, have been studied. Reports (Whiteaves, 1879, 1895, 1896, 1903) indicated that *Calva* is common in Late Cretaceous deposits of southern Vancouver Island [1–2], British Columbia, but few specimens are available, and Nanaimo Basin *Calva* are represented in this study mainly by Campanian, *Hoplitoplacenticeras vancouverense* Zone, specimens from Sucia Island [3], Washington. Most of the specimens from Baja California, Mexico, are from the Rosario Formation and are of early Maastrichtian age, but a few specimens from formations as old as Cenomanian are available. California has provided the bulk of specimens and species over the most extensive time range and the best geographic distribution. However, Albian and Cenomanian deposits are unknown in Southern California, and the most studied deposits of Coniacian, Santonian, and early Campanian age of Southern California were laid down in moderately deep or deeper water and have as yet yielded no specimens of *Calva.*

The phylogenetic relationship between *Calva* s.s. and *Calva* (*Egelicalva*) is not known. *Egelicalva* appears in our records before *Calva* (*Calva*), and the shape of the earliest typical *Calva, C.* (*C.*) *heliaca,* which is probably of Cenomanian age, resembles that of *C.* (*E.*) *taffi* of Santonian age rather than *C.* (*E.*) *nitida* of latest Albian–Cenomanian age or *C.* (*E.*) *byblidis* of early Albian age. No *Calva* s.s. species can be unequivocally derived from a species of *Egelicalva,* but *Calva* and *Egelicalva* are so similar in hinge structures and shape that they are probably related.

Whiteaves (1879, p. 150; 1903, p. 377) listed specimens that would now be assigned to *Calva* as *Cytherea* (*Caryatis*) *plana* Sowerby or *Meretrix nitida* Gabb from several Nanaimo Basin [1–3] localities. Unfortunately, not all of his specimens are available. His localities included Departure Bay, near Nanaimo, northwest side of Hornby Island, "2¼ miles up the Nanaimo River," Texada Island, and Sucia Island. Work of Muller and Jeletzky (1970), Ward (1978), and Haggart (1989) suggests that Whiteaves' localities on Sucia Island, Texada Island, "2¼ miles up the Nanaimo River," and possibly near Nanaimo are from the Cedar District Formation; localities at Departure Bay and near Nanaimo may have been from the Pender or Haslam Formations, and the Northumberland and Spray Formations are mapped on the northwest side of Hornby Island. The Cedar District Formation is considered to be of early late Campanian age *Hoplitoplacenticeras vancouverense* and *Metaplacenticeras pacificum* zones; *Calva* from this formation on Sucia Island are *Calva* (*Egelicalva*) *bowersiana* and *Calva* (*Microcalva*) *haggarti.* We have not seen specimens from Departure Bay or near Nanaimo; the age range of the Haslam and Pender Formations is late Santonian to early Campanian (Ward, 1978; Haggart, 1989). In California, beds of late Santonian age have yielded *C.* (*E.*) *taffi,* and beds of early Campanian age have yielded *C.* (*E.*) *buttensis.* Four small specimens from Hornby Island identified by Whiteaves as *Meretrix nitida* Gabb are similar to *Calva* (*Microcalva*) *haggarti,* new species (see the discussion under this species); Northumberland and lower Spray Formations are of late Campanian age, and the upper Spray is early Maastrichtian in age (Haggart, 1989).

Figure 3 depicts the known latitudinal range of each species. Chronologic and geographic ranges are based largely on specimens in the collections of the Natural History Museum of Los Angeles County, the University of California, Berkeley, Museum of Paleontology, and the California Academy of Sciences, with additional data from collections of the U.S. Geological Survey, Menlo Park, Royal Provincial Museum, Victoria, British Columbia, and Geological Survey of Canada, Ottawa, Ontario.

←

Loma; **8**—Price Hollow; **34**—Punta Abreojos; **31**—Punta Baja; **29**—Punta Banda; **17**—Quinto Creek; **7**—Rancheria Gulch; **8**—Redding; **4**—Rock Creek; **17**—Salado Creek; **30**—San Antonio del Mar; **18**—San Luis Reservoir; **22**—San Rafael primitive area; **26**—Santa Ana Mts.; **25**—Santa Monica Mts.; **26**—Santiago-Aliso Creek divide; **26**—Silverado Canyon; **24**—Simi Hills; **7**—Siskiyou Mts.; **22**—Sisquoc River; **13**—Sites; **8**—Stinking Creek; **12**—Stony Creek; **3**—Sucia Island; **20**—Sunflower Valley; **5**—Suplee; **1**—Texada Island; **9**—Texas Springs; **13**—Thompson Creek; **2**—Vancouver Island; **33, 34**—Vizcaíno Peninsula; **23**—Warm Springs Mountain; **26**—White Canyon; **26**—Wildcat Canyon; **26**—Williams Canyon; **7**—Young Ranch.

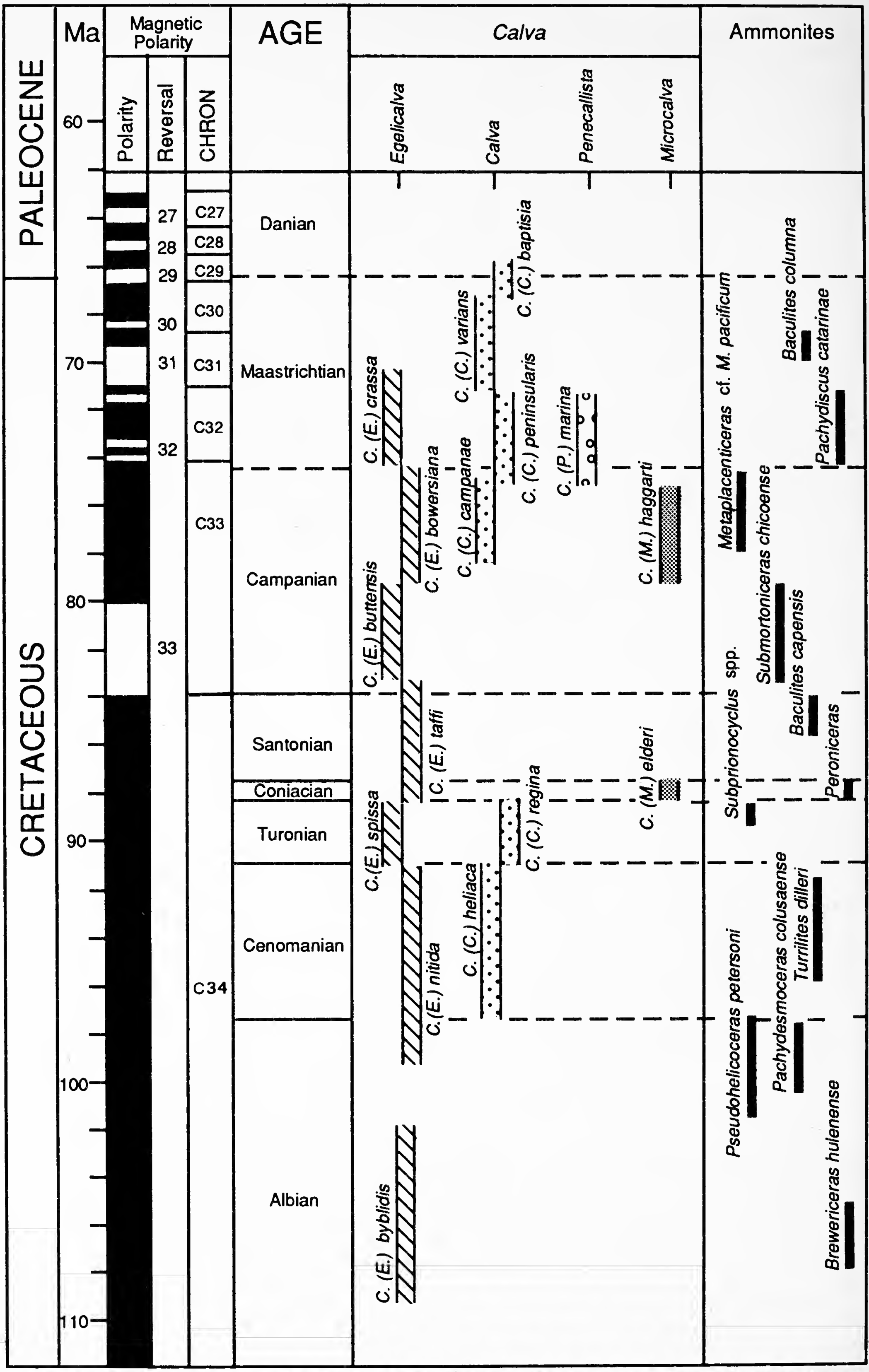


Figure 2. Geologic ranges of species of *Calva* from the Pacific Slope of North America plotted against geochronologic time scale, magnetic polarity (after Palmer, 1983), and selected ammonite ranges.

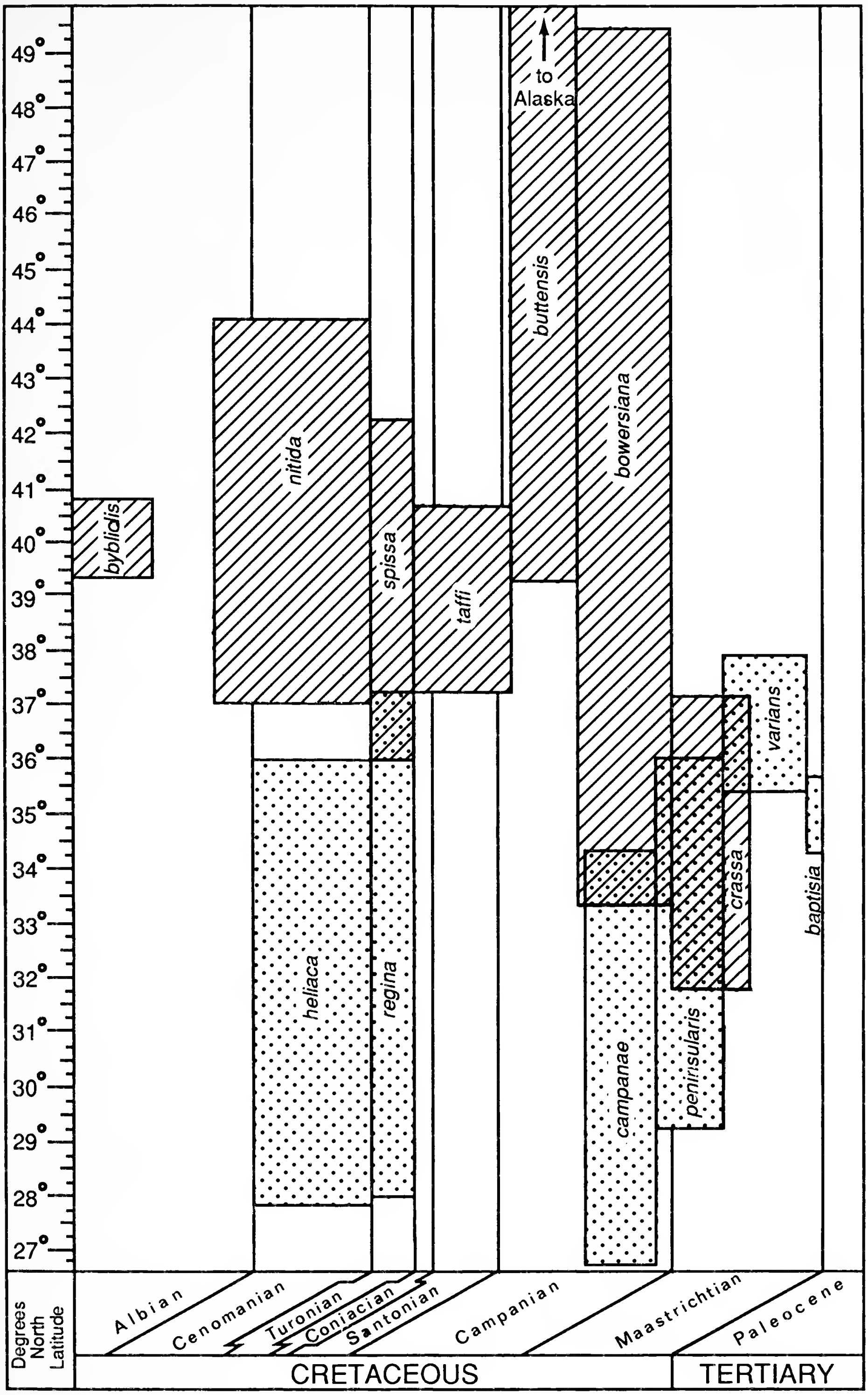


Figure 3. Latitudinal distribution of species of *Calva* and *Egelicalva,* based on range end points of Table 1. All occurrences of C. (C.) *regina,* C. (C.) *campanae,* and C. (C.) *baptisia* are west of the San Andreas fault. All occurrences of C. (E.) *byblidis,* C. (E.) *spissa,* C. (E.) *taffi,* and C. (E.) *buttensis* are east of the San Andreas fault. The northernmost occurrence of C. (C.) *heliaca,* C. (C.) *peninsularis,* C. (E.) *nitida,* C. (E.) *bowersiana,* and C. (E.) *crassa* is east and the southernmost occurrence west of the fault. Northern range ends are rounded-off north and plotted on the next northern quarter degree; southern range ends are rounded-off south and plotted on the next southern quarter degree. Species known only from essentially a single locality are given a latitudinal range of one degree.

Table 1. Range end points for *Calva* species.

	Northern end point	Southern end point
Calva (*Calva*)		
heliaca	36°N, McClure Ridge [20]	27°45′N, NW Vizcaíno Peninsula [33]*
regina	37°15′N, Quinto Creek [17]	28°N, Cedros Is. [31]*
campanae	34°15′N, Simi Hills [24]*	26°45′N, Vizcaíno Peninsula [34]*
peninsularis	36°N, Coalinga [19]	29°30′N, Santa Catarina [31]*
varians	38°N, Martinez [15]	35°45′N, Lake Nacimiento [21]*
baptisia	35°45′N, Lake Nacimiento [21]*	34°30′N, Warm Springs Mtn. [23]*
Calva (*Egelicalva*)		
byblidis	40°30′N, Texas Springs [9]	39°30′N, Sites, Colusa Co. [13]
nitida	44°N, Suplee, Oregon [5]	38°N, Martinez [15]
spissa	42°15′N, Jackson Co., Oregon [6]	36°N, Garza Peak [20]
taffi	40°30′N, Redding [8]	37°15′N, Orestimba [17]
buttensis	56°30′N, Chignik Bay, Alaska	39°50′N, Pentz [11]
bowersiana	49°30′N, Vancouver Is. [2]	33°30′N, Santa Ana Mts. [26]*
crassa	37°N, Ortigalita Creek [18]	31°45′N, Punta Banda [29]*
Calva (*Microcalva*)		
elderi	37°N, San Luis Reservoir [18]	
haggarti	49°30′N, Vancouver Is. [2]	48°45′N, Suicia Is. [3]
Calva (*Penecallista*)		
marina	35°45′N, Pebblestone Shut-In [21]*	31°N, San Antonio del Mar [30]*

* West of the San Andreas Fault.

These compiled latitudinal ranges (Table 1) are filtered through the usual deficiencies of the geologic record—incomplete sections, wrong ecotope preserved, and imperfect preservation of specimens, as well as tectonic transport. However warped by this filter, the occurrences of *Calva* (*Calva*) and *Calva* (*Egelicalva*) form a north–south pattern with species of *Calva* (*Calva*) displaying a more southerly distribution vis à vis contemporaneous species of the subgenus *Egelicalva*. Available Alaskan and Canadian collections surveyed suggest that many northern occurrences are unreported. Both the northerly distribution of several species of *Egelicalva* and the southerly distribution of species of *Calva* s.s. are likely to be extended by additional collecting. In general, specimens of *Calva* (*Egelicalva*) sp. show more accentuated growth checks than do specimens of *Calva* (*Calva*) sp. As strength of growth checks may be encouraged by a more seasonal climate with greater summer–winter food supply differential affecting growth potential, specimens from higher latitudes might be expected to exhibit stronger growth checks.

Actual latitudinal ranges have not only been obscured by deficiencies of the geologic record but have been additionally confounded by the unknown amount of terrane displacement between various *Calva*-bearing outcrops of similar age. Paleomagnetic data suggest a northward translation of many of the Cretaceous deposits (Fry et al., 1985), but the Figure 3 ranges are plotted at the present geographic positions of the rocks from which the specimens were collected. The best documented displacements are those of the San Andreas Fault system, which are relatively northward on the west. Some species have their entire geographic occurrence either east or west of this system, but others straddle it. *Calva* (*C.*) *peninsularis, C.* (*Egelicalva*) *bowersiana,* and *C.* (*E.*) *crassa* all have their southernmost occurrence to the west of this system, on the north moving block, and their northernmost occurrence east of the system. Their present apparent latitudinal range is less than their original distribution by the total displacement on the San Andreas system (approx. 500–600 km). Despite distributional offset due to terrane displacement, latitudinal ranges of time equivalent species of the *Calva* s.s. group are to the south of the ranges of the *Calva* (*Egelicalva*) group. Any terrane displacements across the San Andreas system appear to have been less than the original latitudinal ranges of these species.

Latitudinal ranges in the Cretaceous may have been broad, but the pattern of the *Calva* ranges argues for latitudinal restrictions not too unlike those of the present North American Pacific Coast. Sliter (1968), dealing with foraminiferal faunas of early Maastrichtian age, postulated four marine climatic zones remarkably similar to those of the present. The molluscan equivalent of his south-central fauna includes such tropical forms as the rudist bivalve *Coralliochama* but would be equated to a modern warm temperate rather than a tropical fauna. Although the subgenus *Egelicalva* is of more northern distribution, its range probably extended south into the northern part of the warm temperate zone. The southern distributions of *Calva* (*E.*) *taffi* and *C.* (*E.*) *buttensis* are probably truncated by the lack of beds bearing *Calva* of early Senonian age south of Stanislaus Co. [17], California, and the northward distribution of *C.* (*E.*) *crassa* may also be more reflective of geologic preservation than original distribution. None of the faunas in which *Calva* is present appear to be truly tropical. But some, e.g., northern California Albian, Oregon Cenomanian, northern California Turonian, and southern California late Campanian, include a few genera of tropical aspect, suggesting that these were warm temperate faunas. If the distributions of *Calva* (*Calva*) spp. and *Calva* (*Egelicalva*) spp. are in part temperature dependent, the ranges in Figure 3 suggest a warm Turonian followed by a cooler Coniacian and Santonian. The late Campanian appears to have been slightly warmer than the early Campanian. The early Maastrichtian may have been the coolest interval, but it was followed by a considerable late Maastrichtian warming.

FEATURES MEASURED

In addition to the usual three measurements taken on bivalves, (1) valve height (H), measured perpendicular to the ligament, (2) valve length (L), measured parallel to the ligament, and (3) valve inflation (I), four other measurements were made: (1) distance from the beak to the anterior end (B); (2) lunule length (LL); (3) lunule width (LW); (4) the angle made by drawing lines through lateral teeth (LTA) AII and PII or sockets for AII and PII. The number of specimens measured ranged from only 2 specimens of *C.* (*Microcalva*) *elderi* to 16 of *C.* (*Egelicalva*) *taffi* and depended upon available specimens of sufficient completeness and the amount of time required to remove obscuring matrix. Figure 4 diagrams the features measured on specimens of *Calva*. Figure 5 compares ratios of these measurements and the angle through the lateral teeth. Although these measurements show specific differences, they provide no directional trends in these lineages.

CHANGES IN *CALVA* THROUGH TIME

Most of the changes recognized between species appear undirected within lineages. Even size does not increase regularly. The largest species, *Calva* (*Calva*) *peninsularis*, *C.* (*Egelicalva*) *crassa*, and *Calva* (*Penecallista*) *marina*, are all of early Maastrichtian age. Some specimens of Cenomanian age *C.* (*E.*) *nitida* are larger than any known specimens of Turonian age *C.* (*E.*) *spissa*, Coniacian–Santonian age *C.* (*E.*) *taffi*, or early Campanian age *C.* (*E.*) *buttensis*; some specimens of late Campanian *C.* (*E.*) *bowersiana* approach the size of *C.* (*E.*) *crassa*. Late Maastrichtian *Calva* are of average size. Species of *Microcalva* are considerably smaller than are species of other subgenera of *Calva* and are comparable to *Microcallista* in size. *Calva* (*Calva*) *heliaca* of Cenomanian age and *C.* (*E.*) *taffi* of Coniacian–Santonian age are represented by smaller specimens than are other species of their lineages. Only in the hinge do some developmental trends appear. The anterior laterals become shorter and smoother, losing the striation of the early species. Cardinal tooth 1 moves dorsally from its early position at the hinge plate edge with its dorsal end ventral to that of 3a, whereas in later species its dorsal end is in a more beakward position than that of 3a, and its ventral end is no longer at the hinge plate edge. In *C.* (*C.*) *heliaca* cardinals 3a and 3b are connected dorsally by a low arched ridge; in later species this connection is broken as 1 moves into its more dorsal position.

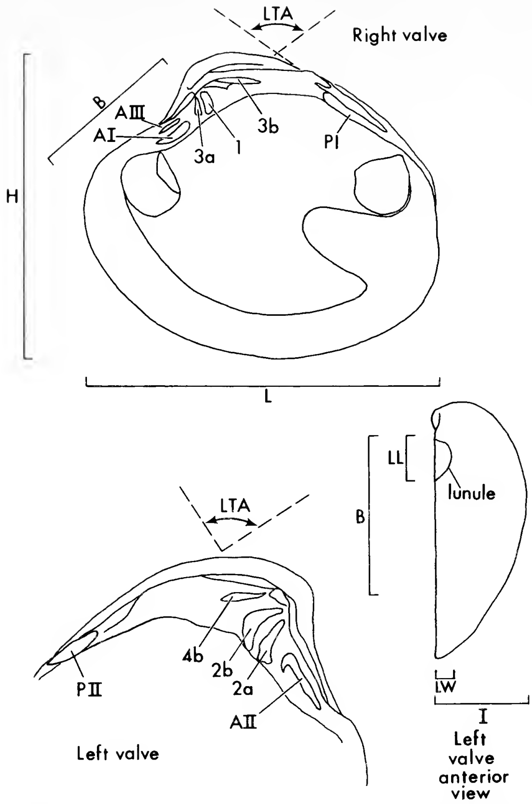


Figure 4. Diagrams of right valve interior view of *Calva* (*Penecallista*) *marina*, left valve anterior view of *Calva* (*Calva*) *peninsularis*, and left valve interior of *Calva* (*Egelicalva*) *crassa* with cardinal teeth labeled and measured features indicated. H, height measured perpendicular to the ligament; L, length measured parallel to the ligament; I, inflation of a single valve; B, distance from the beak to the anterior end; LL, length of the lunule; LW, width of the lunule; LTA, lateral tooth angle, the angle made by drawing a line through the sockets for the laterals AII and PII in the right valve or through the lateral teeth AII and PII in the left valve. Measurement LTA used as an alternative to beak angle, which is more difficult to measure consistently.

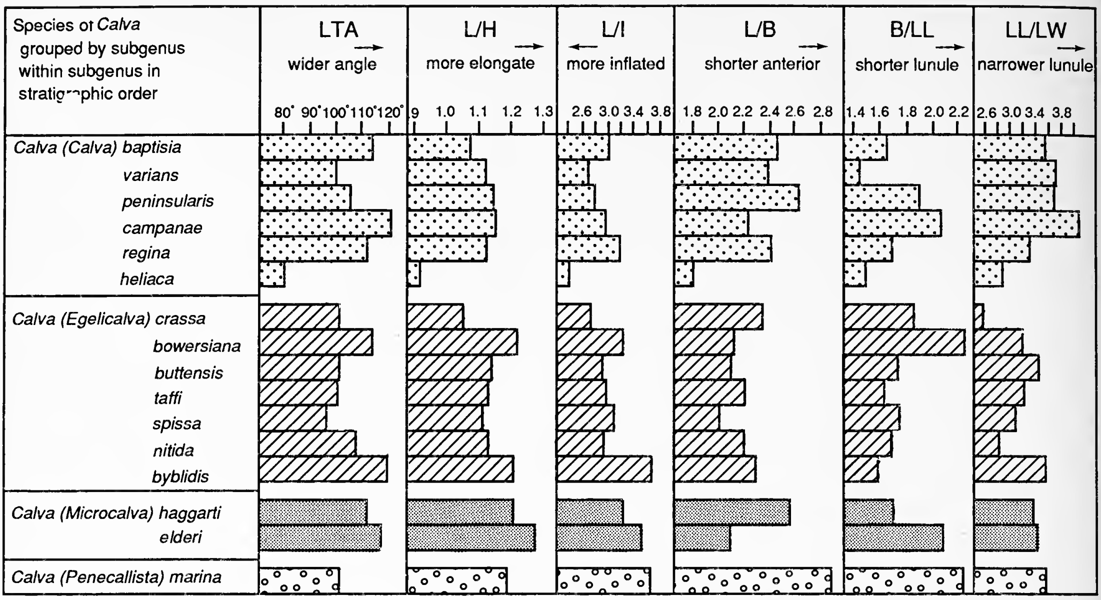


Figure 5. Ratios of measurements made on specimens of 16 species of *Calva*. Measurements from Tables 2–17. Features measured are described and abbreviations decrypted in Figure 4.

SUMMARY

Although for the past century *Venus varians* Gabb, 1864, and *Meretrix nitida* Gabb, 1864, have appeared on faunal lists from the same locality, they do not occur together and are not of the same age. These and 14 other species constitute the genus *Calva,* which is subdivided into four subgenera, two of which, *Calva* s.s. and *Egelicalva,* range through the Late Cretaceous of the Pacific Slope. Species of *Calva* are difficult to distinguish but can be discriminated and are diagnostic of discrete chronologic intervals.

Geographic distributions of *Calva* s.s. and *Calva* (*Egelicalva*), which result in *Egelicalva* having a more northerly distribution, suggest that terrane displacement was not equal to the latitudinal ranges of *Calva* s.l. species and that climatically there was a Coniacian–Santonian cooling, a warming in the late Campanian, and an early Maastrichtian cooling, followed by a warming through the late Maastrichtian.

Only the hinges of *Calva* display any evolving morphologic trends. The anterior lateral teeth become progressively smoother sided, and the central cardinal tooth of the left valve moves into a more beakward position.

ABBREVIATIONS

ANSP	Academy of Natural Sciences of Philadelphia
CAS	California Academy of Sciences, Golden Gate Park, San Francisco
CIT	California Institute of Technology (collections now housed at Natural History Museum of Los Angeles County)
CSMB	California State Mining Bureau
GSC	Geological Survey of Canada
LACMIP	Natural History Museum of Los Angeles County, Invertebrate Paleontology Section
SDSNH	San Diego Society of Natural History
SDSU	San Diego State University
SU	(= LSJU) Stanford University (collections now housed at the California Academy of Sciences, Golden Gate Park, San Francisco)
UCMP	University of California, Berkeley, Museum of Paleontology
UCLA	University of California, Los Angeles (collections now housed at Natural History Museum of Los Angeles County)
USGS	United States Geological Survey, Washington, D.C.
USGSM	United States Geological Survey, Menlo Park, California
USNM	United States National Museum

SYSTEMATIC PALEONTOLOGY

Phylum Mollusca Linnaeus, 1758
Class Bivalvia Linnaeus, 1758
Order Veneroida H. and A. Adams, 1856
Family Veneridae Rafinesque, 1815
Genus *Calva* Popenoe, 1937

TYPE SPECIES. By original designation *Calva regina* Popenoe, 1937, Turonian, Ladd Formation, Holz Shale Member, Santa Ana Mountains, California.

DIAGNOSIS. Veneriform bivalves having growth lines and, generally, well-marked growth checks and a depressed lunule set off by an incised line. Hinge with three cardinals in each valve, two anterior and two posterior lateral teeth in the right valve, and one anterior and one posterior lateral tooth in the left valve; posterior cardinal of the right valve 3b narrowly bifid; anterior lateral AII long, parallel to the lunular border, and terminated posteriorly in a short, ventrally directed prong; left posterior lateral a salient projection of the posterior dorsal margin fitting into an elongate socket in the right valve bounded dorsally by the right posterior dorsal shell margin, and ventrally by elongate lateral tooth PI. Nymphs smooth. Pallial sinus moderately deep. The anterior adductor muscle scar impressed and immediately at the anterior end of the hinge plate.

DISCUSSION. In *Calva,* the posterior lateral tooth of the left valve is not set on the hinge plate but is instead a salient portion of the valve margin that fits into the well-developed posterior lateral socket of the right valve. This tooth is not obvious in plane view but is noticeable in profile as a triangular extension of the valve margin. The dorsal or outer posterior lateral of the right valve is also on the valve margin, and as it is not clearly distinguished from the valve margin, an argument could be made for recognizing only the one posterior lateral interior to the lateral socket. Casey (1952) has, as have we, considered that the clasping structures of the right valve are both posterior lateral teeth even if the exterior one is on the valve margin. Popenoe (1937) noted that posterior laterals are a rare feature in venerid shells, but they are common in Jurassic and Early Cretaceous arcticid precursors of the venerids (Casey, 1952). Posterior laterals are present in some Cretaceous venerids, e.g., *Resatrix* Casey, 1952, *Pseudaphrodina* Casey, 1952, *Trigonocallista* Rennie, 1930, *Loxo* Dailey and Popenoe, 1966, and *Calva* Popenoe, 1937, and in the Late Cretaceous–early Tertiary *Dosiniopsis* Conrad, 1864. Posterior laterals, thus, seem to be a feature derived by venerids from their arcticid ancestors and dispensed with in various lineages through the Cretaceous. The impetus for the removal of the posterior laterals may lie in the need to burrow faster. Strong posterior laterals would inhibit the rocking action of the valves that has been shown to assist burrowing (Trueman et al., 1966).

Sufficiently well-preserved individuals of all species of *Calva* display regularly spaced, fine concentric grooves on the beak area. These grooves rarely extend beyond the first prominent growth check.

Two lineages of *Calva* can be recognized in Pacific Slope deposits. The typical lineage comprises *C. heliaca, C. regina, C. campanae, C. peninsularis, C. varians,* and *C. baptisia.* All have a slightly to moderately arched hinge plate in which the major flexure is posterior to posterior cardinal tooth 3b. The hinge plate is relatively broad, and the lunule is moderately impressed and of moderate width. Posterior lateral PI of the right valve stands high enough to extend beyond the plane of commissure and bounds a relatively broad socket for PII. The lineage, herein assigned to the new subgenus *Egelicalva,* comprises *C. byblidis, C. nitida, C. spissa, C. taffi, C. buttensis, C. bowersiana,* and *C. crassa.* All are of medium to large size and have a lunule that is relatively wider and more deeply impressed than that of *Calva* s.s. They have hinge plates that are relatively narrow and moderately to well arched in which the major flexure is between cardinals 1 and 3b. Species of Albian–early Campanian age have laterals that are more coarsely striated than those of the typical lineage. Additionally, three other subgenerically distinct species are present. Two of these, *Calva elderi* and *C. haggarti,* have small shells displaying fine, round-topped concentric ribs and a small depressed lunule; *Calva haggarti* typifies the new subgenus *Microcalva. Calva* (*Penecallista*) *marina* has a large shell resembling a *Callista* Poli, 1791; its anterior lateral is shorter than that of other *Calva* spp., and it typifies the new subgenus *Penecallista.*

Popenoe (1937) described *Calva* as having smooth laterals, and Casey (1952, p. 172), who examined specimens sent to him by Popenoe, also stated that the anterior lateral teeth and sockets are smooth, not striated. Popenoe (1940) had recognized *Trigonocallista* Rennie, 1930, as the senior synonym of *Calva,* but Casey (1952) considered the genera distinct because *Calva* has smooth laterals, whereas those of *Trigonocallista* are striate. However, at 20× magnification the anterior lateral AII of *C. regina* is finely striate on its dorsal side; PI is finely striate on its dorsal side; and both sides of the socket for AII are finely striate. Striae are unrecognizable on the laterals of late Campanian and younger species of *Calva.* In *Trigonocallista umzambiensis* (Woods, 1906) from the Umzamba Formation of Santonian–early Campanian age (Klinger and Kennedy, 1980), however, the laterals are coarsely striate. According to Keen (*in* Moore, 1969, p. N679) cardinal 3b of *Trigonocallista* is entire, but Rennie (1930) described it as superficially grooved, and illustrations show it narrowly bifid. *Calva* bears a strong resemblance to *Trigonocallista* Rennie, 1930, but *Trigonocallista* has the anterior laterals curved and subparallel to the lunular margin, the nymph border wrinkled, a shallow pallial sinus, and a distinctly demarked escutcheon. The more coarsely striated anterior laterals of pre-Campanian species of the subgenus *Egelicalva* are suggestive of *Trigonocallista,* but the escutcheon of *Egelicalva* is less well defined than that of *Calva* s.s. and much less well defined than that of *Trigonocallista.* The anterior lateral of *Calva* is hooked. It parallels the lunular margin but is straight and has at its dorsal end a short, abruptly inward turned prong. The resultant angle faces toward the interior of the shell. The anterior lateral of *Trigonocallista* is arched but not hooked. The portion of the hinge plate bearing the anterior laterals is narrow, whereas in *Calva* this portion of the hinge plate is much broader. The posterior lateral socket of *Calva* is wider and deeper than that of *Trigonocallista.*

Trigonocallista has more in common with the Late Cretaceous–early Tertiary genus *Dosiniopsis* Conrad, 1864, than either have with *Calva*. Both these Atlantic Basin venerids have conspicuously striated laterals and rugose nymphae.

According to Casey (1952, p. 173) the earliest stratigraphic record of *Calva* s.s. is the British upper Albian species *Calva subrotundata* (J. de C. Sowerby, 1836). *Calva subrotundata* is very similar to Pacific Slope *Calva* but has a better defined escutcheon and, judging from Woods' (1908, pl. 28, figs. 1–6) illustrations, lacks the posterior hook on the anterior lateral AII. Casey (1952) derives *Calva* from *Dosiniopsella* Casey, 1952, of early and middle Albian age by way of *Chimela* Casey, 1952, of late Albian age, which he considers to be a subgenus of *Calva*. *Chimela* does not have the lunule in a depressed area, and the anterior lateral AII does not appear to be hooked. Casey (1952, fig. 93) does not draw an inscribed lunule on *Calva* (*Chimela*) *caperata* (J. de C. Sowerby, 1836), but Woods (1908, pl. 28, figs. 7–10) shows one. Both *C. subrotundata* and C. (*Chimela*) *caperata* are more like *Dosiniopsella* than is the earliest Pacific Slope *Calva*, C. (*Egelicalva*) *byblidis* of late early Albian age. The latter has a hooked anterior lateral rather than the convexly arched lateral of *Dosiniopsella*. The posterior right cardinal of C. (*E.*) *byblidis* is narrowly bifid; the posterior arm is decidely the longer and in echelon to the shorter anterior arm, a condition not found in *Dosiniopsella*. These differences suggest that although *Calva* may be derived from *Resatrix* Casey, 1952, the ancestor of *Dosiniopsella*, it was probably not derived from *Resatrix* by way of *Dosiniopsella* and *Chimela*.

Calva is recognized with certainty only in Pacific Slope deposits from Alaska to Baja California Sur, Mexico, of early Albian to late Maastrichtian age.

Subgenus *Calva* Popenoe, 1937

DIAGNOSIS. Species of *Calva* of subquadrate shape having an apparent posterior truncation and smooth exterior except for growth lines and growth checks. Hinge plate relatively broad and slightly arched with maximum flexure posterior to cardinal 3b; posterior lateral PI realtively short and high. Pallial sinus broad with steeply ascending ventral arm and nearly horizontal dorsal arm.

Calva (*Calva*) *heliaca*, new species

Figures 6–19

DIAGNOSIS. A very high, short, thick-shelled *Calva*.

DESCRIPTION. Shell thick, of moderate size, higher than long, inflated, with subdued posterior angulation; beaks prominent, anterior to the midlength of the shell, prosogyrous, lunular margin convex; anterior end rounded; ventral border arched; posterior end bluntly truncate vertically; posterior dorsal border long, slightly arched; lunule heart-shaped, relatively large, moderately deep, delimited by an inscribed line; escutcheon long, obscurely demarked by rounded angulation.

Ligament groove relatively short, arched behind strong nymphs. Hinge of right valve with anterior tooth 3a and median cardinal tooth 1 short but sturdy, 3a closer to the beak than 1 and joined to 3b by a low arched ridge dorsal to 1, ventral end of 1 at the hinge plate margin; posterior cardinal 3b bifid, long, subparallel to the nymph; AIII low, elongate, obscurely separated from valve margin by shallow groove; AI low, elongate, with a prominence at beakward end; socket for lateral AII very long, rather wide, deep, parallel to the lunular border of the shell, finely striate on both sides; socket for PII moderately deep, bounded below by large projecting tooth PI; PI finely striate on dorsal side. Hinge of left valve with anterior cardinal 2a very slender; cardinal 2b trigonal, sturdy; posterior cardinal 4b elongate, separated from the nymph by a shallow groove; anterior lateral AII long, heavy, parallel to lunular valve margin, posteriorly hooked, finely striate on dorsal side; posterior lateral tooth PII a salient portion of the shell-margin just posterior to the posterior end of the nymph. Pallial sinus and muscle scars unknown.

HOLOTYPE. LACMIP cat. no. 8200.

PARATYPES. LACMIP cat. nos. 8201–8204 from LACMIP loc. 28788, north of Sunflower Valley, Kings Co.; USNM cat. no. 456070 from USGS loc. M8573, Garza Peak Quadrangle, Kings Co. [20], California.

TYPE LOCALITY. LACMIP loc. 28788, north of Sunflower Valley, Reef Ridge Quadrangle, Kings Co. [20], California.

GEOLOGIC AGE. Cenomanian.

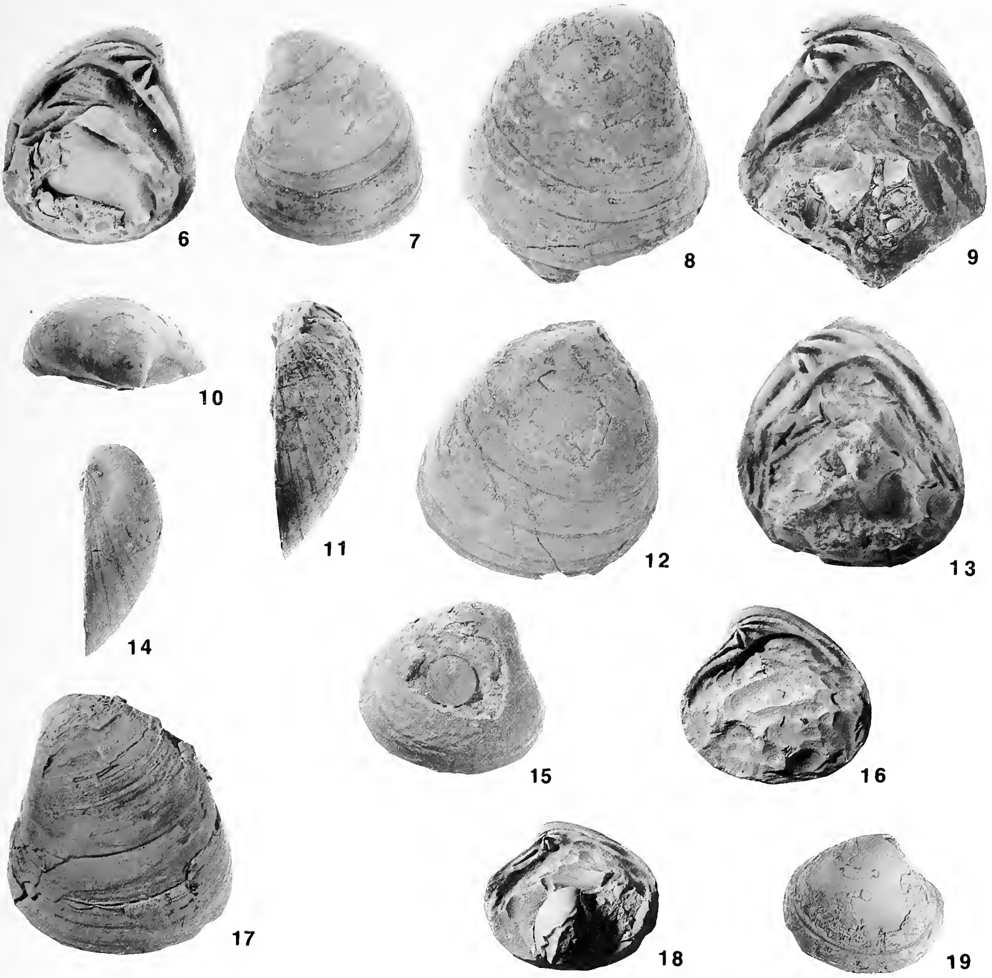
DISTRIBUTION. Boulders in a Panoche Formation conglomerate that crops out between Big Tar Canyon and Sunflower Valley, Kings Co. [20], California; Valle Formation, northern Vizcaíno Peninsula [33], Baja California Sur, Mexico.

DIMENSIONS. See Table 2.

REMARKS. *Calva heliaca* is tentatively included in *Calva* s.s. because of the very fine striations on its lateral teeth, relatively short, high PI, and bluntly truncated posterior. Within *Calva* s.s., C. (C.) *heliaca*'s attached 3a and 3b and distant 1 give it the most primitive hinge. It differs from other *Calva* s.s. in having the hinge plate strongly arched and from all other known *Calva* in being higher than long. Small specimens are relatively elongate and proportioned like other *Calva*, but those over 25 mm in length are higher than long. *Calva* (C.) *heliaca* resembles C. (*Egelicalva*) *taffi* in shape but is relatively higher, has a more bluntly truncated posterior, and has longer, stronger anterior lateral teeth.

At its type locality in redeposited boulders in a Panoche Formation conglomerate, *Calva* (C.) *heliaca* is associated with *Anthonya cultriformis* Gabb, 1864, and *Nelltia roddana* Saul, 1973, both indicative of Cenomanian age.

ETYMOLOGY. The species name, derived from



Figures 6–19. *Calva* (*Calva*) *heliaca,* new species. All ×1; all specimens whitened with ammonium chloride. **6, 7, 10, 14,** LACMIP cat. no. 8200, holotype, from LACMIP loc. 28788; **6,** hinge, **7,** exterior, **10,** dorsal view, **14,** anterior view. **8, 9,** LACMIP cat. no. 8201, paratype, from LACMIP loc. 28788, **8,** exterior, **9,** hinge. **11–13,** LACMIP cat. no. 8202, paratype, from LACMIP loc. 28788, **11,** posterior view, **12,** exterior, **13,** hinge. **15, 16,** LACMIP cat. no. 8154, paratype, from UCLA loc. 6973, **15,** exterior, **16,** hinge. **17,** USNM cat. no. 456070, paratype, from USGS loc. M8573, exterior. **18, 19,** LACMIP cat. no. 8203, paratype, from LACMIP loc. 28788, **18,** hinge, **19,** exterior. Photos 6–14 by Saul; 15–19 by De Leon.

Greek, *helios,* sun, refers to the type locality north of Sunflower Valley.

Calva (*Calva*) *regina* Popenoe, 1937

Figures 20–29

Calva regina Popenoe, 1937, p. 395, pl. 48, figs. 6–7, 13–14; Popenoe, 1954, fig. 4 (8); Keen *in* Moore, 1969, p. N677, fig. E145, 1a–1c; Jones, Sliter, and Popenoe, 1978, pl. 2, fig. 32.

Trigonocallista regina (Popenoe) Popenoe, 1940, p. 163; Anderson, 1958, p. 140.

DIAGNOSIS. A *Calva* with a subdued posterior angulation, strong posterior truncation, slightly concave lunular margin, and finely striated lateral teeth.

DESCRIPTION. Shell moderately thick, of moderate size, nearly as high as long, inflated, having a subdued posterior angulation; beaks prominent, anterior to the mid-length of the shell, prosogyrous; lunular margin slightly concave; anterior end sharply rounded; ventral border broadly arched; posterior end bluntly truncate vertically; posterior dorsal border moderately short, slightly arched; lunule heart-shaped, moderately large, deep, delimited by an inscribed line; escutcheon moderately wide, smooth, demarked by rounded angulation.

Ligament groove arched behind moderate nymphs. Hinge of right valve with anterior tooth 3a and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; posterior

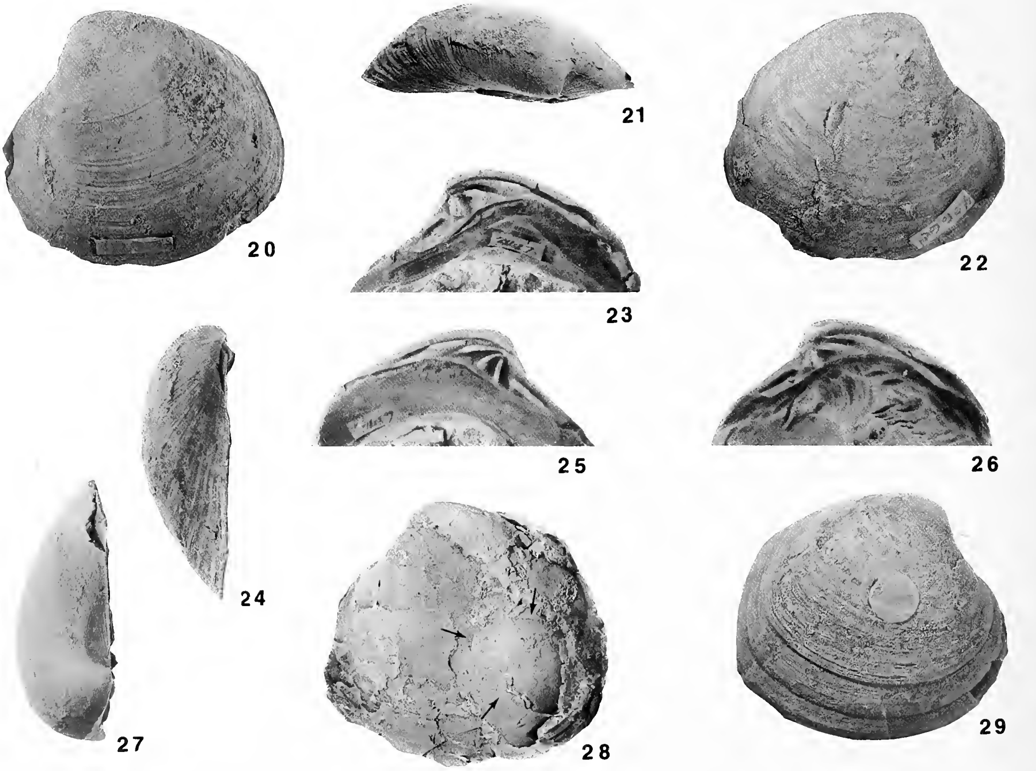
Table 2. Measurements of *Calva* (*Calva*) *heliaca*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8154	22.8	24.6		12.5	8.5	2.5	100°	1.1	—	2.0	1.5	3.4
LACMIP 8200	27.8	25.0	10.5	15.5	9.6	3.6	78°	0.9	2.4	1.6	1.6	2.7
LACMIP 8201	37.5	32.4	15.7	18.8	12.6	4.7	75°	0.9	2.1	1.7	1.5	2.7
LACMIP 8202	33.7	31.1	12.4	16.6	11.8	3.9	75°	0.9	2.5	1.9	1.4	3.0
LACMIP 8203	19.0	22.4	7.5	9.8	6.2	2.8	105°	1.2	3.0	2.3	1.6	2.2
USNM 456070	37.0	32.8	13.7	20.0	13.5	4.8	80°	0.9	2.4	1.6	1.5	2.8

cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, parallel to the lunular border of the shell, finely striate on both sides; socket for PII deep, bounded below by rather large projecting tooth PI; PI finely striate on dorsal side. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; cardinal 2b thicker than 2a, trigonal, directed posteriorly; posterior cardinal 4b slightly longer than the anterior teeth, slender; anterior lateral AII long, parallel to lunular valve margin, posteriorly hooked, finely striate on dorsal side; posterior lateral tooth PII a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broad, rounded, extending about to mid valve length; dorsal arm convex, almost horizontal; ventral arm arcuate, steeply ascending. Adductor muscle scars lightly impressed; anterior oval; posterior round.

SYNTYPES. UCLA cat. nos. 40660–40661 (ex CIT cat. no. 3447). UCLA 40661 was figured inadvertently as the holotype by Jones et al. (1978, pl. 2, fig. 32).

HYPOTYPES. LACMIP cat. nos. 8205 from UCLA loc. 2323, Santa Ana Mts. [26]; 8206 from



Figures 20–29. *Calva* (*Calva*) *regina* Popenoe. All ×1; all specimens whitened with ammonium chloride. **20, 21, 24, 25, 27,** UCLA cat. no. 40661, syntype, from CIT loc. 1164, **20,** exterior, **21,** dorsal view, **24,** posterior view, **25,** hinge, **27,** anterior view. **22, 23,** UCLA cat. no. 40660, syntype, from CIT loc. 1164, **22,** exterior, **23,** hinge. **26, 29,** LACMIP cat. no. 8205, hypotype, from UCLA loc. 2323, hinge, **29,** exterior. **28,** LACMIP cat. no. 8206, hypotype, from LACMIP loc. 10135, pallial sinus. Photos 20, 21, 23, 28, 29 by De Leon; 22, 24–27 by Saul.

Table 3. Measurements of *Calva* (*Calva*) *regina*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
UCLA 40660	33.7	38.0	10.3	16.0	9.5	3.0	109°	1.1	3.7	2.4	1.7	3.2
UCLA 40661	33.0	37.0	11.7	14.8	10.0	3.0	112°	1.1	3.2	2.5	1.5	3.3
LACMIP 8205	33.5	36.5	13.5	19.4	10.8	3.0	118°	1.1	2.7	1.9	1.8	3.6

LACMIP loc. 10135, Santa Ana Mts. [26], Orange Co., California.

TYPE LOCALITY. CIT loc. 1164, south side of Silverado Canyon opposite Holz Ranch house [26], Santa Ana Mts., Orange Co., California.

GEOLOGIC AGE. Turonian; associated with *Subprionocyclus neptuni* (Geinitz).

DISTRIBUTION. Ladd Formation, sandstone beds in the Baker Canyon Conglomerate Member, Santa Ana Mts. [26], Orange Co., California; Valle Formation, Cedros Island [32], Baja California Sur, Mexico.

DIMENSIONS. See Table 3.

REMARKS. *Calva* (*C.*) *regina* is thinner shelled, has a narrower hinge plate and a subdued angulation delimiting the escutcheon, and is more quadrate than the contemporaneous C. (*Egelicalva*) *spissa* with which it has been confused. C. (C.) *regina* is shorter and has a narrower, more arched hinge plate than C. (C.) *campanae.* The laterals of C. (C.) *regina* are finely striate, but those of C. (C.) *campanae* and geologically younger species of *Calva* s.s. are smooth. In overall shape C. (C.) *regina* is most like C. (C.) *peninsularis,* but all specimens of C. (C.) *regina* are smaller than average sized C. (C.) *peninsularis.* The specimens of C. (C.) *regina* figured by Popenoe (1937) are, however, relatively small, and specimens twice as large are common but usually crushed or broken. *Calva* (C.) *regina* is less inflated and has a more subdued posterior angulation and a larger lunule than C. (C.) *peninsularis. Calva* (C.) *varians* is more inflated and trigonal than C. (C.) *regina,* and C. (C.) *baptisia* has cardinal 4b longer than lateral AII.

Calva (*Calva*) *campanae,* new species

Figures 30–49

DIAGNOSIS. A relatively elongate *Calva* with straight lunular margin, weak posterior angulation, nearly straight hinge plate, and smooth laterals.

DESCRIPTION. Shell moderately thick, of moderate size, longer than high, moderately inflated; beaks prominent but low, anterior to the midlength of the shell, prosogyrous; lunular margin straight; anterior end rounded; ventral border broadly arched; posterior end bluntly truncate vertically; posterior dorsal border moderately short, slightly arched; lunule heart-shaped, moderately large, delimited by an inscribed line; escutcheon narrow, smooth, demarked by subdued angulation. Ligament groove arched behind moderate nymphs. Hinge of right valve with anterior tooth 3a and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; posterior cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, parallel to the lunular border of the shell; socket for PII deep, bounded below by a rather large projecting tooth PI. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; cardinal 2b thicker than 2a, trigonal, directed posteriorly; posterior cardinal 4b slightly longer than the anterior teeth, slender; anterior lateral AII long, parallel to lunular valve margin, posteriorly hooked; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broad, bluntly angulate, extending across two-fifths the valve length; dorsal arm nearly straight, horizontal; ventral arm slightly arcuate, steeply ascending.

HOLOTYPE. LACMIP cat. no. 8207.

PARATYPES. LACMIP cat. nos. 8208 from LACMIP loc. 10710, Bell Canyon [24]; 8209 from UCLA loc. 6020, Bell Canyon [24]; 8210–8212 from LACMIP loc. 10709, Bell Canyon [24]; 8213–8215 from UCLA loc. 6232, Bell Canyon [24], Simi Hills, Ventura Co.; 8216–8217 from LACMIP loc. 10096, Santa Ana Mts. [26], Orange Co., California.

HYPOTYPE. LACMIP cat. no. 8218 from LACMIP loc. 11944, Vizcaíno Peninsula [34], Baja California, Mexico.

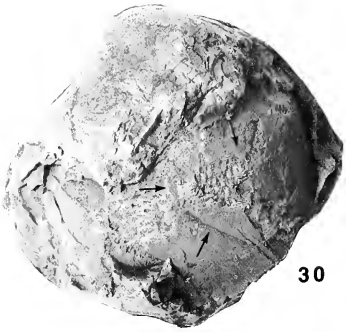
TYPE LOCALITY. LACMIP loc. 10710, Bell Canyon, Ventura Co. [24], California.

GEOLOGIC AGE. Mid and late Campanian.

DISTRIBUTION. Chatsworth Formation, Bell Canyon [24], Simi Hills, Ventura Co.; Uppermost Holz Shale Member of the Ladd Formation and Pleasants Sandstone Member of the Williams Formation, Santa Ana Mts., Orange Co. [26], California. Valle Formation, Vizcaíno Peninsula [34], Baja California Sur, Mexico.

DIMENSIONS. See Table 4.

REMARKS. *Calva* (*C.*) *campanae* has commonly been misidentified as *C.* (*Egelicalva*) *bowersiana* (Cooper). It is, however, generally smaller with a lower beak and has a relatively heavier hinge and a less depressed lunule. The ventral margin of the hinge plate of C. (C.) *campanae* is nearly straight from the ventral end of the posterior cardinal to the anterior end of the anterior cardinal, but in C. (E.) *bowersiana* the ventral margin of the hinge



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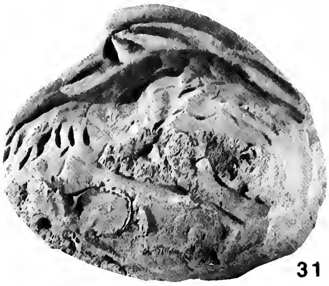

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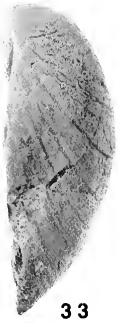

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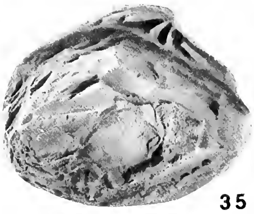

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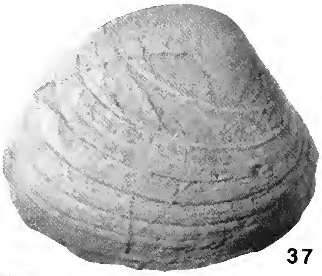

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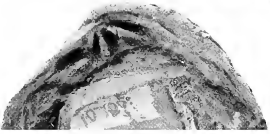

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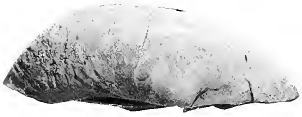

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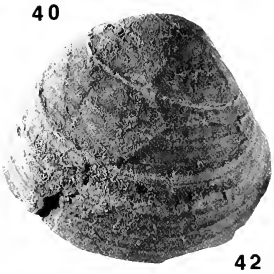

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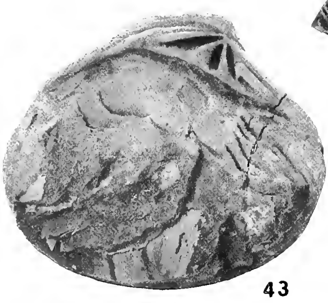

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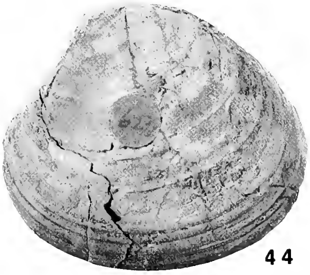

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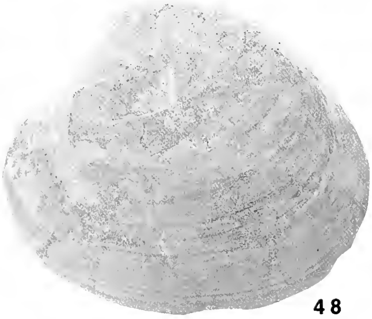

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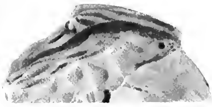

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Table 4. Measurements of *Calva* (*Calva*) *campanae*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8207	37.0	44.1	15.0	18.9	9.7	3.7	118°	1.2	2.9	2.3	1.9	2.6
LACMIP 8208	41.8	47.8	13.5	22.2	9.5	2.0	114°	1.1	3.5	2.2	2.3	4.8
LACMIP 8210	32.0	34.7	12.5	15.8	8.2	3.3	102°	1.1	2.8	2.2	1.9	2.5
LACMIP 8211	35.4	33.7	17.0	15.7	8.8	3.0		1.0	2.0	2.1	1.8	2.9
LACMIP 8213	35.4	40.0	15.8	18.2	11.4	2.5	120°	1.1	2.5	2.2	1.6	4.6
LACMIP 8214	29.0	35.3	12.3	15.9	15.9	1.6	120°	1.2	2.9	2.2	1.0	9.9
LACMIP 8216	25.7	32.0	10.4	16.5	6.4	1.8	120°	1.2	3.1	1.9	1.3	3.6
LACMIP 8217	19.8		7.8	10.8	4.7	1.0	120°	—	—	—	2.3	4.7

plate is arched. The anterior cardinal is relatively shorter than that of *C.* (*E.*) *bowersiana* but not as short as that of *Loxo decore* Dailey and Popenoe, 1966; unlike that of *L. decore,* the anterior lateral parallels the valve margin. The socket for 3b is relatively wider than that in *C.* (*E.*) *bowersiana,* and the posterior end of the anterior lateral is between the ventral end of 2a and the valve margin.

Calva (*C.*) *campanae* is more elongate and more inflated and has a broader, less arched hinge plate and a weaker posterior angulation than *Calva* (*C.*) *regina*. *Calva* (*C.*) *campanae* has a straighter hinge plate, and a broader lunule and lacks the distinctive angulation of *C.* (*C.*) *peninsularis.*

A large left valve, CAS cat. no. 66296.01, from "6 miles north of Rosario Canyon," Baja California, Mexico, may belong to this species, although no other specimen of *Calva* (*C.*) *campanae* approaches its length of 75 mm. The specimen is broken around the ventral margin and was probably at least 10 mm longer. The margin that would provide the posterior lateral is missing as is the posterior cardinal tooth 4b. The specimen also resembles C. (*C.*) *varians* but is larger than most specimens of C. (*C.*) *varians* and its anterior lateral is closer to the beak. It is comparable in size to *C.* (*Egelicalva*) *crassa* but has a straighter hinge line, the anterior lateral closer to the beak, and a less concave lunule. If this specimen is indeed *C.* (*C.*) *campanae* and the locality information is acurate, this is the first indication that beds of mid to late Campanian age crop out that far north of El Rosario.

ETYMOLOGY. The species is named for its type locality in Bell Canyon, *campana,* Latin, bell.

Calva (*Calva*) *peninsularis* (Anderson and Hanna, 1935)

Figures 50–66

Corbis peninsularis Anderson and Hanna, 1935, p. 31, pl. 10, fig. 1.

Corbis sp. aff. *C. peninsularis* Anderson and Hanna, Moore, 1968, p. 22, pl. 9a.

Trigonocallista sp., Sundberg, 1979, p. 176, pl. 1, fig. 9.

Calva sp., Sundberg and Riney, 1984, p. 104, fig. 2 (11).

DIAGNOSIS. A rounded *Calva* with slightly concave lunular margin, a posterior angulation, and smooth lateral teeth.

DESCRIPTION. Shell of moderate size, nearly as high as long, inflated, rather thick, having a posterior angulation extending from beak to posteroventral border; beaks prominent, rather high, placed anterior to the mid-length of the shell, prosogyrous; lunular margin slightly concave; anterior end rather sharply rounded; ventral border broadly arched; posterior end bluntly truncate vertically; posterior dorsal border of moderate length, slightly arched; lunule relatively small, deep, delimited by an inscribed line; escutcheon demarked by rounded angulation.

Ligament groove arched behind moderate nymphae. Hinge of right valve with anterior tooth 3a very short and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; 1 extending from very near the hinge plate edge to as

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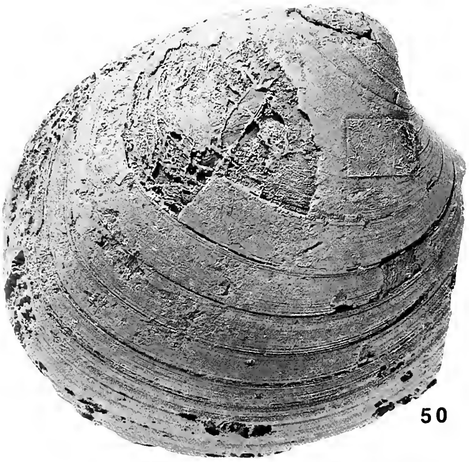
Figures 30–49. *Calva* (*Calva*) *campanae,* new species. All ×1; except as indicated, all specimens whitened with ammonium chloride. **30,** LACMIP cat. no. 8209, paratype, from UCLA loc. 6020, pallial sinus, without whitening. **31–34, 37,** LACMIP cat. no. 8207, holotype, from LACMIP loc. 10709, **31,** hinge, **32,** anterior view, **33,** posterior view, **34,** dorsal view, **37,** exterior. **35, 36,** LACMIP cat. no. 8216, paratype, from LACMIP loc. 10096, **35,** hinge, **36,** exterior. **38, 39,** LACMIP cat. no. 8214, paratype, from UCLA loc. 6232, **38,** exterior, **39,** hinge, **40, 42, 43,** LACMIP cat. no. 8210, paratype, from LACMIP loc. 10709, **40,** hinge, **42,** exterior, **43,** hinge. **41, 44,** LACMIP cat. no. 8213, paratype, from UCLA loc. 6232, **41,** dorsal view, **44,** exterior. **45, 46,** LACMIP cat. no. 8215, paratype, from UCLA loc. 6232, **45,** exterior, **46,** hinge. **47, 48,** LACMIP cat. no. 8208, paratype, from LACMIP loc. 10709, **47,** hinge, **48,** exterior. **49,** LACMIP cat. no. 8217, paratype, from LACMIP loc. 10096, hinge. Photos 30, 32, 33, 40, 43, 44, 47, 48 by Saul; 31, 34–39, 41, 42, 45, 46, 49 by De Leon.



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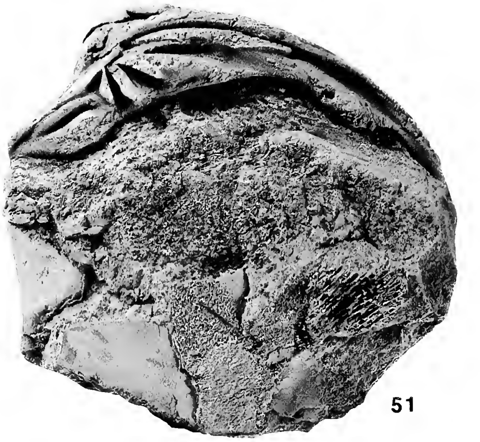

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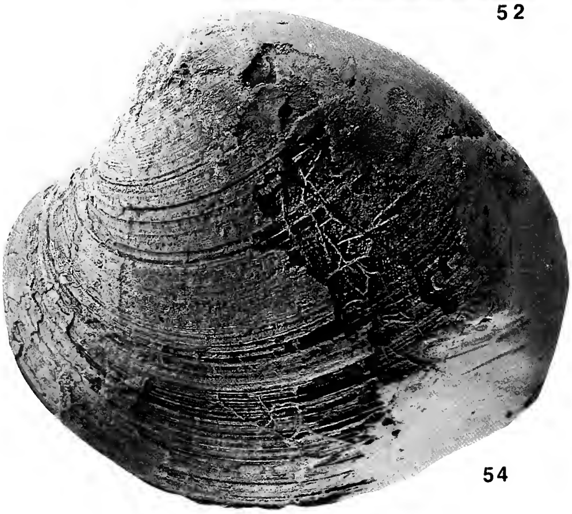

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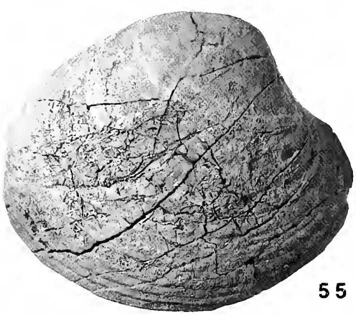

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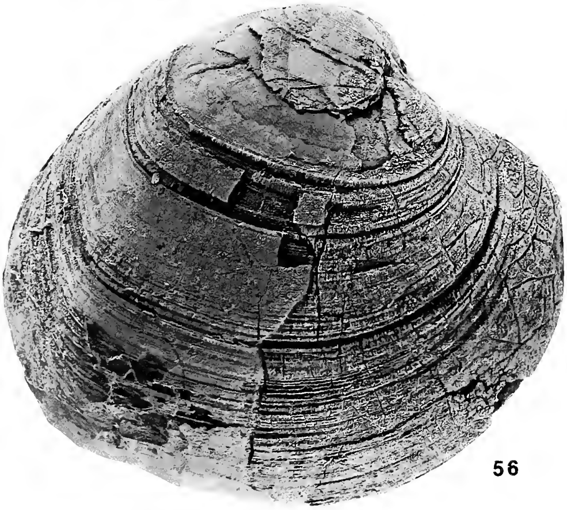

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close to beak as 3a; posterior cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, smooth, parallel to the lunular border of the shell; socket for PII deep, bounded below by a rather large projecting tooth. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; cardinal 2b thicker than 2a, trigonal, directed obliquely backward; posterior cardinal 4b continuous with the ventral side of the nymph, slightly longer than the anterior teeth, not very massive; anterior lateral AII long, wedge-shaped, parallel to the hinge border below the lunule, smooth sided; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broad, bluntly angulate, extending about to the posterior valve quarter length, arms nearly equal; dorsal arm slightly descending; ventral arm steeply ascending, slightly concave. Anterior adductor scar deeply set, semicircular; posterior adductor scar lightly impressed, rather round.

HOLOTYPE. UCMP cat. no. 36119.

HYPOTYPES. CAS cat. no. 66512.01 from CAS loc. 66512, Point Loma [28], San Diego Co.; SDSNH cat. no. 25994 from SDSNH loc. 3162-A, Carlsbad Research Center [27], San Diego Co.; LACMIP cat. nos. 7746 from LACMIP loc. 22629 (= SDSU loc. 6), La Jolla [28], San Diego Co.; 8219–8220 from UCLA 2415, Bee Canyon [26], El Toro Quadrangle, Orange Co., California; 8221 from LACMIP loc. 2855, Arroyo Santa Catarina [31]; 8222 from LACMIP loc. 5989, Arroyo Santa Catarina [31]; 8223–8224 from UCLA loc. 3268, Arroyo Santa Catarina [31]; UCMP cat. no. 38658 from UCMP loc. A-467, north of San Antonio del Mar [30], Baja California, Mexico.

TYPE LOCALITY. UCMP loc. A-467, 6.5 miles [10.4585 km] north of San Antonio del Mar [30], Baja California, Mexico.

GEOLOGIC AGE. Latest Campanian and early Maastrichtian.

DISTRIBUTION. Panoche Formation on Los Gatos Creek [19], Fresno Co., California; Williams Formation, Pleasants Sandstone at Bee Canyon [26], Santa Ana Mts., Orange Co., California; basal Point Loma Formation at La Jolla [28], and reworked into Cabrillo Formation on Point Loma [28], San Diego Co., California; Rosario Formation at Punta Banda [29], near San Antonio del Mar [30], and Arroyo Santa Catarina [31], Baja California, Mexico.

DIMENSIONS. See Table 5.

REMARKS. Anderson and Hanna (1935) did not describe a hinge for this species. The hinge of the holotype was exposed by W. P. Popenoe permitting a more appropriate familial and generic assignment. The posterior angulation readily distinguishes *Calva* (*C.*) *peninsularis* from all other species of *Calva*. It is less elongate than *C.* (*C.*) *varians*, more inflated than *C.* (*C.*) *campanae*, and smaller but more inflated than *C.* (*Penecallista*) *marina* and does not have as deep a lunule as *C.* (*Egelicalva*) *crassa*. It resembles *C.* (*C.*) *regina* but has smooth laterals.

In the Panoche Formation on the north side of Los Gatos Creek [19], Fresno Co., *Calva* (*C.*) *peninsularis* occurs in beds just below those yielding *Pachydiscus* (*Neodesmoceras*) cf. *P.* (*N.*) *catarinae* (Anderson and Hanna, 1935) and well above strata that yield *Metaplacenticeras* sp. At Bee Canyon [26], El Toro Quadrangle, Orange Co., specimens intermediate between *C.* (*C.*) *campanae* and *C.* (*C.*) *peninsularis* (Figs. 52, 53, 55) occur with compressed, fine-ribbed, tricarinate *Metaplacenticeras pacificum* (Smith, 1900). These *Metaplacenticeras* resemble the holotype of *M. pacificum*, and this typical morph is the youngest of the Pacific Slope forms that have commonly been referred to the *Metaplacenticeras pacificum* Zone (John Alderson, pers. communication).

Corbis aff. *Calva peninsularis* Anderson and Hanna, *in* Anderson, 1958 (p. 58), from CAS loc. 28118, Quinto Silt on north bank of Las Baños Creek [18], *Corbis peninsularis* Anderson and Hanna, *in* Anderson, 1958 (p. 61), from CAS loc. 2359, Upper Asuncion, Garzas Member, south side of Deer Valley [15], and *Corbis peninsularis* Anderson and Hanna, *in* Anderson, 1958 (p. 61), from CAS loc. 25707, Upper Asuncion, Garzas Member, SW¼ Sec. 27, T1N, R2E [15], are all *Calva* (*C.*) *varians* (Gabb).

Aphrodina major (Packard) of Anderson and Hanna (1935, p. 28) from CAS loc. 1431, near Santa Catarina Landing is *C.* (*C.*) *peninsularis*.

Calva (*Calva*) *varians* (Gabb, 1864)

Figures 67–89

Venus varians Gabb, 1864, p. 161 (in part), pl. 23, fig. 140–140a, only. Not fig. 141 = *Calva buttensis* Anderson, 1958.

Aphrodina varians (Gabb) Stewart, 1930, p. 249, pl. 6, fig. 6.

"*Trigonocallista*" *varians* (Gabb) Anderson, 1958, p. 138. Not *Trigonocallista* cf. *T. varians* (Gabb) Hall, 1958, p. 54, pl. 7, fig. 2 = *Calva* (*Egelicalva*) *spissa*, new species. Not *Calva varians* (Gabb)

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Figures 50–57. *Calva* (*Calva*) *peninsularis* (Anderson and Hanna). All ×1; all specimens whitened with ammonium chloride. **50, 51,** UCMP cat. no. 36119, holotype, from UCMP loc. A-467, **50,** exterior, **51,** hinge. **52,** LACMIP cat. no. 8219, hypotype, from UCLA loc. 2415, hinge. **53, 55,** LACMIP cat. no. 8220, hypotype, from UCLA loc. 2415, **53,** hinge, **55,** exterior. **54, 56, 57,** UCMP 38658, hypotype, from UCMP loc. A-467, **54,** exterior left valve, **56,** exterior right valve, **57,** anterior view. Photos 50, 51, 54, 56, 57 by Susuki; 52, 53 by Saul; 55 by De Leon.

Table 5. Measurements of *Calva* (*Calva*) *peninsularis.* Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8219			17.8		10.4	3.3	105°	—	—	—	—	3.2
LACMIP 8220	39.6	46.4	16.5	20.4	10.7	3.0	93°	1.2	2.8	2.3	1.9	3.6
LACMIP 8221	65.8	75.0	29.0	29.0	15.5	4.5	103°	1.1	2.6	2.6	1.9	3.4
LACMIP 8222	61.5	67.4	24.7	25.7	14.5	3.7	100°	1.1	2.7	2.6	1.8	3.9
LACMIP 8223	58.2	66.8	24.0	24.0	12.3	3.5	113°	1.1	2.8	2.8	2.0	3.5

Dailey and Popenoe, 1966, p. 16, pl. 4, figs. 1–4; Saul, 1970, p. 80, fig. 16 = C. (*Egelicalva*) *crassa,* new species. Not *Calva varians* (Gabb) Saul, 1986, p. 26, figs. 7–9 = *Loxo quintense* Saul, in press.

DIAGNOSIS. A *Calva* with nearly straight lunular margin, smooth lateral teeth, and cardinal tooth 1 longer than and approaching closer to the beak than 3a.

DESCRIPTION. Shell of moderate size, nearly as high as long, inflated, thick; beaks prominent, moderately high, anterior to the mid-length of the shell, strongly prosogyrous; lunular margin straight to slightly convex; anterior end broadly rounded; ventral border slightly arched, medially flattened; posterior end bluntly truncate vertically; posterior dorsal border long, slightly arched; lunule moderately large, shallow, delimited by an inscribed line; escutcheon obscurely delimited.

Ligament groove arched behind low nymphae. Hinge of right valve with anterior tooth 3a shortest and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; 1 extending from near the hinge plate edge closer to the beak than 3a; posterior cardinal 3b long, straight, shallowly bifid, subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, smooth, parallel to the lunular border of the shell; socket for PII deep, bounded below by a rather large projecting tooth. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; cardinal 2b thicker than 2a, trigonal, directed obliquely backward; posterior cardinal 4b continuous with the ventral side of the nymph, slightly longer than the anterior teeth, not very massive; anterior lateral AII long, wedge-shaped, parallel to the hinge border below the lunule, smooth sided; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broad, bluntly angulate, extending across one-half of valve length; dorsal arm nearly horizontal and straight; ventral arm steeply ascending, a little concave. Anterior adductor muscle scar deeply impressed, ovoid; posterior adductor muscle scar impressed, rather round.

LECTOTYPE. ANSP cat. no. 4383, designated by Stewart, 1930.

PARALECTOTYPES. ANSP cat. no. 76481 (eight specimens) and UCMP cat. nos. 39832–39833 from Martinez [15], Contra Costa Co., California.

HYPOTYPES. UCMP cat. no. 38656 from UCMP loc. 2609, near Martinez [15], Contra Costa Co., California. LACMIP cat. nos. 8226–8229 from UCLA loc. 3313, south side Deer Valley [15]; 8230 from UCLA loc. 3957, south side Deer Valley [15], Contra Costa Co.; 8231–8232 from UCLA loc. 6345, south of Ortigalita Creek [18], Merced Co.; 8233 from LACMIP loc. 29217, Cantinas Creek [21], San Luis Obispo Co., California.

TYPE LOCALITY. Martinez, Contra Costa Co., California.

GEOLOGIC AGE. Late Maastrichtian.

DISTRIBUTION. Great Valley Series near Martinez [15] and Deer Valley Formation of Colburn (1964) Deer Valley [15], Contra Costa Co.; Garzas Member of the Moreno Formation, east border of the Diablo Range, Stanislaus [17] and Merced Counties [18]; El Piojo Formation, near Lake Nacimiento [21], San Luis Obispo Co., California.

DIMENSIONS. See Table 6.

REMARKS. Gabb's name is apt for this species of variable elongation. The lectotype is more elongate and has a lower beak than most specimens of *Calva* (*C.*) *varians* from the type locality. It resembles specimens of *Loxo quintense* Saul (in press), but like other specimens of *C.* (*C.*) *varians* has a longer anterior lateral that parallels the lunular margin, and the shell is more roundly inflated than that of *L. quintense.*

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Figures 58–66. *Calva* (*Calva*) *peninsularis* (Anderson and Hanna). All ×1; all specimens whitened with ammonium chloride. **58, 60,** LACMIP cat. no. 8223, hypotype, from UCLA loc. 3268, **58,** hinge, **60,** exterior. **59, 61–63, 66,** LACMIP cat. no. 8221, hypotype, from LACMIP loc. 2855, **59,** dorsal view, **61,** anterior view, **62,** posterior view, **63,** exterior, **66,** hinge. **64,** LACMIP cat. no. 8222, hypotype, from LACMIP loc. 5989, interior. **65,** LACMIP cat. no. 8224, hypotype, from UCLA loc. 3268, pallial sinus. Photos 58, 59, 64, 66 by Saul; 60–63, 65 by De Leon.

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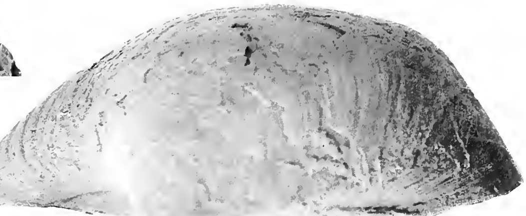

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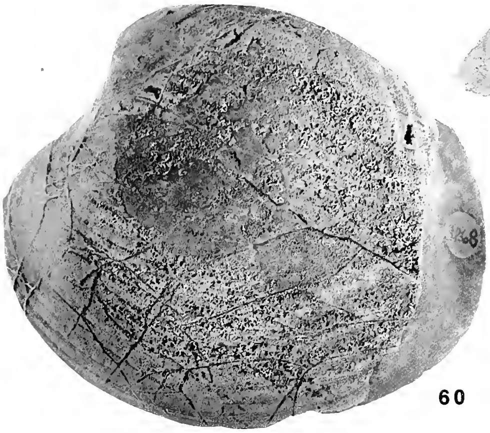

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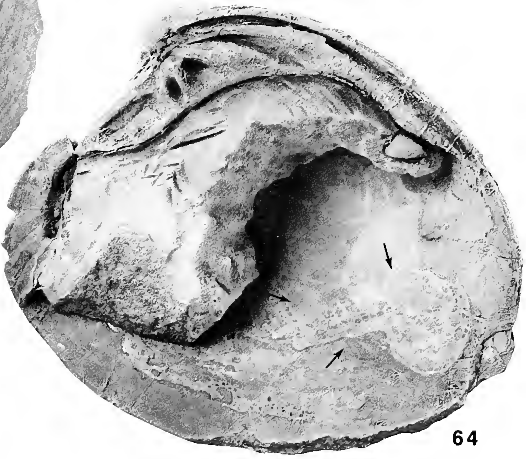

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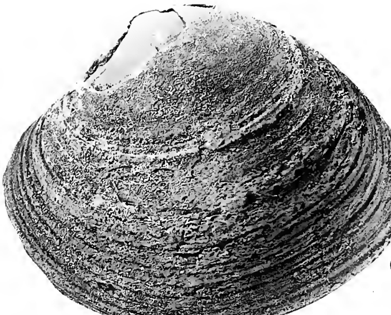
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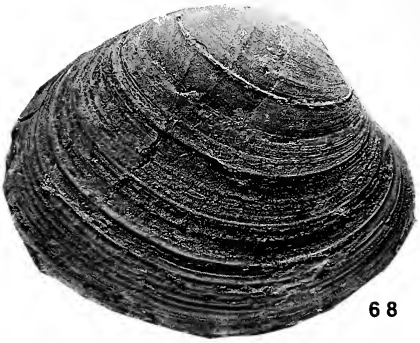
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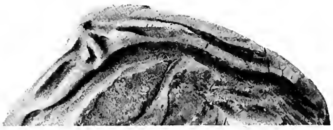
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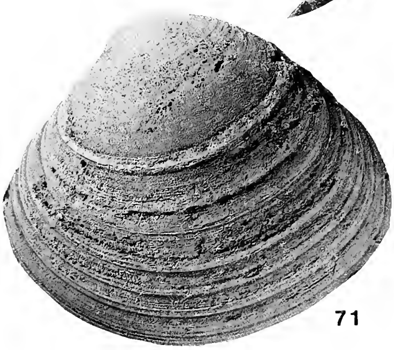
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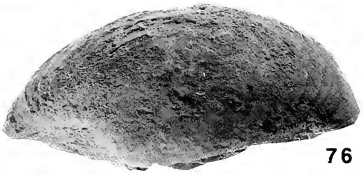
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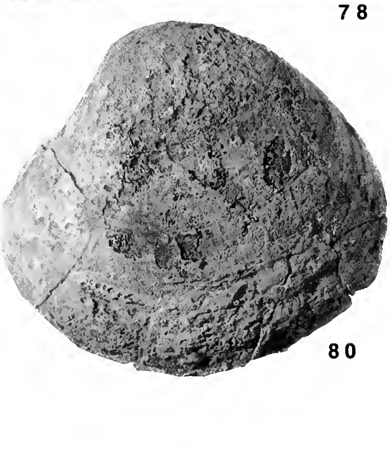
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Table 6. Measurements of *Calva* (*Calva*) *varians.* Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
UCLA 36284*	40.7	49.0	16.0	22.0	13.7	3.7	105°	1.2	3.1	2.2	1.6	3.7
UCLA 36285*	43.0	48.7	15.5	23.6	12.3	3.7		1.1	3.1	2.1	1.9	3.3
UCLA 36286*	41.5	49.7	16.5	20.7	13.0	3.5		1.2	3.0	2.4	1.6	3.7
LACMIP 8225	45.4	50.8	19.0	20.0	13.7	4.4	113°	1.1	2.7	2.5	1.4	3.1
LACMIP 8226	37.0		16.0	18.0	11.5	3.0	110°	—	—	—	1.6	3.8
LACMIP 8227	54.3	61.0	25.8	21.8	15.5	5.5	97°	1.1	2.4	2.8	1.4	2.8
LACMIP 8228	44.4	48.0	18.0	22.4	16.5	3.9	91°	1.1	2.7	2.1	1.4	4.2
LACMIP 8229	48.6	50.4	21.8	21.7	15.4	5.7	90°	1.0	2.3	2.3	1.4	2.7
LACMIP 8231	41.6	48.0	18.9	21.0	15.0	4.0	99°	1.2	2.5	2.3	1.4	3.8
LACMIP 8232	48.0	53.0	18.9	22.4	11.4	3.0	98°	1.1	2.8	2.4	2.0	3.8

* Plaster casts of ANSP 4383, 76481a, 76481b.

Gabb (1864, p. 231) listed *Venus varians* from 12 localities now known to range in age from Cenomanian to late Maastrichtian. Among these localities only the type locality, Martinez, provides specimens conspecific with the lectotype. Although all of the specimens Gabb identified as *Venus varians* could have been considered to be syntypes, Stewart (1927, 1930) did not use this term, nor, after he had selected the lectotype, did he refer to remaining specimens identified by Gabb as paralectotypes. Gabb's specimens of *Venus varians* from his 12 localities belong to several of the species described in this paper, and only his specimens from the type locality are treated as paralectotypes of *Calva* (*Calva*) *varians* (Gabb, 1864). Two of the specimens, UCMP cat. nos. 39832–39833, in a box labeled (in a hand resembling Gabb's) "*Venus varians* G. Siskiyou Mts." are C. (C.) *varians* and have the preservation and matrix of specimens from Martinez. A fragment of a *Meekia sella* Gabb, 1864, a species common at Martinez but not found in the Siskiyou Mountains is in the matrix of UCMP cat. no. 39832, and UCMP cat. nos. 39832–39833 are considered to be paralectotypes of C. (C.) *varians.* Merriam (1895) listed *Venus* (*Chione*) *varians* Gabb; vol. I, pl. 23, fig. 140, among the type specimens in the Geological Museum of the University of California, but Stewart (1930) did not record its catalogue number and said that it should be in the Museum of Paleontology. A specimen, marked "type," labeled as from the Siskiyou Mountains, was considered by Stewart to be possibly the specimen referred to by Merriam, but despite several searches, this specimen is not now recognizable.

None of the specimens of *Calva* (C.) *varians* is as large as large specimens of C. (*Egelicalva*) *crassa. Calva* (C.) *varians* is more elongate than C. (E.) *crassa,* and whereas the lunular border in C. (E.) *crassa* is concave, in C. (C.) *varians* it is nearly straight or slightly convex, and the lunule is relatively narrow, more elongate oval than heart-shaped or lanceolate. The stratigraphic ranges of C. (E.) *crassa* and C. (C.) *varians* overlap as both are present in the Moreno Formation at UCLA loc. 6345, south of Ortigalita Creek [18], Merced Co., California. Although other occurrences of C. (E.) *crassa* are from deposits of early Maastrichtian age, this overlap is considered to be of mid Maastrichtian age because C. (C.) *varians* occurrences are of mid and late Maastrichtian age. Three other specimens in the box are *Calva* (E.) *spissa* and undoubtedly from the lower Hornbrook Formation of the Siskiyou Mountains.

In shape *Calva* (C.) *varians* varies from somewhat elongate subquadrate resembling C. (C.) *campanae* to shorter subquadrate. It differs from C. (C.) *campanae* in being more inflated and having a slightly higher beak. *Calva* (C.) *varians* is less inflated than C. (C.) *peninsularis* and does not have the distinctive strong posterior angulation of that

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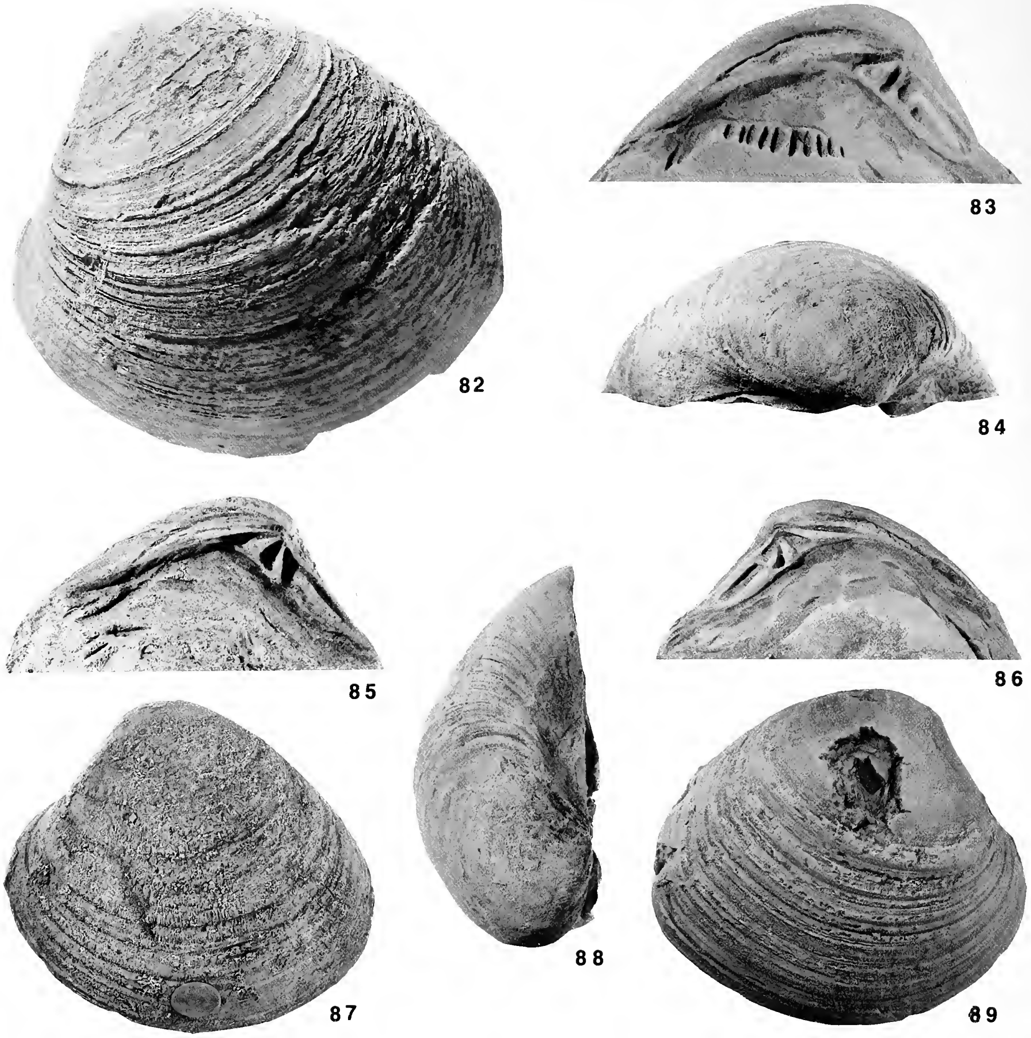
Figures 67–81. *Calva* (*Calva*) *varians* (Gabb). All ×1; all specimens whitened with ammonium chloride. **67, 69, 72,** ANSP cat. no. 4383, lectotype, from Martinez, **67,** exterior, **69,** hinge, **72,** dorsal view. **68,** ANSP cat. no. 76481a, paralectotype, from Martinez, exterior. **70,** LACMIP cat. no. 8226, hypotype, from UCLA loc. 3313, hinge. **71,** ANSP cat. no. 76481b, paralectotype, from Martinez, exterior. **73, 74, 77,** LACMIP cat. no. 8228, hypotype, from UCLA loc. 3313, **73,** hinge, **74,** posterior view, **77,** exterior. **75, 76, 81,** LACMIP cat. no. 8229, hypotype, from UCLA loc. 3313, **75,** hinge, **76,** dorsal view, **81,** anterior view. **78, 80,** LACMIP cat. no. 8232, hypotype, from LACMIP loc. 29217, **78,** hinge, **80,** exterior. **79,** LACMIP cat. no. 8230, hypotype, from UCLA loc. 3957, pallial sinus. Photos 67–69, 71, 72 by Susuki; 70, 73–75 by Saul; 76–81 by De Leon.



Figures 82–89. *Calva* (*Calva*) *varians* (Gabb). All ×1; all specimens whitened with ammonium chloride. **82–84, 88,** LACMIP cat. no. 8227, hypotype, from UCLA loc. 3313, **82,** exterior, **83,** hinge, **84,** dorsal view, **88,** anterior view. **85, 87,** LACMIP cat. no. 8231, hypotype, from UCLA loc. 6345, **85,** hinge, **87,** exterior. **86, 89,** UCMP cat. no. 38656, hypotype, from UCMP loc. 2609, **86,** hinge, **89,** exterior. Photos 82 by Susuki; 83–89 by De Leon.

species. *Calva* (*C.*) *baptisia* has a shorter more swollen anterior lateral AII. *Calva* (*C.*) *varians* differs from *Loxo quintense,* new species, with which it occurs north of Lake Nacimiento [21] and at Garzas Creek [17], in being relatively less elongate, having more prominent beaks, and having anterior lateral tooth AII and its socket parallel to the lunular margin and more distant from the cardinal teeth.

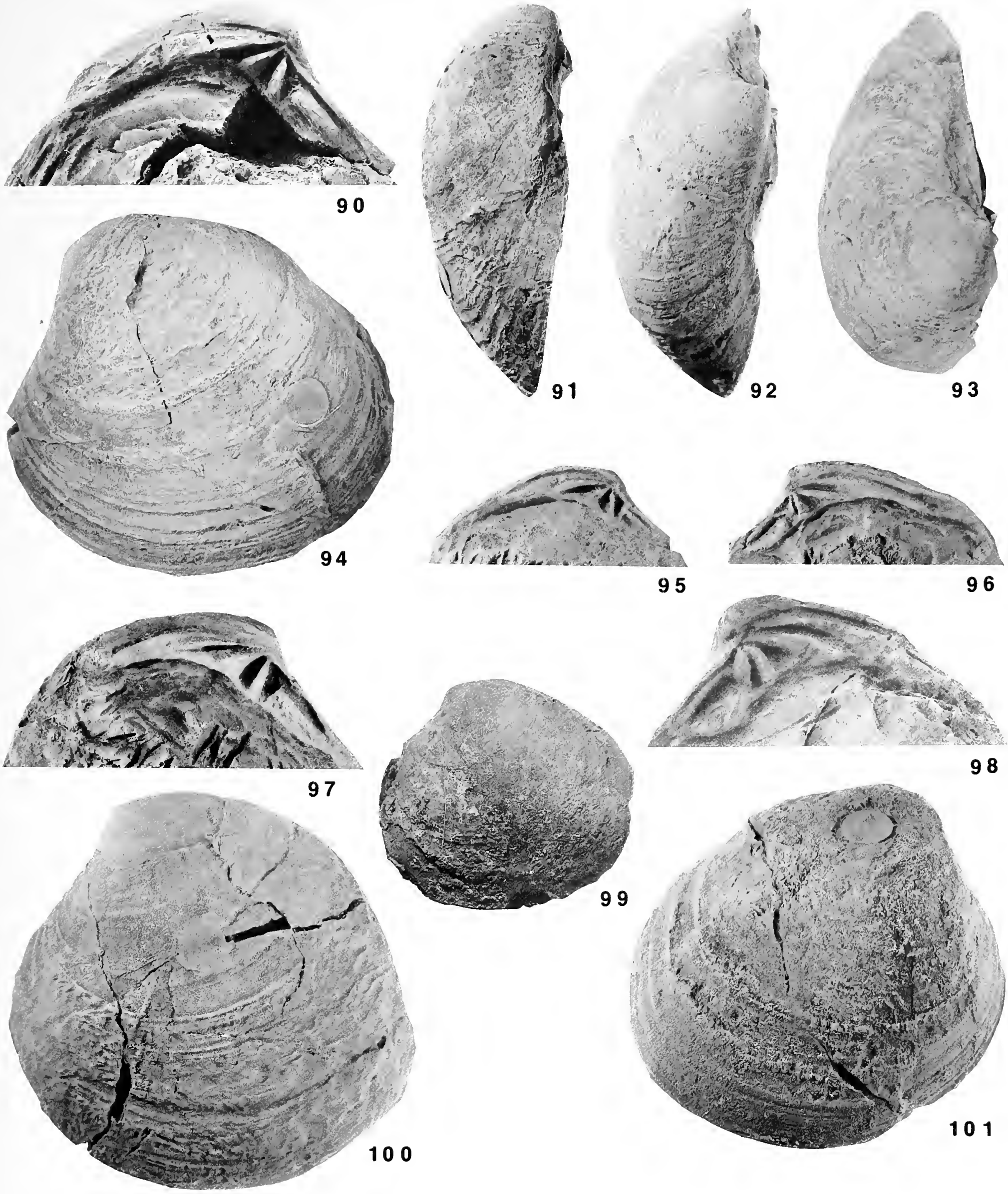
Venus varians, Trigonocallista varians, or *Calva varians* appear on faunal lists from many Pacific Slope Cretaceous localities of various geologic ages, but only those specimens from rocks of mid to late Maastrichtian age are likely to be *Calva* (*C.*) *varians.* Hall's (1958) specimen of supposed latest Jurassic or earliest Cretaceous age is discussed under *C.* (*Egelicalva*) *spissa.* Dickerson's (1914) *Venus varians* from UCMP loc. 783, one-half mile west of Lower Lake, Lake Co., California, is closer to *Lucina alcatrazis* Anderson, 1938, than to *C.* (*C.*) *varians* and may be of Cenomanian rather than Maastrichtian age.

Calva (*Calva*) *baptisia,* new species

Figures 90–101

Calva cf. *C. varians* (Gabb) Saul, 1986, p. 29, figs. 41–43.

DIAGNOSIS. A relatively short, rounded *Calva* with anteriorly placed beak, straight lunular margin, smooth lateral teeth, and cardinal 3a noticeably shorter than 1; 1 extending from near the hinge



Figures 90–101. *Calva* (*Calva*) *baptisia*, new species. All ×1; all specimens whitened with ammonium chloride. All from UCLA loc. 6526. **90–94,** LACMIP cat. no. 7559, holotype, **90,** hinge, **91,** posterior view, **92,** dorsal view, **93,** anterior view, **94,** exterior. **95, 99,** LACMIP cat. no. 8235, paratype, **95,** hinge, **99,** exterior. **96,** LACMIP cat. no. 8234, paratype, hinge. **97, 100,** LACMIP cat. no. 8183, paratype, **97,** hinge, **100,** exterior. **98, 101,** LACMIP cat. no. 7560, paratype, **98,** hinge, **101,** exterior. Photos 90, 98 by Saul; 91–97, 99–101 by De Leon.

plate edge and approaching the beak more closely than 3a; lateral AII enlarged, swollen, shortened.

DESCRIPTION. Shell of moderate size, nearly as high as long, inflated, thick; beaks prominent, moderately high, placed anterior to the mid-length of the shell, prosogyrous; lunular margin slightly convex to straight; anterior end rounded; ventral border arched; posterior end rounded; posterior dorsal border long, slightly arched; lunule moderately large, impressed, delimited by an inscribed line; escutcheon delimited by blunt angulation.

Ligament groove long, arched, nymph strong, smooth. Hinge of right valve with anterior cardinal tooth 3a and median cardinal tooth 1 sturdy, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks, 1 noticeably longer than 3a and more closely approaching beak; posterior cardinal 3b long, arched, shallowly bifid, subparallel to the nymph; socket for lateral AII

Table 7. Measurements of *Calva* (*Calva*) *baptisia*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 7559	49.5	54.5	19.7	23.3	12.0	3.4	103°	1.1	2.8	2.3	1.9	3.5
LACMIP 7560	49.4	50.2	20.0	18.3	13.0	5.0	101°	1.0	2.5	2.7	1.4	2.6
LACMIP 8183	53.2	55.3?	17.3	24.0	15.7	4.4		1.0	3.2	2.3	1.5	3.6
LACMIP 8234					7.7	2.2	124°	—	—	—	—	3.5
LACMIP 8235	31.5	34.3	10.8	13.5?	7.7	2.4	123°	1.1	3.2	2.5	1.8	3.2

moderately long, deep, smooth, parallel to the lunular border of the shell; socket for PII deep, bounded below by a rather large projecting tooth. Hinge of left valve with anterior cardinal 2a prominent, slender, somewhat posteriorly directed; cardinal 2b slightly thicker than 2a, directed posteriorly; posterior cardinal 4b nearly twice as long as 2a and 2b, sturdy; anterior lateral AII moderately long, parallel to the hinge border below the lunule, smooth sided, thick, a little hooked at the dorsal end; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus and muscle scars unknown.

HOLOTYPE. LACMIP cat. no. 7559.

PARATYPES. LACMIP cat. nos. 7560, 8234–8235 from UCLA loc. 6526, Dip Creek [21], San Luis Obispo Co., California.

TYPE LOCALITY. UCLA loc. 6526, Dip Creek [21], Lime Mountain Quadrangle, San Luis Obispo Co., California.

GEOLOGIC AGE. Latest Maastrichtian and ?earliest Danian.

DISTRIBUTION. Dip Creek Formation of Taliaferro (1944) on Dip Creek [21], San Luis Obispo Co.; basal San Francisquito Formation on Warm Springs Mountain, Los Angeles Co. [23], California.

DIMENSIONS. See Table 7.

REMARKS. *Calva* (*C.*) *baptisia* differs from *C.* (*C.*) *varians* in being more equant and in having a shorter anterior end, a wider LTA, a shorter lunule, a straighter lunular margin, and a shorter anterior lateral. The posterior margin of the right valve LACMIP 7560 is smashed (Fig. 98), obscuring the posterior lateral and socket, but the posterior portion of the right hinge is preserved in LACMIP 8234 (Fig. 96). "*Dosiniopsis*" *stewartvillensis* Clark and Woodford, 1927, from the Meganos Formation of Contra Costa Co. [15], California, resembles *C.* (*C.*) *baptisia*. "*Dosiniopsis*" *stewartvillensis* is rounder than *C.* (*C.*) *baptisia*, has a shorter anterior lateral, and lacks posterior laterals, although the posterior shell margin is grooved. As in *C.* (*C.*) *baptisia*, the anterior laterals of "*D.*" *stewartvillensis* are not striated, and it is not a *Dosiniopsis*. Its right posterior cardinal 3b differs from that of *Calva* in being widely bifid and curved anteriorly as in *Nitidavenus* Vokes, 1939, and "*D.*" *stewartvillensis*, despite its superficial resemblance to *C.* (*C.*) *baptisia*, is an unlikely descendent. The cardinal teeth of *Calva* suggest that descendents might more likely be found in *Callista* Poli, 1791.

ETYMOLOGY. The specific name is from Greek, *baptisis*, a dipping, dyeing, for the type locality on Dip Creek [21], San Luis Obispo Co., California.

Subgenus *Egelicalva*, new subgenus

TYPE SPECIES. *Cucullaea bowersiana* Cooper, 1894.

DIAGNOSIS. *Calva* spp. of trigonal shape, smooth except for growth lines and checks, having the lunule impressed and wide and the escutcheon very obscurely developed. Hinge plate moderately to strongly arched, with the major flexure at or in front of cardinal tooth 3b, the posterior lateral socket relatively long and narrow, and posterior lateral PI well developed but low. Pallial sinus linguiform.

DISCUSSION. *Egelicalva*, the *Calva nitida* lineage, comprises *C.* (*E.*) *byblidis*, *C.* (*E.*) *nitida*, *C.* (*E.*) *spissa*, *C.* (*E.*) *taffi*, *C.* (*E.*) *buttensis*, *C.* (*E.*) *bowersiana*, and *C.* (*E.*) *crassa*. Species of *Egelicalva* of Albian through early Campanian age have laterals that are more coarsely striated than those of the typical lineage. Their vertical striations are localized on longitudal welts, and the sockets are wider below the welts. The ventral side of the posterior lateral socket, both sides of the anterior lateral socket, and the dorsal side of the anterior lateral tooth have these finely striate welts. Species of the *C. nitida* lineage are of medium to large size and have a moderately to well arched hinge plate that is relatively narrow and a lunule that is wide and deeply impressed. Posterior lateral PI of the right valve barely extends beyond the plane of the commissure and bounds a socket that is relatively narrower than that of *Calva* s.s. The pallial sinus of *Egelicalva* is narrower at the pallial line and of more linguiform shape than that of *Calva* s.s.

Egelicalva bears a greater resemblance to *Trigonocallista* Rennie, 1930, than does *Calva* s.s. *Egelicalva* has striations on the laterals of Turonian and earlier species that are similar in size to the striations on the laterals of *Trigonocallista*. Both *Egelicalva* and *Trigonocallista* have a more trigonal shape, whereas *Calva* s.s. is more truncate posteriorly and has a more quadrate shape. *Egelicalva* differs from *Trigonocallista* in having the escutcheon obscurely indicated rather than clearly demarked, a deeper pallial sinus, anterior lateral AII straight but with a sharp posterior interiorward bend rather than being slightly arched concavely to the exterior, and the anterior arm of the bifid cardinal 3b shorter than the posterior arm rather than equal to or longer than the posterior arm.

ETYMOLOGY. The subgeneric name is compounded from Latin *egelidus,* lukewarm, tepid, chilly, refering to the apparently cooler, more northern distribution of this group, and *Calva* and is of feminine gender.

Calva (*Egelicalva*) *byblidis,* new species

Figures 102–113

DIAGNOSIS. An *Egelicalva* with striated lateral teeth. Cardinal tooth 1 extending to the hinge plate margin and somewhat distant from the beak; cardinal 3a shorter than 1 and extending closer to the beak than 1.

DESCRIPTION. Shell of moderate size, slightly longer than high, roundly inflated posteriorly, moderately thick; beaks prominent, high, anterior to the mid-length of the shell, prosogyrous; lunular margin slightly concave; anterior end produced, rounded, ventral border broadly arched; posterior end barely truncate; posterior dorsal slope long, slightly arched; lunule lanceolate, sunken, circumscribed by a fine line and a ridge; escutcheon faintly marked off, extending the length of the posterior dorsal border; shell surface polished, marked by growth lines and distant, lightly impressed growth checks.

Ligament groove long, behind smooth, posteriorly salient nymphs. Hinge of right valve with anterior cardinal 3a short, narrow, overhanging the socket for 2a; medial cardinal 1 narrowly triangular, based at the ventral hinge plate margin and not extending as far beakward as 3a and 3b; posterior cardinal 3b long, barely arched, shallowly bifid; socket for lateral AII long, moderately deep, parallel to the lunular border of the shell; socket for PII long, deep, bounded below by a long, projecting tooth. Hinge of left valve with anterior cardinal 2a prominent, narrowly trigonal, aligned almost vertically beneath the beak; cardinal 2b thicker than 2a, trigonal, directed obliquely backward; posterior cardinal 4b longer than the anterior teeth, slender, high, slightly arcuate, set off from nymph by marked groove; anterior lateral AII long, parallel to the lunular margin, wedge-shaped, posteriorly hooked; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broadly linguiform, ascending, extending to mid valve length; dorsal arm slightly convex, nearly horizontal; ventral arm barely concave, ascending at angle of about 35° to pallial line. Anterior adductor muscle scar impressed.

HOLOTYPE. LACMIP cat. no. 8098.

PARATYPES. LACMIP cat. nos. 8099 and 8104 from LACMIP loc. 29231, Texas Springs [9]; 8100 and 8101 from LACMIP loc. 29230, Texas Springs [9]; 8102 from UCLA loc. 3916, Texas Springs [9]; USNM cat. no. 456068 from USGS loc. 1051, Texas Springs [9], Shasta Co., California.

HYPOTYPE. LACMIP cat. no. 8146 from UCLA 4285, from a slump block, south of Sites [13], Colusa Co., California.

TYPE LOCALITY. LACMIP loc. 29231, Texas Springs [9], Shasta Co., California.

GEOLOGIC AGE. Early Albian, *Brewericeras hulenense* Zone.

DISTRIBUTION. Budden Canyon Formation at Texas Springs [9], Shasta Co.; ?Great Valley Series south of Sites [13], Colusa Co., California.

DIMENSIONS. See Table 8.

REMARKS. *Calva* (*Egelicalva*) *byblidis* resembles *Calva* s.s. species in having the escutchon obscurely demarked, but it is less truncate posteriorly, and its anterior lateral is more strongly striate. It is most similar to *C.* (*E.*) *nitida* from which it differs in being slightly more elongate, having a deeper lunule, and having cardinal tooth 1 more distant from 3a and more ventrally placed on the hinge plate.

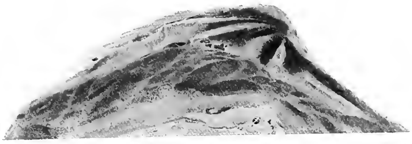
The species is fairly common in deposits of early Albian age near Texas Springs [9], Shasta Co., but because the shells are recrystallized and the matrix is hard, specimens are difficult to extract. Only the seven most complete specimens have been used in this study; all are from the vicinity of Texas Springs, Shasta Co., California. An additional incomplete specimen from a transported block 2.8 miles south of Sites is referred to this species with reservations. Whiteaves (1876) described *Callista* (?) *subtrigona* from the Queen Charlotte Islands, British Columbia, but the whereabouts of his figured specimen is not known. The Royal British Columbia Museum has a number of specimens identified by Whiteaves from localities with *Anagaudryceras sacya* (Forbes, 1846) suggesting that *Callista* (?) *subtrigona* Whiteaves is of late Albian to early Cenomanian age. Whiteaves' (1876, p. 63, pl. 9, fig. 10) original figure is of a much more rounded form than that of any available specimen of *Calva* (*Egelicalva*) *byblidis.* Only LACMIP cat. no. 8099, a specimen considered to be deformed, has an outline approaching that of Whiteaves' figure. Additionally, Whiteaves illustrated and several of the Royal British Columbia Museum specimens show a very trigonal pallial sinus rather than the linguiform shape of *C.* (*E.*) *byblidis*; the two species are doubtless distinct.

ETYMOLOGY. The specific name is derived from Greek, *Byblis,* a nymph changed into a spring.

Calva (*Egelicalva*) *nitida*
(Gabb, 1864)

Figures 114–135

Meretrix nitida Gabb, 1864, p. 165, pl. 23, figs. 145–146. Not *Meretrix nitida* Gabb Whiteaves, 1903, p. 377, includes *Calva* (*Egelicalva*) *buttensis* (Anderson, 1958) and *C.* (*E.*) *bowersiana* (Cooper, 1894).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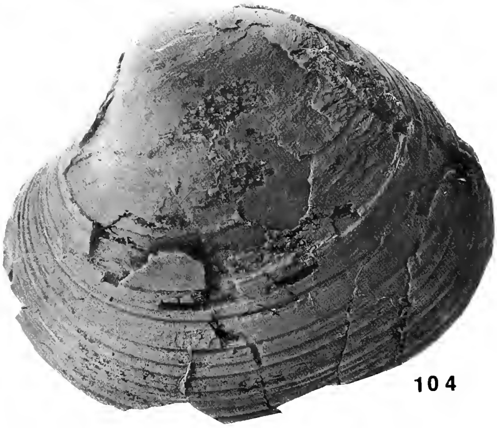
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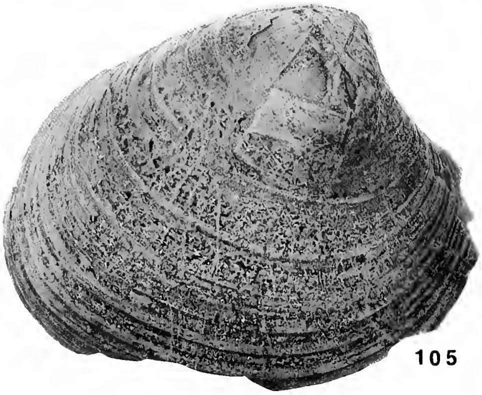
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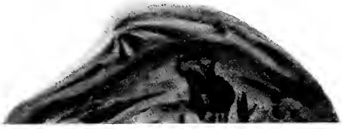
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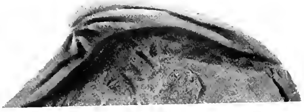
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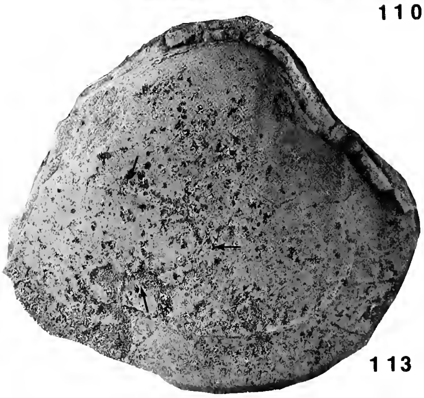
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Figures 102–113. *Calva* (*Egelicalva*) *byblidis,* new species. All ×1; all specimens whitened with ammonium chloride. **102, 104, 108, 109,** LACMIP cat. no. 8100, paratype, from LACMIP loc. 29230, **102,** hinge, **104,** exterior, **108,** posterior view, **109,** anterior view. **103, 105, 111,** LACMIP cat. no. 8098, holotype, from LACMIP loc. 29231, **103,** hinge, **105,** exterior, **111,** dorsal view. **106,** LACMIP cat. no. 8099, paratype, from LACMIP loc. 29231, hinge. **107,** USNM cat. no. 456068, paratype, from USGS loc. 1051, hinge. **110,** LACMIP cat. no. 8101, paratype, from LACMIP loc. 29230, hinge. **112,** LACMIP cat. no. 8104, hypotype, from LACMIP loc. 29231, pallial sinus. **113,** LACMIP cat. no. 8146, hypotype, from UCLA loc. 4285, hinge. Photos 102–112 by Saul; 113 by De Leon.

Table 8. **Measurements of *Calva* (*Egelicalva*) *byblidis*. Dimensional abbreviations defined in Figure 4.**

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8098	49.0	61.8	17.0	27.3	19.4	4.7	118°	1.3	3.6	2.3	1.4	4.1
LACMIP 8099	42.6	46.0	17.0	25.0	14.2	4.3	114°	1.1	2.7	1.8	1.8	3.3
LACMIP 8100	52.6	63.8	16.7	27.0	15.0	4.4	124°	1.2	3.8	2.4	1.8	3.4
LACMIP 8101			13.0		13.0	4.0	116°	—	—	—	—	3.2
LACMIP 8102			17.0		16.4	4.6	121°	—	—	—	—	3.6
LACMIP 8146			18.0		17.5	4.4	108°	—	—	—	—	4.0
USNM 456068	43.8		18.7	24.8	19.0	4.4	124°	—	—	—	1.3	4.3

Caryatis nitida (Gabb) Gabb, 1869, p. 186, pl. 30, fig. 79.

Aphrodina nitida (Gabb) Stewart, 1930, p. 250, pl. 5, fig. 10; pl. 6, fig. 9.

"*Trigonocallista*" *nitida* (Gabb) Anderson, 1958, p. 139. Not *Trigonocallista nitida* (Gabb) Taff, Hanna, and Cross, 1940, p. 1232, pl. 2, figs. 3–4 = *Calva* (*Egelicalva*) *taffi* Anderson, 1958.

DIAGNOSIS. A trigonal, slightly longer than high *Egelicalva* with striated lateral teeth, the lunular border nearly straight. Cardinal tooth 1 extending to the hinge plate margin. Cardinal 3a shorter than 1 and extending closer to the beak than 1.

DESCRIPTION. Shell of moderate size, slightly longer than high, inflated, moderately thick; beaks prominent, high, anterior to the mid-length of the shell, prosogyrous; lunular border nearly straight; anterior end slightly produced, sharply rounded, ventral border broadly arched; posterior end barely truncate; posterior dorsal border long, slightly arched; posterior dorsal slope arched; lunule heart-shaped, sunken, circumscribed by a fine line; escutcheon faintly marked off by obscure angulation, extending the length of the posterior dorsal border; shell surface polished, marked by growth lines and distant barely impressed growth checks.

Ligament groove arched behind smooth, posteriorly salient nymphs. Hinge of right valve with anterior cardinal 3a short, narrow, prominent; medial cardinal 1 narrowly triangular, based at the ventral hinge plate margin; posterior cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, parallel to the lunular border of the shell, finely striate along both sides; socket for PII deep, bounded below by large projecting tooth PI; PI finely striate along dorsal face. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; left median cardinal 2b thicker than 2a, trigonal, directed obliquely backward; left posterior cardinal 4b continuous with the ventral side of the nymph, slightly longer than the anterior teeth, not very massive; anterior lateral AII long, prominent and hooked posteriorly, parallel to the lunular valve margin, finely striate along dorsal face; striae at posterior end of tooth noticeably coarsest; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus linguiform with angulate tip, slightly ascending, extending to valve mid-length; dorsal arm convex, nearly horizontal; ventral arm concavely ascending. Anterior adductor muscle scar impressed, at the anterior end of the hinge plate, posterior adductor muscle scar lightly impressed.

LECTOTYPE. ANSP 4374. Gabb did not designate type specimens or type localities. Stewart (1927, 1930) commonly referred to Gabb's illustrated specimens as holotypes and gave preference in designating lectotypes to figured specimens or to specimens from the same lot or locality as Gabb's figured specimen. Stewart (1930) did not find the specimens of *Meretrix nitida* that Gabb had figured and chose not to designate a lectotype for this species but figured two specimens from the same lot as Gabb's figured specimens. The larger of these, ANSP 4374, is here designated as lectotype.

PARALECTOTYPE. ANSP 4374a from the type locality.

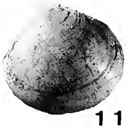
HYPOTYPES. LACMIP cat. nos. 8106–8107 from LACMIP loc. 6165, Andy Bernard Ranch [5], Crook Co., 8111–8113 from UCLA loc. 4669, near Suplee, Crook Co. [5], Oregon; 8105 from LACMIP loc. 28766, Stony Creek, Glenn Co. [12], 8108–8109 from LACMIP 10871, Elder Creek [10], Tehama Co., California. CAS cat. no. 28104.01 from CAS loc. 28104, Curry Canyon [15], Contra Costa Co., California.

TYPE LOCALITY. "Near Martinez [15], in loose blocks on the shores of the Straits of Carquines" (Gabb, 1864).

GEOLOGIC AGE. Late Albian–Cenomanian; associated with *Turrilites* at Suplee [5], Crook Co., Oregon; from *Turrilites dilleri* Zone in Ono area [9], Shasta Co., California (Rodda, 1959, p. 96).

DISTRIBUTION. Hudspeth Formation, along Rock Creek [4], Wheeler Co., and near Dayville [4], Grant Co., Oregon; Bernard Formation, Suplee [5], Crook Co., Oregon; Osburger Gulch Sandstone Member of the Hornbrook Formation near Jacksonville [6], Jackson Co., Oregon; Bald Hills Member of the Budden Canyon Formation, near Ono [9], Shasta Co., California. Redeposited (?) clasts, of possible or probable late Albian age, in Cenomanian strata, at Curry Canyon [15], Contra Costa


114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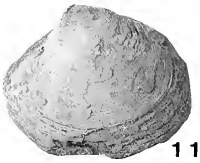
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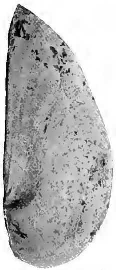
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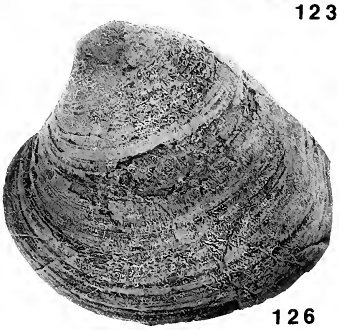
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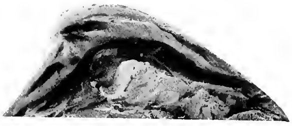
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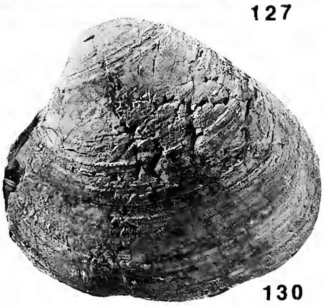
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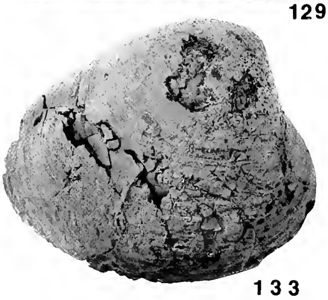
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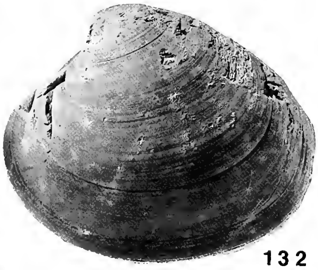
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Figures 114–135. *Calva* (*Egelicalva*) *nitida* (Gabb). All ×1; except as indicated, all specimens whitened with ammonium chloride. **114, 118,** CAS cat. no. 28104.01, hypotype, from CAS loc. 28104, **114,** hinge, **118,** exterior. **115,** ANSP cat. no. 4374, paralectotype, from Martinez, exterior, without whitening. **116,** ANSP cat. no. 4374a, lectotype, from Martinez, exterior, without whitening. **117, 120,** LACMIP cat. no. 8108, hypotype, from LACMIP loc. 10871, **117,** hinge, **120,** exterior. **119, 121, 124,** LACMIP cat. no. 8106, hypotype, from LACMIP loc. 6165, **119,** anterior view, **121,** hinge, **124,** exterior. **122, 123, 126,** LACMIP cat. no. 8107, hypotype, from LACMIP loc. 6165, **122,** posterior view, **123,** hinge, **126,** exterior. **125, 128, 129, 133,** LACMIP cat. no. 8112, hypotype, from UCLA loc. 4669, **125,** anterior view,

Table 9. Measurements of *Calva* (*Egelicalva*) *nitida*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
UCLA 28770*	14.7	15.7	6.6					1.1	2.4	—	—	—
UCLA 28771*	29.5	35.5	11.4					1.2	3.1	—	—	—
LACMIP 8105	53.0?	62.0	22.7	28.0?	15.0	5.6	108°	1.2	2.7	2.2	1.9	2.7
LACMIP 8106	33.7	37.8	12.8	17.8	10.8	4.0	107°	1.1	2.9	2.1	1.6	2.7
LACMIP 8107	37.7	41.8	14.8	20.1	12.0	4.5	106°	1.1	2.8	2.1	1.7	2.7
LACMIP 8108	19.5	23.7	7.3	11.0	6.0	2.3	107°	1.2	3.2	2.1	1.8	2.6
LACMIP 8109	32.8	36.4	7.0	17.0	10.0	3.7	111°	1.1	5.2	2.1	1.7	2.7
LACMIP 8110	19.4	24.0	8.4	10.7	7.0	2.7	127°	1.2	2.9	2.2	1.5	2.6
LACMIP 8111	35.0	40.4	16.0	16.5	12.0?	3.5	101°	1.2	2.5	2.4	1.4	3.4
LACMIP 8112	34.5	40.5	12.8	18.7	11.2	4.1	102°	1.2	3.2	2.2	1.7	2.7

* Plaster casts of ANSP 4374 and 4374a.

Co., Sites, Antelope Creek, and Peterson Ranch [13], Colusa Co., Elder Creek [10], Tehama Co., North Fork of Cottonwood Creek [9], Shasta Co., etc., along the western border of the northern Great Valley (Rodda, 1959; Brown and Rich, 1960).

DIMENSIONS. See Table 9.

REMARKS. *Calva* (*Egelicalva*) *nitida* and *Calva* (*Calva*) *varians* have commonly been confused and reported to co-occur. Gabb (1864, p. 165) remarked upon the great resemblance between *Meretrix nitida* and *Venus varians* but used the smaller size, polished surface, fewer and less distinct lines of growth, and the presence of a deeply impressed line bordering the lunule of *M. nitida* to distinguish it from *V. varians*. However, those characters, which depend in part upon conditions of preservation or of growth, cannot define species (Stewart, 1930), and both species have an inscribed line bordering the lunule. *Calva* (*E.*) *nitida* has a more prominent beak, is more strongly concave just anterior to the beak, and has a straighter, more steeply sloping posterior dorsal margin than *C.* (*C.*) *varians*. The anterior laterals of *C.* (*E.*) *nitida* are striated but those of *C.* (*C.*) *varians* are smooth. *Calva* (*E.*) *nitida* is more trigonal than *C.* (*C.*) *regina*, *C.* (*C.*) *peninsularis*, *C.* (*C.*) *baptisia*, *C.* (*E.*) *byblidis*, *C.* (*E.*) *bowersiana*, and *C.* (*Penecallista*) *marina*. Its anterior end is relatively longer than that of *C.* (*C.*) *regina*, *C.* (*C.*) *peninsularis*, *C.* (*C.*) *varians*, or *C.* (*C.*) *baptisia*. It never develops the hunched over aspect of the posterodorsal area exhibited by *C.* (*E.*) *taffi*, usually by *C.* (*E.*) *crassa*, and sometimes by *C.* (*C.*) *varians*. It resembles *C.* (*E.*) *bowersiana*, but striations on its lateral teeth are visible without magnification, whereas those on the laterals of *C.* (*E.*) *bowersiana* are present only on small specimens and require a magnification of at least 30×. The anterior lateral socket in the right valve does not connect with the socket for 2a. Cardinal tooth 1 of *C.* (*E.*) *nitida* has a more triangular shape and is in a more ventral position closer to the hinge plate margin than that of any geologically younger *Calva*.

For both *Meretrix nitida* and *Venus varians* the type locality is in the vicinity of Martinez [15], but they do not occur in the same beds there or elsewhere. Gabb's specimens from the "loose blocks on shore of Carquines Strait" have a distinctly different matrix from that of the type material of *V. varians*. The matrix additionally contains some other fossils not found in association with *V. varians* but that are found in collections from Curry Canyon [15], on the slope of Mt. Diablo, Contra Costa Co. The matrix, furthermore, resembles that from Curry Canyon [15], and specimens of *M. nitida* identical in appearance to Stewart's (1930) figured specimens (Figs. 115, 116) are found at Curry Canyon [15] (Figs. 114, 118).

The age of the Curry Canyon [15] occurrences of *Calva* (*Egelicalva*) *nitida* is possibly late Albian or more probably Cenomanian. *Calva* (*E.*) *nitida* has been found in the Bald Hills Member of the Budden Canyon Formation, near Ono [9], Shasta Co., which contains Cenomanian ammonites (Rodda, 1959; Murphy and Rodda, 1960), and in Oregon with Cenomanian ammonites.

Calva (*Egelicalva*) *nitida* occurs from central Oregon [4] to Contra Costa Co. [15], California. Although Whiteaves (1903) identified it from the Nanaimo Basin Deposits in British Columbia, those of his specimens that have been examined are *Calva* (*E.*) *bowersiana* or, as is the case of some specimens

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←
128, dorsal view, **129**, hinge, **133**, exterior. **127, 130,** LACMIP cat. no. 8111, hypotype, from UCLA loc. 4669, **127**, hinge, **130**, exterior. **131, 132,** LACMIP cat. no. 8109, hypotype, from LACMIP loc. 10871, **131**, hinge, **132**, exterior. **134**, LACMIP cat. no. 8105, hypotype, from LACMIP loc. 28766, hinge. **135**, LACMIP cat. no. 8113, hypotype, from UCLA loc. 4669, pallial sinus. Photos 114, 118–120, 123, 129, 131, 134 by De Leon; 115, 116, 130, 132 by Susuki; 117, 121, 122, 124–128, 133, 135 by Saul.

at the Royal British Columbia Museum that were labeled as *Caryatis nitida* by Whiteaves, are *C.* (*Microcalva*) *haggarti,* new species. If, as seems likely, some of his specimens came from lower horizons than the specimens presently available, they might well be *C.* (*E.*) *buttensis* (Anderson, 1958).

Calva (*Egelicalva*) *spissa*, new species

Figures 136–154

Trigonocallista cf. *T. varians* (Gabb, 1864) Hall, 1958, p. 54, pl. 7, fig. 2.

DIAGNOSIS. A trigonal *Egelicalva* with nearly straight lunular margin and finely striate lateral teeth. Cardinal tooth 1 extending barely to hinge plate edge; 3a short.

DESCRIPTION. Shell thick, of moderate size, nearly as high as long, rather trigonal; beaks prominent, moderately high, anterior to the mid-length of the shell, prosogyrous; lunular margin nearly straight; anterior end bluntly rounded; ventral border broadly arched; posterior end obscurely truncated, arched into the posterior dorsal border; lunule heart-shaped, moderately large, delimited by an inscribed line; escutcheon not delimited; shell surface polished, marked by growth lines and distant, well-impressed growth checks.

Ligament groove long, arched, behind moderate nymphs. Hinge plate broad. Hinge of right valve with anterior tooth 3a short, vertically directed immediately beneath the beak; median cardinal 1 longer but narrower, close to 3a, directed a little posteriorly; 3b elongate, bifid; socket for AII long, deep, subparallel to the lunular valve margin, finely striate on both sides; socket for PII deep, narrow, bounded below by prominent projecting lateral PI; PI finely striate on dorsal side. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; left median cardinal 2b thicker than 2a, trigonal, directed posteriorly; posterior cardinal 4b longer than the anterior cardinals, slender; anterior lateral AII posteriorly hooked, parallel to the lunular valve margin, striate along dorsal face; striae noticeably coarsest at posterior end; posterior lateral tooth PII a salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus extending across two-fifths of valve length, ascending, broadly linguiform with subangulate tip; dorsal arm slightly convexly ascending; ventral arm concavely ascending at angle of about 50° to pallial line. Anterior adductor muscle scar ovoid; posterior adductor muscle scar bean-shaped.

HOLOTYPE. LACMIP cat. no. 8114.

PARATYPES. LACMIP cat. nos. 8115 from LACMIP loc. 10782, Stinking Creek [8], Shasta Co., 8116–8119 from UCLA loc. 5422, Rancheria Gulch [7], Siskiyou Co., 8120 from UCLA loc. 4251, Young Ranch [7], Siskiyou Co., 8121 from UCLA loc. 5522, SE ridge of Garza Peak [20], Kings Co., 8129–8139 from UCLA loc. 4250, Young Ranch [7], Siskiyou Co., 8131 from UCLA loc. 6370, Cooper Canyon [19], Fresno Co., California. CAS cat. nos. 31920.02–31920.03 from CAS loc. 31920, Thompson Creek [13], Yolo Co., 29491.01 from CAS loc. 29491, Salado Creek [17], Stanislaus Co., California. UCMP cat. no. 39829–39831 from Siskiyou Mts. [7], Oregon–California border. USNM cat. no. 456069 from USGS loc. 660 = USGS loc. 21369, 1 mile southeast of Buckeye [8], vicinity of Dry Creek, Shasta Co., California. LACMIP cat. nos. 8125–8126 from LACMIP loc. 10903, Ashland Creek [6], Jackson Co., Oregon.

TYPE LOCALITY. LACMIP loc. 10769, Dry Creek [8], Shasta Co., California.

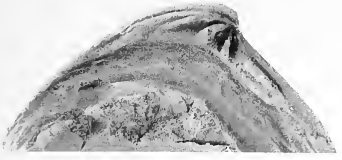
GEOLOGIC AGE. Turonian; associated with *Tragodesmoceras ashlandicum* (Anderson, 1902) and *Subprionocyclus* spp.

DISTRIBUTION. Hornbrook Formation, Osburger Gulch Member, Ashland region [6], Jackson Co., Oregon; Hornbrook Formation, Osburger Gulch Member, Rancheria Gulch [7], near Henley, Siskiyou Co.; Redding Formation, Bellavista Sandstone Member, Redding area [8], Shasta Co.; basal Yolo Shale, Thompson Creek [13], Yolo Co.; Great Valley Series in Arroyo del Valle, Alameda Co. [15]; lower Panoche Formation on Salado Creek [17], Stanislaus Co., California. Well-preserved specimens are from a clast in the Panoche Formation on an eastward trending spur of Garza Peak [20], Kings Co., California.

DIMENSIONS. See Table 10.

REMARKS. Three paratypes of *Calva* (*Egelicalva*) *spissa,* UCMP cat. nos. 39823–39830, are labeled in a hand resembling Gabb's "*Venus varians* G. Siskiyou Mts." and are probably the basis for Gabb's (1864, p. 231) listing *V. varians* from the Siskiyou Mountains. Also in the same box were paralectotypes of *Calva* (*C.*) *varians* discussed herein under that species. This agglomeration of specimens probably led Stewart (1930, p. 250) to say that University of California, Berkeley, had specimens from the Siskiyou Mountains conspecific with the lectotype of *C.* (*C.*) *varians. Calva* (*E.*) *spissa* is higher and more trigonal and has a longer lunule and longer lateral teeth than *C.* (*C.*) *varians,* and the lateral teeth of *C.* (*E.*) *spissa* are striate.

Calva (*Egelicalva*) *spissa* resembles *C.* (*E.*) *nitida* in being equantly trigonal but differs in having a steeper posterior slope, blunter anterior, broader umbonal area, less deeply impressed lunule, and broader pallial sinus. The anterior lateral of *C.* (*E.*) *spissa* is prominent and strongly hooked posteriorly, its socket is very deep and strongly hooked, and the striae at the posterior end of AII and on the dorsal face of AI are coarse enough to be seen under low magnification. Specimens of *C.* (*E.*) *spissa* have been identified as *C.* (*C.*) *regina,* but *C.* (*E.*) *spissa* is trigonal rather than subquadrate in shape and has more coarsely striated lateral teeth. *C.* (*E.*) *spissa* differs from *C.* (*E.*) *taffi* in lacking the hunched-over aspect to the beak and in having more coarsely striated laterals. Early Coniacian specimens are intermediate between *C.* (*E.*) *spissa* and *C.* (*E.*)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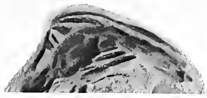
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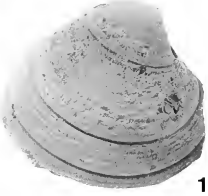
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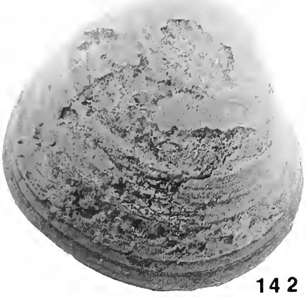
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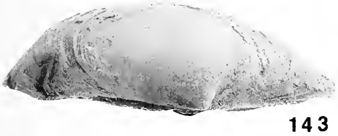
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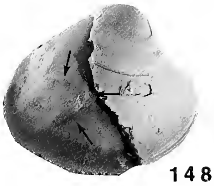
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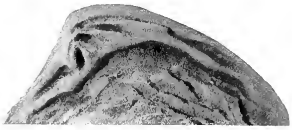
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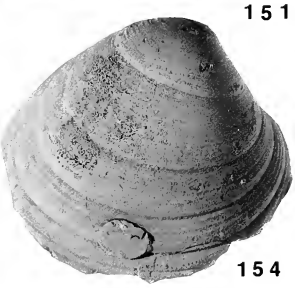
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Figures 136–154. *Calva* (*Egelicalva*) *spissa,* new species. All ×1; all specimens whitened with ammonium chloride. **136, 139, 143,** LACMIP cat. no. 8114, holotype, from CIT loc. 1203, **136,** hinge, **139,** exterior, **143,** dorsal view. **137, 140, 141,** CAS cat. no. 29491.01, paratype, from CAS loc. 29491, **137,** hinge, **140,** exterior, **141,** dorsal view. **138, 142,** LACMIP cat. no. 8115, paratype, from LACMIP loc. 10782, **138,** hinge, **142,** exterior. **144,** LACMIP cat. no. 8116, paratype, from UCLA loc. 5422, hinge. **145, 146,** LACMIP cat. no. 8117, paratype, from UCLA loc. 5422, **145,** hinge, **146,** posterior view. **147, 150,** CAS cat. no. 31920.02, paratype, from CAS loc. 31920, **147,** anterior view, **150,** dorsal view. **148,** LACMIP cat. no. 8120, paratype, from UCLA loc. 4251, pallial sinus. **149, 152,** CAS cat. no. 31920.03, paratype, from CAS loc. 31920, **149,** hinge, **152,** exterior. **151, 154,** LACMIP cat. no. 8121, paratype, from UCLA loc. 5522, **151,** hinge, **154,** exterior. **153,** LACMIP cat. no. 8129, hypotype, from UCLA loc. 4250, exterior resembling C. (*E.*) *taffi.* Photos 136, 138, 140, 142, 143, 145–147, 150 by Saul; 137, 141, 144, 148, 149, 151–154 by De Leon; 139 by Susuki.

Table 10. Measurements of *Calva* (*Egelicalva*) *spissa*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8114	40.5	44.0	13.8	23.0	13.7	2.8	99°	1.1	3.2	1.9	1.7	4.9
LACMIP 8115	40.0	41.7	14.5	23.0	13.0	4.3	94°	1.0	2.9	1.8	1.8	3.0
LACMIP 8116	40.5	44.7	14.3	21.0	13.8	4.5	96°	1.1	3.1	2.1	1.5	3.1
LACMIP 8117	37.6	41.7	14.0	21.8	12.8	3.0	92°	1.1	3.0	1.9	1.7	4.3
LACMIP 8121	35.6	38.5	14.4	19.5	10.8	4.3	104°	1.1	2.7	2.0	1.8	2.5
LACMIP 8122	30.3	35.9	11.3	14.2	9.3	1.9	110°	1.2	3.2	2.5	1.5	4.9
LACMIP 8129	29.5	35.7	11.1	14.4	8.1	2.9		1.2	3.2	2.5	1.8	2.8
CAS 29491.01	25.0	28.0	9.9	14.5	7.6	2.8	95°	1.1	2.8	1.9	1.9	2.7

taffi; they have the shape of C. (*E.*) *spissa* with the teeth of C. (*E.*) *taffi*.

The specimen figured by Hall (1958, pl. 7, fig. 2) (LSJU cat. no. 8458 = CAS cat. no. 66237.01) is a *Calva spissa*. This specimen, purported to be from the Oakland Conglomerate of ?Late Jurassic–Early Cretaceous age, is labeled as being collected in 1906, ½ mile [0.8045 km] northeast of Niles, in conglomerate along road up south side of Niles Canyon, Niles Quadrangle, Alameda Co., California. Crandall (1907) also reported a specimen of *Venus varians* from 1¼ miles [2.01125 km] northeast of Niles, but says that it was from a hard flinty limestone concretion. On-going studies of the Oakland Conglomerate by D. L. Jones (letter, 1990) show that previous workers have confused two conglomerates; one, the actual Oakland Conglomerate, is younger than mid-Cenomanian age, and the other, associated with beds containing *Buchia*, is not younger than Valanginian.

The specimen figured by Hall is a fairly well-preserved but recrystallized shell in an immature sandstone matrix that contains other similarly preserved pieces of shell. A sandstone so replete with fossils should have produced a considerable faunal list, but Hall (1958, p. 47) records only *T. varians* and *Aucella lahuseni* Pavlow from this locality. This sandstone and preservation of the enclosed fossils resemble preservation and matrix at CAS loc. 33706, Arroyo del Valle, Alameda Co., where *Calva* (*Egelicalva*) *spissa* also occurs. Matsumoto (1960, pp. 71, 95) has considered ammonites from this locality to indicate an early Turonian age. The matrix of Hall's figured specimen is moderately hard sandstone. None of the pieces of shell in the matrix of "*T. varians*" is from an "*Aucella*" = *Buchia*. Other than this specimen, no *Calva* of older than Albian age has been recognized. No strata of Turonian age have been recognized in Niles Canyon [15], but eastward in Arroyo del Valle [15], Alameda Co., beds of Turonian age are present (Matsumoto, 1960, p. 71). This specimen is so clearly a *Calva* (*E.*) *spissa* and its matrix so dissimilar to that of the Lower Cretaceous of the Pleasanton area, that a strong suspicion arises of specimens being transposed sometime between the collecting of fossils from Niles Canyon by Robert Anderson in 1906 and the figuring of this specimen by Hall in 1958.

ETYMOLOGY. The specific name is from Latin, *spissus*, close, dense, thick, slow.

Calva (*Egelicalva*) *taffi* (Anderson, 1958)

Figures 155–190

Trigonocallista nitida (Gabb) Taff, Hanna, and Cross, 1940, p. 1322, pl. 2, figs. 3–4. Not *Meretrix nitida* Gabb, 1864; *Caryatis nitida* (Gabb), Gabb, 1869; nor *Aphrodina nitida* (Gabb), Stewart, 1930; all = *Calva* (*Egelicalva*) *nitida* (Gabb, 1864).

Calva sp. aff. *C. regina* Popenoe, Casey, 1952, p. 173, text figs. 90–91.

"*Trigonocallista*" *taffi* Anderson, 1958, p. 139, pl. 59, fig. 2–2a.

DIAGNOSIS. A nearly equant *Egelicalva* with a large lunule, strongly arched posterodorsal margin, giving the umbos a hunched-over aspect, and slightly convex lunular margin. Lateral teeth with fine striations localized on elongate welts, cardinal tooth 1 reaching barely to hinge plate edge, lateral AI large and swollen.

DESCRIPTION. Shell of moderate size, nearly as high as long, inflated, especially near the beak, thick; beaks prominent but rather low, anterior to the mid-length of the shell, prosogyrous; lunular margin slightly convex; anterior end rounded; ventral border broadly arched; posterior end subtruncate vertically; posterior dorsal border well arched; lunule large, clearly demarked by an inscribed line; escutcheon bounded by blunt angulation; shell surface polished, marked by growth lines and impressed growth checks.

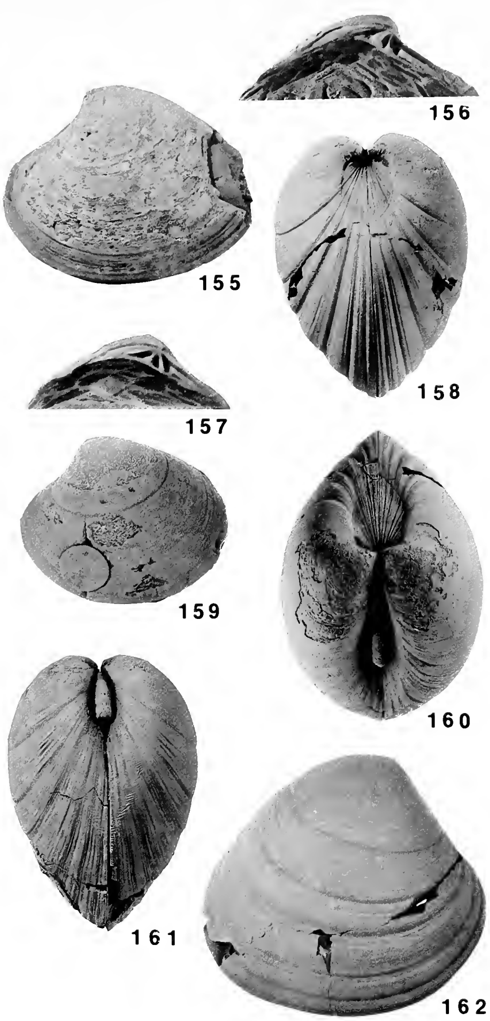
Ligament groove long, arched, behind moderate nymphs. Hinge of right valve with anterior tooth 3a and median cardinal tooth 1 short, narrow, prominent, close together, nearly equant in length, slightly divergent ventrally, situated directly beneath and having dorsal ends equally close to the beaks; right posterior cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, deep, parallel to the lunular border of the shell, finely striate along narrow, raised welts along both sides; socket for PII deep, bounded below by a rather large projecting tooth PI; PI finely striate along welt; welt lower on tooth at anterior, angling higher posteriorly. Hinge of left valve with anterior cardinal 2a prominent, very slender, aligned almost vertically beneath the beak; left median cardinal 2b thicker than 2a, trigonal, directed obliquely backward; left posterior cardinal 4b continuous with the ventral side of the nymph, slightly longer than the anterior teeth, not very massive; anterior lateral AII long, parallel to the hinge border below the lunule, finely striate on dorsal face; striae confined to raised longitudinal welt at mid tooth height; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broadly linguiform with subangulate tip, ascending, extending to near mid valve length; dorsal arm convexly gently ascending; ventral arm concavely ascending at angle of about 50° to pallial line. Adductor muscle scars moderately impressed, roundish.

HOLOTYPE. CAS cat. no. 27836.01 [= CAS cat. no. 5789].

HYPOTYPES. LACMIP cat. nos. 8133 from LACMIP loc. 10847 [= CIT loc. 1016], Chico Creek [11], 8134 from UCLA loc. 3625, Chico Creek [11], 8135 from UCLA loc. 3623, Chico Creek [11], 8136–8138 from UCLA loc. 3627, Chico Creek [11], 8139 from LACMIP loc. 10849 [= CIT loc. 1017], Chico Creek [11], Butte Co., 8140, 8143 from UCLA loc. 4219, Oak Run, 8147 from UCLA loc. 4209, Clover Creek [8], 8149–8150 from LACMIP loc. 10824 [= CIT loc. 1232], Price Hollow [8], 8152–8153 from UCLA loc. 4106, Clover Creek [8], 8155–8157 from UCLA loc. 4217, Clover Creek [8], Shasta Co., California. CAS cat. nos. 27854.02 from CAS loc. 27854, Orestimba Creek [17], Stanislaus Co., California.

TYPE LOCALITY. Chico Creek [11], Butte Co., California. The holotype was reported to have come from CAS loc. 27836 (Taff et al., 1940, explanation of pl. 2, figs. 3–4; Anderson, 1958, p. 139), which is approximately 200–233 m (675 feet) above the base of the section. UCLA localities at this stratigraphic position yielded no specimens of *Calva* (*Egelicalva*) *taffi*. There is very little other material from CAS loc. 27836 at the California Academy of Sciences; one small tray, so numbered, of poorly preserved fossils in a matrix similar to that at UCLA loc. 3617 contains no *Calva*. The type specimen is beautifully preserved; the locality number 27835 was written upon it in black ink; the last digit was changed to a 6 in blue ink. *Calva* (*E.*) *taffi*, often in an excellent state of preservation, is common to abundant at several localities near the stratigraphic position of CAS loc. 27835, approximately 450–550 m (1600 feet) above the base of the section (Taff et al., 1940, p. 1316, fig. 1).

GEOLOGIC AGE. Coniacian–Santonian, associated with *Hyphantoceras oshimai* (Yabe, 1904), *H.* cf. *H. venustum* (Yabe, 1904) and *Baculites capensis* (Woods, 1906).



Figures 155–162. *Calva* (*Egelicalva*) *taffi* (Anderson). All ×1; all specimens whitened with ammonium chloride; all of Coniacian age. **155, 156,** CAS cat. no. 27854.02, hypotype, from CAS loc. 27854, **155,** exterior, **156,** hinge. **157, 159,** LACMIP cat. no. 8147, hypotype, from UCLA loc. 4209, **157,** hinge, **159,** exterior. **158, 160–162,** LACMIP cat. no. 8271, hypotype, from UCLA loc. 4245, **158,** anterior view, **160,** dorsal view, **161,** posterior view, **162,** exterior. Photos 155, 156 by De Leon; 157, 159, 162 by Saul; 158, 160 by Susuki.

DISTRIBUTION. Redding Formation (Members IV through VI? of Popenoe, 1943), east of Redding [8], Shasta Co.; Musty Buck Member of the Chico Formation on Chico Creek [11] and Butte Creek [11], Butte Co.; Lower Panoche Formation, Orestimba Creek [17], Stanislaus Co., California.

DIMENSIONS. See Table 11.

REMARKS. Anderson (1958) based this species on the figures of *Trigonocallista nitida* in Taff et al. (1940) but provided no description. His holotype is small and double valved, and the above hinge description is based upon probable topotype specimens. Specimens larger than the holotype and of Santonian age develop the most distinctive form of *Calva* (*Egelicalva*) *taffi*. They are relatively high and have a hunched-over aspect to the posterodorsal margin (Figs. 167, 170, 175, 178, 180, 181). *Calva* (*E.*) *taffi* specimens of Coniacian age (Figs. 155–162) are similar to *C.* (*E.*) *spissa* in shape and are relatively longer than are specimens from the vicinity of the type locality (Fig. 167). In outline these Coniacian specimens resemble *C.* (*E.*) *buttensis* or *C.* (*E.*) *bowersiana*. Specimens of late Santonian age are again predominantly more elongate (Figs. 182–190) and grade into *C.* (*E.*) *buttensis*. The three taxa *C.* (*E.*) *taffi*, *C.* (*E.*) *buttensis*, and *C.* (*E.*) *bowersiana* constitute an intergrading series in which mature specimens of the two end members are distinct, but small specimens cannot usually be allocated. Some relatively elongate specimens of *C.* (*E.*) *taffi* cannot be distinguished from *C.* (*E.*) *buttensis*, but the two forms are treated as separate species because the distinctive, relatively short *C.* (*E.*) *taffi* appears to be confined to the Santonian. Those with a less distinctive shape are separable from *C.* (*E.*) *buttensis* on the basis of the lunular margin, which is usually convex in *C.* (*E.*) *taffi* but straight to slightly concave in *C.* (*E.*) *buttensis*.

The specimen figured by Casey (1952) was provided by Popenoe. In Casey's (1952) figure 91, the escutcheon and lunule are indicated by dashed lines as though they were equally recognizable, but on specimens the lunule is depressed and delimited by an incised line and the escutcheon is indistinctly bounded by an obscure angulation (Fig. 177).

Calva (*Egelicalva*) *taffi* is relatively lower and longer than *C.* (*C.*) *heliaca* but relatively higher than other species of *Calva*; its lunule appears larger than that of *C.* (*E.*) *buttensis* and *C.* (*E.*) *bowersiana*. Like *C.* (*E.*) *nitida*, it has a trigonal shell. Its outline is similar to that of *C.* (*E.*) *crassa*, but it has striated laterals, and the largest specimens of *C.* (*E.*) *taffi* are a third as large as the largest *C.* (*E.*) *crassa*. *Calva* (*E.*) *taffi* resembles *C.* (*E.*) *spissa* in being thick shelled, trigonal, and heavy hinged, but *C.* (*E.*) *spissa* has a higher beak, lacks the hunched-over aspect to the posterodorsal margin, and has a proportionately longer and more prominent anterior lateral that is noticeably more coarsely striate at its dorsal end.

Specimens of *Calva* at CAS loc. 27854, Orestimba Creek [17], Stanislaus Co., ?base of the Panoche, occur with *Meekia louella* Popenoe, 1962. They are shaped more like *C.* (*Egelicalva*) *buttensis* but have a hinge like *C.* (*E.*) *taffi*. CAS loc. 27854 is the type locality of *Didymoceras orestimbense* Anderson, 1958, which Matsumoto (1959, p. 158; 1960, p. 84) considered to be *Hyphantoceras oshimae* (Yabe, 1904) and indicative of late Turonian or Coniacian age (Matsumoto, 1960, p. 84). These *Calva* and the *M. louella* suggest an early Coniacian age for this locality.

We have not seen Whiteaves' (1879, p. 149) specimen of *Cytherea* (*Caryatis*) *plana* (Sowerby) from the Productive Coal Measures, Division A (= Haslam or Pender Formation of Ward, 1978, late Santonian or early Campanian age) at the entrance to Departure Bay [2], Vancouver Island. The age and association with *Inoceramus schmidti* Michael, 1899, suggest that it and others identified from that vicinity as *Cytherea leonensis* Conrad by Etheridge (*in* Hector, 1861) may be *Calva* (*Egelicalva*) *taffi* or *C.* (*E.*) *buttensis*. Whiteaves (1903) later included all of these in *Meretrix nitida* Gabb. Although Etheridge referred to *Cytherea leonensis* Conrad, 1857, as the commonest fossil near Nanaimo, no worker since Whiteaves has mentioned *Calva*-like bivalves from that vicinity.

Specimens of *Calva* from the Chignik Formation west of Chignik Bay, Alaska Peninsula, Alaska (USGS loc. 6981), are similar to those of latest Santonian to earliest Campanian age in the Chico Formation. *Inoceramus schmidti* and *Canadoceras newberryanum* (Meek, 1857) are distributed throughout the Chignik Bay section of the Chignik Formation (Jones, 1963, p. 8). The *Calva* is referred to *C.* (*Egelicalva*) *buttensis* despite its large lunule, because the lunular margin is barely concave rather than convex as in typical *C.* (*E.*) *taffi*.

Calva (*Egelicalva*) *buttensis* (Anderson, 1958)

Figures 191–210

Venus varians var.? Gabb, 1864, p. 161, in part, pl. 23, fig. 141 only (specimens from "Pence's Ranch," Butte Co.).

Trigonocallista varians (Gabb) Taff, Hanna, and Cross, 1940, p. 1321, pl. 2, figs. 10–11. Not *Venus varians* Gabb, 1864.

"Trigonocallista" buttensis Anderson, 1958, p. 140, pl. 59, fig. 1–1a.

DIAGNOSIS. An *Egelicalva* with very fine striations on the lateral teeth localized on elongate welts. The lunular margin is nearly straight. Cardinal tooth 1 extending barely to hinge plate edge; 3a shorter than 1; lateral AI not swollen; hinge plate relatively narrow.

DESCRIPTION. Shell thick, of moderate size,

→

Figures 163–181. *Calva* (*Egelicalva*) *taffi* (Anderson). All ×1; all specimens whitened with ammonium chloride; all of early Santonian age. **163, 164,** CAS cat. no. 27836.01, holotype, from CAS loc. 27836, **163,** exterior left valve, **164,** dorsal view. **165, 171,** LACMIP cat. no. 8143, hypotype, from UCLA loc. 4219, **165,** exterior, **171,** hinge. **166, 169,**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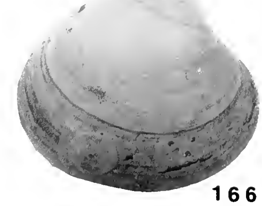
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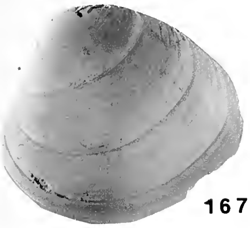
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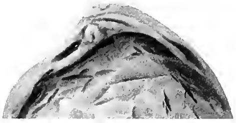
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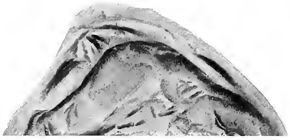
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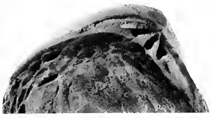
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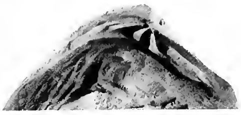
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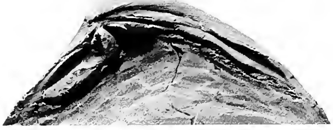
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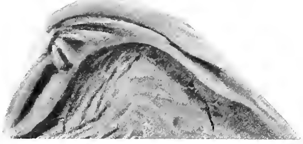
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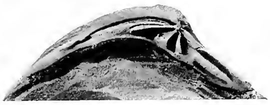
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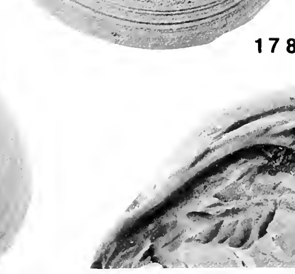
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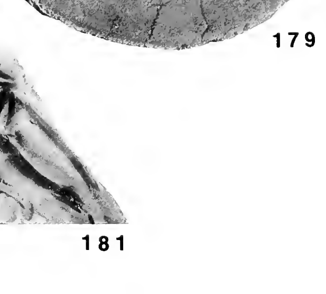
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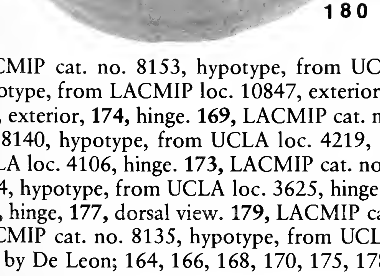
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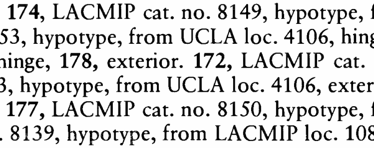
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LACMIP cat. no. 8153, hypotype, from UCLA loc. 4106, **166,** exterior, **169,** hinge. **167,** LACMIP cat. no. 8133, hypotype, from LACMIP loc. 10847, exterior. **168, 174,** LACMIP cat. no. 8149, hypotype, from LACMIP loc. 10824, **168,** exterior, **174,** hinge. **169,** LACMIP cat. no. 8153, hypotype, from UCLA loc. 4106, hinge. **170, 178,** LACMIP cat. no. 8140, hypotype, from UCLA loc. 4219, **170,** hinge, **178,** exterior. **172,** LACMIP cat. no. 8152, hypotype, from UCLA loc. 4106, hinge. **173,** LACMIP cat. no. 8273, hypotype, from UCLA loc. 4106, exterior. **175,** LACMIP cat. no. 8134, hypotype, from UCLA loc. 3625, hinge. **176, 177,** LACMIP cat. no. 8150, hypotype, from LACMIP loc. 10824, **176,** hinge, **177,** dorsal view. **179,** LACMIP cat. no. 8139, hypotype, from LACMIP loc. 10849, pallial sinus. **180, 181,** LACMIP cat. no. 8135, hypotype, from UCLA loc. 3623, **180,** exterior, **181,** hinge. Photos 163, 165, 167, 169, 171, 172 by De Leon; 164, 166, 168, 170, 175, 178–181 by Saul; 173, 174, 176, 177 by Susuki.

Table 11. Measurements of *Calva* (*Egelicalva*) *taffi*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
CAS 27836.01	25.2	27.5	9.7	12.0	9.0	2.6		1.1	2.8	2.3	1.3	3.5
CAS 27854.02	32.0	38.0	13.0	16.7	10.6	3.2	107°	1.2	2.9	2.3	1.6	3.3
LACMIP 8133	30.6	34.3	12.7	13.5	10.0	3.0		1.1	2.7	2.5	1.4	3.3
LACMIP 8135	46.4	48.7	20.7	25.4	15.4	4.8	84°	1.0	2.4	1.9	1.6	3.2
LACMIP 8136	36.0	41.0	15.8	17.0	12.0	3.8	99°	1.1	2.6	2.4	1.4	3.2
LACMIP 8137	34.0	37.6	11.5	16.8	13.7	4.3	90°	1.1	3.3	2.2	1.2	3.2
LACMIP 8138	15.4	18.1	6.2	8.7	5.4	1.4	107°	1.2	2.9	2.1	1.6	3.8
LACMIP 8140	37.0	39.0	15.4	20.5	12.3	3.6	86°	1.0	2.5	1.9	1.7	3.4
LACMIP 8143	26.6	28.0	12.5	13.0	8.1	2.8	97°	1.0	2.2	2.2	1.6	2.9
LACMIP 8147	21.6	26.9	9.3	11.4	7.0	1.9	113°	1.2	2.9	2.4	1.6	3.7
LACMIP 8149	37.0	42.0	14.6	17.5	11.0	3.3	100°	1.1	2.9	2.4	1.6	3.3
LACMIP 8150	29.7	35.4	12.3	17.4	10.0	3.0	107°	1.2	2.9	2.0	1.7	3.3
LACMIP 8152	32.0	35.0	11.0	14.5	10.0	3.7	95°	1.1	3.2	2.4	1.4	2.7
LACMIP 8153	28.0	31.8	12.5	14.9	8.9	2.8	99°	1.1	2.5	2.1	1.7	3.2
LACMIP 8155	24.6	27.4	11.0	13.8	8.5	3.2	95°	1.1	2.5	2.0	1.6	2.7
LACMIP 8156	21.6	25.7	9.8	12.4	7.0	3.0	102°	1.2	2.6	2.1	1.8	2.3

longer than high, inflated; beaks prominent, of moderate height, anterior to the mid-length of the shell, prosogyrous; lunular margin nearly straight; anterior end broadly rounded; ventral border broadly arched; posterior end abruptly rounded; posterior dorsal border moderately long, slightly arched; lunule elongate, depressed, moderately wide, well demarked by inscribed line; escutcheon delimited by angulation sharp near the beak, rounding to obscurity near the margin.

Ligament groove one-third length of dorsal border. Hinge of right valve with anterior tooth 3a and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; right posterior cardinal 3b long, straight, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, moderately deep, smooth, parallel to the lunular border of the shell; socket for PII deep, bounded below by a rather large projecting tooth. Hinge of left valve with anterior cardinal 2a prominent, very slender, long, slightly concavely arched anteriorly, directed nearly vertically; left median cardinal 2b thicker than 2a, trigonal, directed obliquely backward; left posterior cardinal 4b parallel to ventral side of the nymph, twice as long as 2b, bladelike but sturdy; anterior lateral AII long, sturdy, hooked at its dorsal end, parallel to the hinge border below the lunule and the lunule margin, smooth sided except for fine striae along the upper dorsal edge; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the ligament groove. Pallial sinus broadly linguiform, angulate at the tip, extending to about the midline of the valve; dorsal arm barely ascending, nearly straight; ventral arm concavely ascending at about 50° to the ventral pallial line.

HOLOTYPE. CAS cat. no. 27838.15 [= CAS cat. no. 5788].

HYPOTYPES. USNM 456072 from USGS loc. M6981, near Chignik Lagoon, Alaska Peninsula, Alaska; LACMIP cat. nos. 8159 from UCLA loc. 3635, Chico Creek [11]; 8161 from UCLA loc. 3637, Chico Creek [11]; 8162 from UCLA loc. 3642, Chico Creek [11]; 8163 from UCLA loc. 3641, Chico Creek [11]; 8164–8165 from UCLA loc. 3643, Chico Creek [11]; 8168, 8170–8171 from LACMIP loc. 10834, Butte Creek [11], UCMP cat. no. 39834 (Gabb, 1864, pl. 23, fig. 141) from "Pence's Ranch" [11], Butte Co., California.

TYPE LOCALITY. CAS loc. 27838, Chico Creek [11], Butte Co., California (approx. 830 m above base of formation).

GEOLOGIC AGE. Early Campanian; associated with early occurrences of *Submortoniceras chicoense* (Trask, 1856).

DISTRIBUTION. Chignik Formation, Alaska Peninsula, Alaska; probably Pender Formation, Texada Island [1] and Vancouver Island [2], British Columbia; Chico Formation, Ten Mile Member, from approximately 600 m to 970 m above the base of the formation on Chico Creek [11], Butte Co.; Chico Formation, Ten Mile Member, Butte Creek [11], Butte Co.; Chico Formation, Pentz [11], Butte Co., California.

DIMENSIONS. See Table 12.

REMARKS. Anderson (1958) named but did not describe this species. The above description is based in part upon hypotypes from localities along Chico Creek [11] near the type locality. Popenoe (1964) considered *Calva* (*Egelicalva*) *buttensis* indistinguishable from *C.* (*E.*) *bowersiana,* but it is equally similar to *C.* (*E.*) *taffi*. The earliest *C.* (*E.*) *buttensis* are as difficult to distinguish from the preceeding *C.* (*E.*) *taffi* as are the latest from the succeeding *C.* (*E.*) *bowersiana. Calva* (*E.*) *buttensis* is transitional between *C.* (*E.*) *taffi,* which is relatively short and has a relatively large lunule and a narrower lateral tooth angle, and C. (*E.*) *bowersiana,* which is more elongate and has a more depressed lunule and a wider tooth angle. If preservation were better and the matrix more amenable, the striations on the lateral teeth might be more useful in distinguishing these species, as the striations are better developed on laterals of C. (*E.*) *taffi* than on laterals of C. (*E.*) *buttensis* and are lacking on mature C. (*E.*) *bowersiana.* The lunular margin of C. (*E.*) *taffi* is convex, that of C. (*E.*) *buttensis* is nearly straight, and that of C. (*E.*) *bowersiana* is concave. Gabb's (1864, pl. 23, fig. 141) three specimens of *Venus varians* var. ? from "Pence's Ranch," which are in the University of California, Berkeley, Museum of Paleontology, resemble the holotype of C. (*E.*) *buttensis.* The specimens from the Chignik Formation, near Chignik Bay, Alaska, are on the C. (*E.*) *taffi* end of this transition. They occur with *Inoceramus schmidti* Michael, 1899, and *Canadoceras newberryanum* Meek, 1857, which are found throughout the Chignik Bay section of the Chignik Formation and imply an early Campanian age (Jones, 1963).

Specimens identified as *Cytherea* (*Caryatis*) *plana* (Sowerby, 1812) by Whiteaves (1879, p. 149) and as *Cytherea leonensis* Conrad by Etheridge *in* Hector (1861) from the Pender Formation are probably *Calva* (*Egelicalva*) *buttensis.* The true *Cytherea* (*Caryatis*) *plana* lacks posterior laterals and is the type of *Callistina* Jukes-Brown, 1908. In 1903, Whiteaves referred all of these specimens from the Nanaimo vicinity to *Meretrix nitida* Gabb.

Calva (*Egelicalva*) *bowersiana* (Cooper, 1894)

Figures 211–238

? *Cytherea* (*Caryatis*) *plana* (Sowerby) Whiteaves, 1879, p. 149, in part, probably pl. 17, fig. 14–14b. Not *Venus planus* Sowerby, 1812.
Cucullaea bowersiana Cooper, 1894, p. 48, pl. 5, figs. 61–62; Coan, 1981, p. 152.
Meretrix nitida Gabb Whiteaves, 1903, p. 377, in part. Not *Meretrix nitida* Gabb, 1864.
Chione varians (Gabb) Waring, 1917, p. 8, fig. 13. Not *Venus varians* Gabb, 1864. Specimen not found, not transferred from Stanford to California Academy of Sciences.
Meretrix nitida var. *major* Packard, 1922, p. 425, pl. 31, fig. 2.
Meretrix (?) sp. Packard, 1922, p. 426, pl. 33, fig. 2.
Calva bowersiana (Cooper) Popenoe, 1937, p. 396; Popenoe, 1954, p. 17, fig. 3 (10); Stadum, 1973, pl. II, fig. 2; Popenoe, 1973, p. 22, pl. 3, fig. 32; Saul and Alderson, 1981, p. 32, pl. 2, fig. 12.
"*Meretrix*" *coronada* Anderson, 1958, p. 136.

DIAGNOSIS. A large, ovately trigonal *Egelicalva* having smooth lateral teeth and the lunular margin concave. Cardinal tooth 1 barely extending to hinge plate edge, extending farther toward beak than 3a, 3a shorter than 1, hinge plate relatively narrow.


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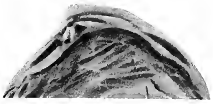
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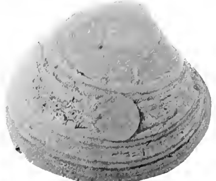
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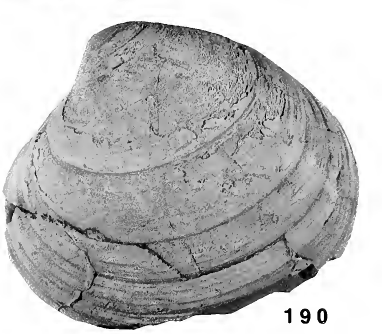
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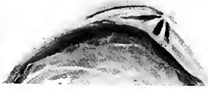
Figures 182–190. *Calva* (*Egelicalva*) *taffi* (Anderson). All hypotypes; all of late Santonian age; all specimens whitened with ammonium chloride. **182, 184, 186,** LACMIP cat. no. 8156, ×1, from UCLA loc. 4217, **182,** hinge, **184,** exterior, **186,** exterior. **183,** LACMIP cat. no. 8138, ×1.5, from UCLA loc. 3627, hinge. **185,** LACMIP cat. no. 8155, ×1, from UCLA loc. 4217, hinge. **187, 189,** LACMIP cat. no. 8136, ×1, from UCLA loc. 3627, **187,** hinge, **189,** exterior. **188, 190,** LACMIP cat. no. 8137, ×1, from UCLA loc. 3627, **188,** hinge, **190,** exterior. Photos 182, 184, 190 by De Leon; 183, 185–189 by Saul.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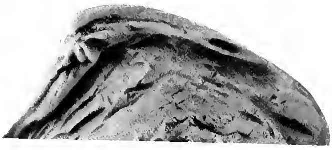
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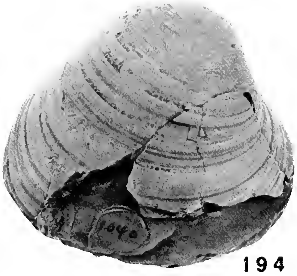
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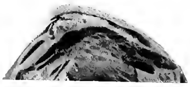
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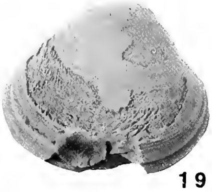
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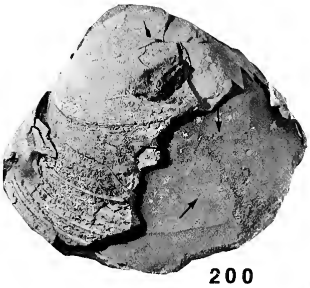
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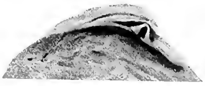
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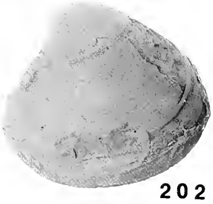
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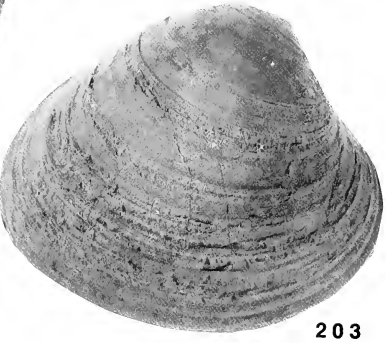
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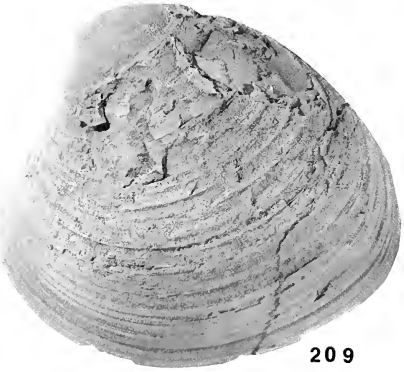
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Table 12. Measurements of *Calva* (*Egelicalva*) *buttensis.* Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
CAS 27838.15	41.0	48.4	16.0	20.4	11.5	3.4	117°	1.2	3.0	2.4	1.8	3.3
LACMIP 8159	38.5	43.7	14.9	18.0	13.0	3.6	100°	1.1	2.9	2.4	1.4	3.6
LACMIP 8161	29.7	34.8	11.2	15.0	10.0	3.2	118°	1.2	3.1	2.3	1.5	3.1
LACMIP 8164	24.8	28.0	9.8	14.4			107°	1.1	2.9	1.9	—	—
LACMIP 8165	21.6	26.4	8.9	13.0	7.0	2.2	126°	1.2	3.0	2.0	1.9	3.2
LACMIP 8168	27.0	30.0	12.0	14.4	9.4	2.6	94°	1.1	2.5	2.1	1.5	3.6
LACMIP 8170	33.7	36.4	15.3	17.5	10.0	4.0	98°	1.1	2.4	2.1	1.8	2.5
LACMIP 8171	22.5	26.3	10.5	14.4	8.7	2.8	101°	1.2	2.5	1.8	1.6	3.1
USNM 456072	31.6	38.5	12.5	27.8	11.4	3.0	110°	1.2	3.1	1.4	2.4	3.8

DESCRIPTION. Shell of moderate to large size, nearly as high as long, inflated, thick; beaks prominent, rather high, placed anterior to the mid-length of the shell, prosogyrous; lunular border slightly concave; anterior end rounded; ventral border broadly arched; posterior end rounded; posterior dorsal border slightly arched; lunule moderately large, impressed, delimited by an inscribed line; escutcheon very narrow, defined by angulation only near the beak.

Ligament groove long, deep, arcuate behind smooth nymphs. Hinge of right valve with anterior tooth 3a very short and median cardinal tooth 1 short, narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; right posterior cardinal 3b long, slightly arched, shallowly bifid subparallel to the nymph; socket for lateral AII long, narrow, deep, smooth, parallel to the lunular border of the shell; socket for PII moderately deep, long, bounded below by a rather large projecting tooth PI; PI aligned with nymph. Hinge of left valve with anterior cardinal 2a prominent, slender; cardinal 2b trigonal, thicker and shorter than 2a, directed obliquely backward; posterior cardinal 4b parallel to nymph, nearly twice as long as 2b, bladelike; anterior lateral AII long, hooked at its dorsal end, parallel to the lunular margin, smooth sided; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the posterior end of the ligament groove. Pallial sinus broadly linguiform, extending across two-fifths of the valve length; dorsal arm nearly horizontal; ventral arm ascending concavely at angle of about 45° to the pallial line. Adductor muscle scars moderately impressed, rounded.

LECTOTYPE. CAS cat. no. 66028.01 (= CAS 615; ex CSMB 13734) herein designated. Popenoe (1937, p. 397) recognized this specimen as the one figured by Cooper and considered it to be the holotype, but Coan (1981, p. 153) regarded it as a syntype.

HYPOTYPES. UCMP cat. nos. 12279 (holotype of *Meretrix nitida* var. *major* Packard) from UCMP loc. 2179, Santa Ana Mountains [26]; 12306 (hypotype of *Meretrix* (?) sp. of Packard, 1922, and holotype of "*Meretrix*" *coronada* Anderson, 1958) from UCMP loc. 2167, Santa Ana Mts. [26], Orange Co., California. UCLA cat. nos. 28710 from LACMIP loc. 10715 [= CIT loc. 86], Santa Ana Mts. [26]; 59076 from UCLA loc. 4207, Santa Ana Mts. [26], Orange Co.; 59214 from LACMIP loc. 10715 [= CIT loc. 1159], Simi Hills [24], Los Angeles Co., California. LACMIP cat. nos. 8173 from UCLA loc. 3976, E of Glenn Cove [14], Solano Co.; 8176 from UCLA loc. 3648, "Fossil Bluff," Chico Creek [11]; 8178–8181 from LACMIP loc. 10861 [= CIT loc. 1183], "Fossil Bluff," Chico Creek [11], Butte Co.; 8182 from LACMIP loc. 10719, Santa Ana Mts. [26]; 8184 from LACMIP loc. 10120 [= CIT loc. 86], Santa Ana Mts. [26]; 8185 from LACMIP loc. 10105 [= CIT loc. 974], Santa Ana Mts. [26], Orange Co.; 8187 from LACMIP loc. 10715 [= CIT

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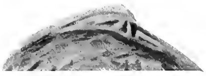
Figures 191–210. *Calva* (*Egelicalva*) *buttensis* (Anderson). All ×1; except as indicated, all specimens whitened with ammonium chloride. **191, 195,** LACMIP cat. no. 8168, hypotype, from LACMIP loc. 10834, **191,** hinge, **195,** exterior. **192, 198,** LACMIP cat. no. 8159, hypotype, from UCLA loc. 3635, **192,** hinge, **198,** exterior. **193,** LACMIP cat. no. 8161, hypotype, from UCLA loc. 3637, hinge. **194, 199,** LACMIP cat. no. 8170, hypotype, from LACMIP loc. 10834, **194,** exterior, **199,** hinge. **196,** LACMIP cat. no. 8171, hypotype, from LACMIP loc. 10834, hinge. **197,** LACMIP cat. no. 8171, hypotype, from LACMIP loc. 10834, exterior. **200,** LACMIP cat. no. 8162, hypotype, from UCLA loc. 3642, pallial sinus, without whitening. **201,** LACMIP cat. no. 8165, hypotype, from UCLA loc. 3643, hinge. **202,** LACMIP cat. no. 8164, hypotype, from UCLA loc. 3643, exterior. **203–205, 207, 208,** CAS cat. no. 27838.15, holotype, from CAS loc. 27838, **203,** exterior, **204,** anterior view, **205,** posterior view, **207,** hinge, **208,** dorsal view. **206, 209,** USNM cat. no. 456072, hypotype, from USGS loc. M6981, **206,** hinge, **209,** exterior. **210,** LACMIP cat. no. 8163, hypotype, from UCLA loc. 3641, hinge. Photos 191, 195, 201, 206, 209 by De Leon; 192–194, 196–200, 201–205, 207, 208, 210 by Saul.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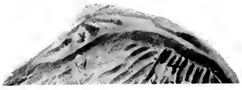
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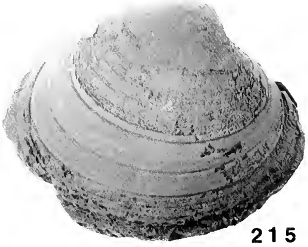
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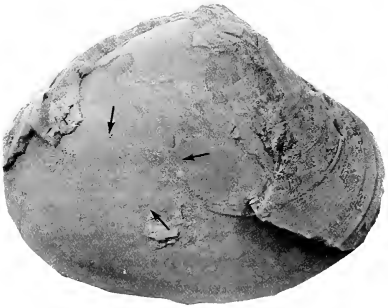
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Table 13. Measurements of *Calva* (*Egelicalva*) *bowersiana*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
UCLA 28710	62.5	68.0	24.6					1.1	2.8	—	—	—
UCLA 59076	60.0	67.5	20.0					1.1	3.4	—	—	—
UCLA 59214	46.7	53.7	19.2					1.2	2.8	—	—	—
LACMIP 8173	39.0	48.0	13.7	19.7	8.7	3.7	124°	1.2	3.5	2.4	2.3	2.4
LACMIP 8176			15.8	27.0	11.4	3.7	109°	—	—	—	2.4	3.1
LACMIP 8178	32.0	39.4	11.8	18.7	7.8	2.4	113°	1.2	3.3	2.1	2.4	3.2
LACMIP 8179	27.5	33.4	11.0	15.0	7.5	2.0	112°	1.2	3.0	2.2	2.0	3.8
LACMIP 8180	23.5	28.8	10.0	14.0	6.0	1.8	126°	1.2	2.9	2.1	2.3	3.3
LACMIP 8182	36.0		13.4	20.5	9.3	2.3	112°	—	—	—	2.0	4.0
LACMIP 8184	48.9	61.0	18.0	22.5	13.0	4.6	114°	1.2	3.4	2.7	1.7	2.8
LACMIP 8185	59.8		22.6	34.0			105°	—	—	—	—	—
LACMIP 8187	62.7		23.2	33.9	18.0	6.0	97°	—	—	—	1.9	3.0
LACMIP 8192	47.2	57.0	15.5	28.0	12.7	3.0	111°	1.2	3.7	2.0	2.2	4.2

loc. 1159], Dayton Canyon [24], Los Angeles Co.; 8192 from LACMIP loc. 10446 [= CIT loc. 1400], Sucia Island, San Juan Co., Washington. Whiteaves' specimen of *Cytherea* (*Caryatis*) *plana* (Sowerby) from 2¼ miles up the Nanaimo River [2], Vancouver Island, British Columbia, and Waring's specimen of *Chione varians* (Gabb) from "loc. 3, south of the Santa Monica Mts." [25], Los Angeles Co., California, are missing.

TYPE LOCALITY. "Cretaceous of Santa Ana Mountains" (Cooper, 1894) [26], Orange Co., California. Of *Meretrix nitida* var. *major,* UCMP loc. 2169, ½ mile south 50° east of B.M. 1271, Corona Sheet. On crest of Santiago–Aliso divide, about ¼ mile north of the road (Packard, 1922, p. 416) [26]. Of "*Meretrix*" *coronada,* UCMP loc. 2167, 2 miles north 10° west of B.M. 1271, Corona Sheet. At a gate about ½ mile below Modjeska Springs in Williams Canyon (Packard, 1922, p. 416) [26].

GEOLOGIC AGE. Late early through late Campanian; associated with late occurrences of *Submortoniceras chicoense* (Trask, 1856) and with *Hoplitoplacenticeras vancouverense* (Meek, 1862) and *Metaplacenticeras* cf. *M. pacificum* (Smith, 1900). The matrix of the lectotype has an impression of a *Turritella chicoensis pescaderoensis* Arnold, 1908, a subspecies of late Campanian age (Saul, 1983).

DISTRIBUTION. Cedar District Formation on Sucia Island [3], San Juan Co., Washington; Great Valley Series, near Benicia [14], Solano Co.; Pigeon Point Formation near Bolsa Point [16], San Mateo Co.; Chatsworth Formation, Simi Hills [24], Los Angeles Co.; Tuna Canyon Formation, Santa Monica Mts. [25], Los Angeles Co.; Williams Formation, Pleasants Sandstone Member, Santa Ana Mts. [26], Orange Co., California.

DIMENSIONS. See Table 13.

REMARKS. Cooper (1894) wrote that he had "many" specimens of this species from the Santa Ana Mountains [26], collected by Dr. Stephen Bower, but only the specimen figured by Cooper, CAS cat. no. 615 = CAS 66028.01, is extant (Coan, 1981, p. 152). Popenoe (1937) found that some matrix had been removed from this specimen exposing the beak and making possible its identification with the common *Calva* of the Pleasants Sandstone in the Santa Ana Mountains [26]. The species is widespread and abundant at many localities.

Calva bowersiana is slightly more elongate than *C. buttensis* and has a more concave lunular margin. Specimens from near the top of the Ten Mile Member of the Chico Formation on Chico Creek have a somewhat more concave lunular margin and shorter anterior laterals than does typical *C.* (*Egelicalva*) *buttensis* and are referred to *C.* (*E.*) *bowersiana,* although at least one specimen from LACMIP loc. 10861, "Fossil Bluff," has very fine striations on a longitudinal ridge on the dorsally facing side of the anterior lateral socket and on an

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Figures 211–226. *Calva* (*Egelicalva*) *bowersiana* (Cooper). All hypotypes; all ×1; all from early Campanian zones of *Submortoniceras chicoense* or *Hoplitoplacenticeras vancouverense*; all specimens whitened with ammonium chloride. **211, 214,** LACMIP cat. no. 8180, from LACMIP loc. 10861, **211,** hinge, **214,** exterior. **212,** LACMIP cat. no. 8176, from UCLA loc. 3648, hinge. **213, 217,** LACMIP cat. no. 8179, from LACMIP loc. 10861, **213,** hinge, **217,** exterior. **215, 216,** LACMIP cat. no. 8178, from LACMIP loc. 10861, **215,** exterior, **216,** hinge. **218, 219, 221, 222, 224,** LACMIP cat. no. 8192, from LACMIP loc. 10446, **218,** posterior view, **219,** anterior view, **221,** hinge, **222,** dorsal view, **224,** exterior. **220,** LACMIP cat. no. 8181, from LACMIP loc. 10861, pallial sinus. **223, 226,** LACMIP cat. no. 8173, from UCLA loc. 3976, **223,** hinge, **226,** pallial sinus. **225,** LACMIP cat. no. 8182, from LACMIP loc. 10719, hinge. Photos 211–217, 220, 223, 225, 226 by Saul; 218, 219, 221, 222, 224 by De Leon.

arcuate slanting ridge on the dorsally facing side of the posterior lateral socket. Specimens from this horizon (Figs. 211, 213–217) have a less depressed lunule and are less inflated than typical *C.* (*E.*) *bowersiana* of the *Metaplacenticeras pacificum* Zone (Figs. 228–233). Specimens from Sucia Island [3] (Figs. 218, 219, 221, 222) have a wider lateral tooth angle than those from the Pleasants Sandstone in the Santa Ana Mountains [26] and, except for a slightly more concave lunular margin, resemble those from the top of the section on Chico Creek [11]. Specimens from the base of the Schultz Conglomerate in the Santa Ana Mountains [26] are also intermediate between *C.* (*E.*) *buttensis* and *C.* (*E.*) *bowersiana.*

Anderson (1958) figured a specimen of *Calva crassa* as *Trigonocallista major* (Packard), although Popenoe (1937) had shown that *T. major* is a junior synonym of *C.* (*Egelicalva*) *bowersiana. Calva* (*E.*) *bowersiana* is more elongate, has a less strongly arched hinge plate, and is less inflated than *C.* (*E.*) *crassa.* Cardinals 2a and 2b of *C.* (*E.*) *bowersiana* are more divergent than those of *C.* (*E.*) *crassa.* Anderson (1958) also provided the new name *Meretrix coronada* for *Meretrix* (?) sp. of Packard (1922). The specimen figured by Packard (UCMP cat. no. 12306) has been rendered unduly elongate for *C.* (*E.*) *bowersiana* by post-depositional crushing. It retains shell mainly on the anterior and displays, as noted by Packard, a lunule bounded by an incised line (Fig. 235). Its pallial sinus can be discerned on the right valve steinkern (Fig. 238); these two features indicate that it is *C.* (*E.*) *bowersiana.* Anderson (1958, p. 137) suggested that "*M.*" *coronada* was congeneric with "*Meretrix*" *marshana* Anderson, 1958, but "*M.*" *marshana,* which appears to have had alate nymphs, is probably not a venerid.

The holotype of *Cyprina denmanensis* Whiteaves, 1903 (p. 380, fig. 25) from the west side of Denman Island, British Columbia, lacks the hinge and part of the beak area. It has a growth line suggestive of *Calva* (*Egelicalva*) *bowersiana* but is at least half again as large as any other specimen of *C.* (*E.*) *bowersiana.* J. M. Haggart has sent two specimens from GSC loc. 83909 on the southern shore of Denman Island, which he suggested might be *Cyprina denmanensis.* Both specimens are bivalved and neither is as large as the holotype. These specimens do not appear to belong in the Veneridae; what can be seen of their hinges suggests that they are mactrids.

Certainly some of *Cytherea* (*Caryatis*) *plana* (Sowerby, 1812) of Whiteaves (1879, p. 149) are *Calva* (*Egelicalva*) *bowersiana* (Cooper). Unfortunately Whiteaves' figured specimens have not been recognized and are not in the collections of the Geological Survey of Canada. His illustrations resemble *C.* (*E.*) *bowersiana* from Sucia Island. Four small specimens, GSC cat. nos. 5716, a–c from the northwest side of Hornby Island, may belong in *Calva* (*Microcalva*). They resemble *Calva* (*Microcalva*) *haggarti* but have concentric sculpture only near the beak, confined to the area circumscribed by the first growth check. They may be juvenile *C.* (*E.*) *bowersiana* but are too incomplete for certain identification. Specimens from the Cedar District Formation on Sucia Island [3], although in some respects intermediate between *C.* (*E.*) *bowersiana* and *C.* (*E.*) *buttensis,* are considered to be *C.* (*E.*) *bowersiana* because of their concave lunular margin. Judging from the inferred ages of the deposits, some of Whiteaves' other specimens are probably *Calva* (*E.*) *bowersiana* (Cooper), but they can best be reassigned when the specimens have been recovered. In 1903, Whiteaves included all of these specimens in *Meretrix nitida* Gabb, but none are likely to be *M. nitida,* which is of late Albian–Cenomanian age.

Calva (*Egelicalva*) *bowersiana* occurs in the Pigeon Point Formation near Bolsa Point [16], San Mateo Co., California. On the basis of a paleomagnetic study, the Pigeon Point Formation has been considered to have been deposited at about 21°N latitude off the coast of southern Mexico (Champion et al., 1981). If the provenance of the Pigeon Point specimens is near 21°N, the geographic range of *C.* (*E.*) *bowersiana* is extended southward by about 13°. Neither *C.* (*E.*) *bowersiana* nor any other species in the fauna is known from the Mexican mainland, but several Pigeon Point species, *Cucullaea* (*Idonearca*) *youngi* (Waring, 1917), *Turritella chicoensis pescaderosensis* Arnold, 1908, and *Tessarolax distorta* Gabb, 1864, also occur in deposits of late Campanian age in the Santa Monica [25] and Santa Ana [26] Mountains.

Calva (*Egelicalva*) *crassa,* new species

Figures 239–254

Venus steineyi Hertlein Anderson and Hanna, 1935, p. 7 (n. nud.).

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Figures 227–238. *Calva* (*Egelicalva*) *bowersiana* (Cooper). All ×1; all from zone of *Metaplacenticeras pacificum*; all specimens whitened with ammonium chloride. **227,** CAS cat. no. 66028.01, holotype, from CAS loc. 66028, exterior. **228, 229, 231–233,** LACMIP cat. no. 8184, hypotype, from LACMIP loc. 10120, **228,** hinge, **229,** exterior, **231,** dorsal view, **232,** anterior view, **233,** posterior view. **230,** LACMIP cat. no. 8185, hypotype, from LACMIP loc. 10105, hinge. **234, 236, 237,** LACMIP cat. no. 8187, hypotype, from LACMIP loc. 10715, **234,** anterior view, **236,** dorsal view, **237,** hinge. **235, 238,** "*Meretrix*" *coronada* Anderson, UCMP cat. no. 12306, holotype, from UCMP loc. 1267, **235,** dorsal view, **238,** right valve pallial sinus. Photos 227, 236 by Saul; 228–235, 237, 238 by De Leon.

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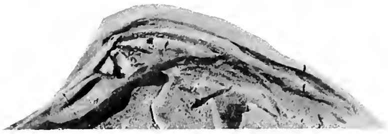

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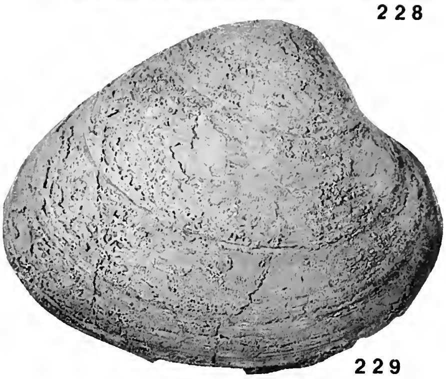

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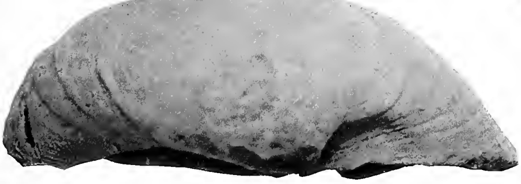

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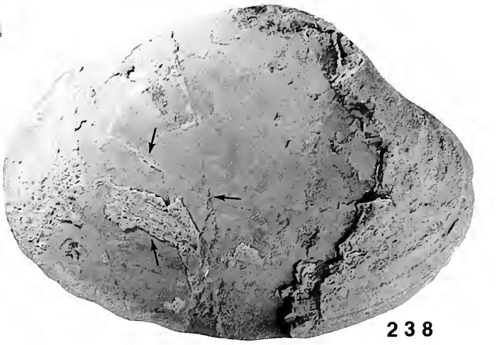

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Calva "*steineyi*" Hertlein MSS Popenoe, 1954, p. 17, fig. 4 (12).

Trigonocallista major (Packard) Anderson, 1958, p. 138, pl. 70, fig. 2–2a. Not *Meretrix nitida major* Packard, 1922 = *Calva bowersiana* (Cooper).

Calva varians (Gabb) Dailey and Popenoe, 1966, p. 16, pl. 4, figs. 1–4; Saul, 1970, p. 80, fig. 16. Not *Venus varians* Gabb, 1864; *Aphrodina varians* (Gabb) Stewart, 1930; "*Trigonocallista*" *varians* (Gabb) Anderson, 1958.

DIAGNOSIS. A large, relatively high, broad-beaked *Egelicalva* with maximum inflation anterior to the mid-length, a concave lunular margin, and smooth lateral teeth. Cardinal tooth 1 not reaching the hinge plate edge, extending farther toward beak than 3a.

DESCRIPTION. Shell thick, of large size, nearly as high as long, inflated, maximum inflation anterior to mid-length; beaks prominent, high, anterior to the mid-length of the shell, strongly prosogyrous; lunular margin strongly concave; anterior end broadly rounded; ventral border slightly arched, medially flattened; posterior end angulately truncate; posterior dorsal border long, slightly arched in small specimens, moderately arched in large specimens; lunule large, wide, deep, delimited by an inscribed line; escutcheon indistinct; shell surface marked by growth lines and distant, impressed growth checks.

Ligament groove arched, nymphs salient posteriorly. Hinge of right valve with anterior tooth 3a short, narrow, prominent, close to 1; median cardinal 1 a third longer than 3a, narrow, prominent, diverging ventrally from 3a, situated directly beneath the beak; posterior cardinal 3b long, arched, shallowly bifid subparallel to the nymph; socket for lateral AII long, deep, smooth, parallel to the lunular border of the shell; socket for PII long, deep, bounded below by PI. Hinge of left valve with anterior cardinal 2a prominent, very slender, directed slightly posteriorly; cardinal 2b thicker than 2a, trigonal, directed obliquely backward, slightly arched; posterior cardinal 4b separated from the nymph by a groove, scarcely longer than the anterior teeth; anterior lateral AII long, hooked posteriorly, parallel to the lunular margin, smooth sided; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus broadly linguiform, extending to near the valve mid-length; dorsal arm nearly horizontal; ventral arm concavely ascending, at an angle of near 40° to pallial line. Anterior adductor muscle scar well impressed, rounded; posterior adductor muscle scar moderately impressed, rounded.

HOLOTYPE. UCLA cat. no. 40421 [= hypotype of *Calva varians* (Gabb) of Dailey and Popenoe, 1966, p. 16, pl. 4, figs. 1–2, 4].

PARATYPES. UCLA cat. nos. 28711 [= "hypotype" of *Calva* "*steineyi*" Hertlein MSS of Popenoe, 1954, p. 19, fig. 4 (12)] from LACMIP loc. 10690 [= CIT loc. 590], Jalama area [22]; 40422 [= hypotype of *C. varians* (Gabb) of Dailey and Popenoe, 1966, p. 16, pl. 4, fig. 3] from UCLA loc. 4118, Jalama area [22]; 59081 [= hypotype of *C. varians* (Gabb) of Popenoe, 1973, p. 24, pl. 4, fig. 41] from UCLA loc. 4143, Jalama area [22], Santa Barbara Co., California. LACMIP cat. nos. 8174 from UCLA loc. 4120, Jalama Creek [22]; 8177 from UCLA loc. 4116, Jalama Creek [22]; 8198 from LACMIP loc. 10695, Jalama Creek [22], Santa Barbara Co.; 8199 from UCLA loc. 6345, 2 miles south of Ortigalita Creek [18], Merced Co.; 8233 from UCLA loc. 4131, Jalama Ranch [22], Santa Barbara Co., California. CAS cat. no. 10645 from CAS loc. 954 (hypotype of *Trigonocallista major* (Packard) of Anderson, 1958) from Punta Banda [29], Baja California, Mexico.

TYPE LOCALITY. UCLA loc. 4118, Jalama area [22], Santa Barbara Co., California.

GEOLOGIC AGE. Early Maastrichtian.

DISTRIBUTION. Moreno Formation, Tierra Loma Sandstone, Ortigalita Peak Quadrangle [18], Merced Co.; cobble in ?El Piojo Formation, at Pebblestone Shut-In [21], San Luis Obispo Co.; Jalama Formation, near Jalama Creek [22], Santa Barbara Co., California; Chatsworth Formation, west end of the Simi Hills [24], Ventura Co., California; Rosario Formation, Punta Banda [29], Baja California, Mexico.

DIMENSIONS. See Table 14.

REMARKS. In some specimens the valves are unevenly inflated and the anterior more inflated part is set off from the posterior by a shallow arching sulcus that extends from about ¼ valve height to the ventral margin (Fig. 250). *Calva* (*Egelicalva*) *crassa* and *C.* (*Penecallista*) *marina* are both large, but *C.* (*E.*) *crassa* is relatively much higher and more inflated and has a larger lunule than *C.* (*P.*) *marina*. *Calva* (*E.*) *crassa* has a typical *Calva* hinge, but *C.* (*P.*) *marina* has 2b short, extending no more than two-thirds across the hinge plate. In shape *C.* (*E.*) *crassa* resembles *C.* (*E.*) *taffi* but has a more concave lunular border, and all specimens of *C.* (*E.*) *taffi* are much smaller. *Calva* (*E.*) *crassa* has been confused with *C.* (*C.*) *varians* from which it

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Figures 239–245. *Calva* (*Egelicalva*) *crassa*, new species. All ×1; all specimens whitened with ammonium chloride. **239–241, 243, 245,** UCLA cat. no. 40421, holotype, from UCLA loc. 4118, **239,** hinge, **240,** anterior view, **241,** exterior, **243,** posterior view, **245,** dorsal view. **242,** LACMIP cat. no. 8174, paratype, from UCLA loc. 4120, hinge. **244,** LACMIP cat. no. 8233, paratype, from UCLA loc. 4131, exterior. Photos 239–241, 245 by Susuki; 242–244 by De Leon.

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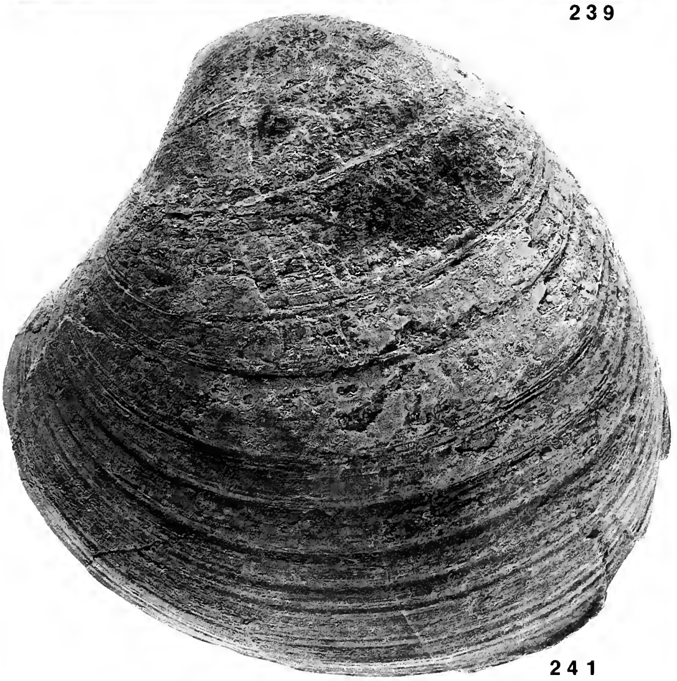

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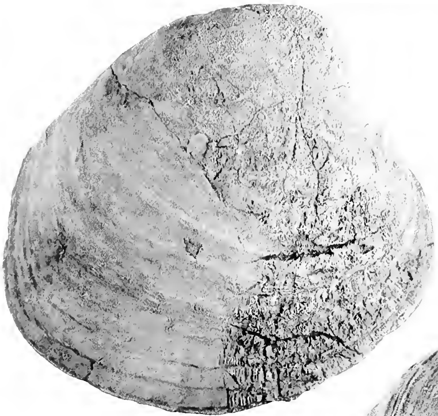

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Table 14. Measurements of *Calva* (*Egelicalva*) *crassa*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
UCLA 28711	89.4	98.7	36.4	39.4	23.8	9.4		1.1	2.7	2.5	1.66	2.5
UCLA 40421	83.6	87.8	36.8	40.5	24.0	9.2	93°	1.0	2.4	2.2	1.7	2.6
UCLA 40422	82.0	85.0	34.4	42.2	22.8	11.0	93°	1.0	2.5	2.0	1.8	2.1
UCLA 59081	80.0	85.8	32.6					1.1	2.6	—	—	—
LACMIP 8177	80.5	85.0	30.8	32.0	17.0	8.6		1.1	2.8	2.7	1.9	2.0
LACMIP 8198	54.5	59.0	20.0	28.7	15.0	4.7	108°	1.1	3.0	2.1	1.9	3.2
LACMIP 8233	58.0	60.5	17.0	26.0	13.5	5.0		1.0	3.6	2.3	1.9	2.7

differs in being relatively higher and having a much wider, deeper, and more heart-shaped lunule and a concave lunular border.

The specimen figured by Anderson (1958, pl. 70, fig. 2–2a) as *Trigonocallista major* Packard is the same specimen earlier called *Venus steineyi* Hertlein by Anderson and Hanna (1935). According to Anderson and Hanna it was collected at Punta Banda [29], Baja California. Although Hertlein never described the species, the name "*steineyi*" was used for this large, robust *Calva* for more than two decades.

Several specimens from a large boulder (LACMIP loc. 12245) in a conglomerate that crops out at the Pebblestone Shut-In [21], San Luis Obispo Co., California, are probably this species as are poorly preserved specimens from at least two localities near Ortigalita Creek [18], Merced Co., California. At one of these localities *Calva* (*Calva*) *varians* is also present, and the temporal ranges of these two species apparently overlapped somewhat.

ETYMOLOGY. The specific name is from Latin, *crassus*, large.

Subgenus *Microcalva*, new subgenus

TYPE SPECIES. *Calva* (*Microcalva*) *haggarti*, new species.

DIAGNOSIS. Small ovately trigonal *Calva* with concentric ribs and lacking a distinct escutcheon. Hinge moderately heavy with 3b narrowly bifid, laterals finely striate, and anterior lateral AII hooked. Pallial sinus linguiform.

DISCUSSION. Hinges of these small venerids are essentially similar to those of *Calva*. *Microcalva* differs from other *Calva* in its small size and in having the polished shell surface sculptured with fine concentric ribs. Compared to other *Calva* of equivalent age its laterals are more strongly striated. Juveniles up to the first growth check of *Egelicalva* are most similar to *Microcalva*, and specimens of *Microcalva* might be considered to be just juveniles of an *Egelicalva* if *Calva* (*Microcalva*) *haggarti* were not so abundant in the Cedar District Formation of the Nanaimo Basin. *Microcalva* is clearly more closely related to *Egelicalva* than to *Calva* s.s. In size and sculpture *Microcalva* is suggestive of *Loxo* Dailey and Popenoe, 1966, but *Microcalva* has round-topped ribs rather than the inscribed lines of *Loxo*. The hinge of *Microcalva* has the anterior lateral AII posteriorly hooked and parallel to the lunular margin as in *Calva*, whereas that of *Loxo* is straight and at an angle to the lunular margin. *Microcalva* resembles *Chimela* Casey, 1952, in lacking an escutcheon but differs in having a well-developed posterior hook to anterior lateral AII. AII is quite long in *Microcalva*, and the pallial sinus is long and linguiform.

ETYMOLOGY. The subgeneric name is compounded from *mikros*, Greek, small, little, and *Calva* and is of feminine gender.

Calva (*Microcalva*) *elderi*, new species

Figures 255–261

DIAGNOSIS. An anteriorly produced *Microcalva* with moderately broad concentric ribs that are steeper on the dorsal side. Hinge with cardinal 3b elongate and lateral AII long.

DESCRIPTION. Shell small, subovoid, gently inflated medially; beaks prominent, near the anterior third-length of the shell, prosogyrous; lunular margin straight; anterior end, slightly produced, rounded; ventral border roundly arched; posterior end roundly truncated; posterior dorsal slope long,

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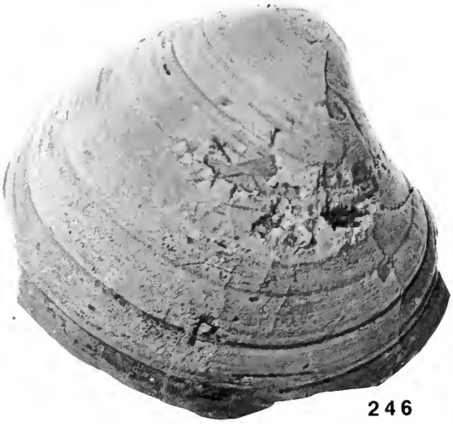
Figures 246–254. *Calva* (*Egelicalva*) *crassa*, new species. All ×1; all specimens whitened with ammonium chloride. **246, 247,** LACMIP cat. no. 8198, paratype, from LACMIP loc. 10695, **246,** exterior, **247,** hinge. **248, 252,** LACMIP cat. no. 8174, paratype, from UCLA loc. 4120, **248,** posterior view, **252,** exterior. **249,** UCLA cat. loc. 40422, paratype, from UCLA loc. 4118, hinge. **250, 251,** LACMIP cat. no. 8177, paratype, from UCLA loc. 4116, **250,** dorsal view, **251,** exterior right valve. **253,** LACMIP cat. no. 8233, paratype, from UCLA loc. 4131, anterior view. **254,** LACMIP cat. no. 8199, paratype, from UCLA loc. 6345, pallial sinus. Photos 246, 247 by Saul; 248, 250–254 by De Leon; 249 by Susuki.



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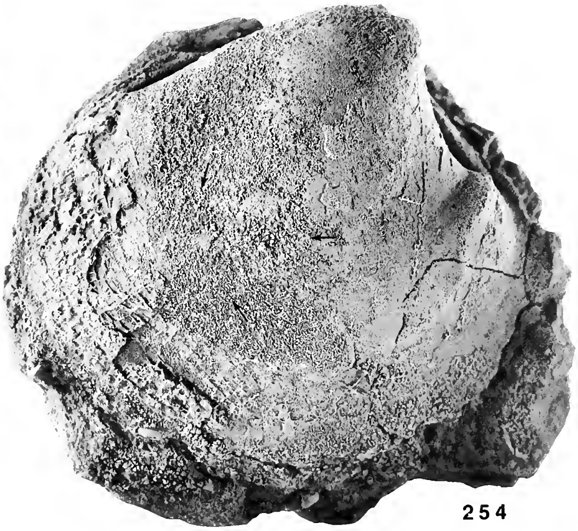

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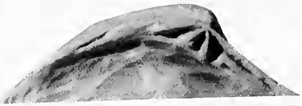
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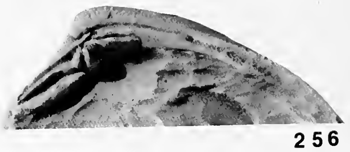
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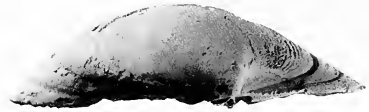
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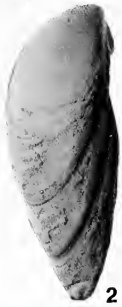
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Figures 255–261. *Calva* (*Microcalva*) *elderi,* new species. All ×2; all specimens whitened with ammonium chloride. **255, 257, 258, 260, 261,** USNM cat. no. 456073, holotype, from USGS loc. M8649c, **255,** hinge, **257,** exterior, **258,** anterior view, **260,** dorsal view, **261,** posterior view. **256, 259,** USNM cat. no. 456074, paratype, from USGS loc. M8649b, **256,** hinge, **259,** exterior. All photos by De Leon.

arched; lunule lanceolate, moderately depressed, circumscribed by a line; shell surface ornamented by evenly spaced, flatly round-topped, concentric ribs over-steepened on the dorsal side, and irregularly spaced, impressed growth checks.

Ligament groove moderately long, barely arched behind smooth nymphae. Hinge of right valve with cardinals 3a and 1 divergent, beneath the beak, 1 longer than 3a; cardinal 3b more than twice as long as 1, bifid; anterior laterals elongate enclosing a moderately deep socket for AII, AI rather thick, AIII very slender; posterior lateral PI well developed, bordering an elongate socket. Hinge of left valve with cardinals 2a and 2b sturdy, nearly equal, divergent; cardinal 4b longer, slender, separated from the nymph by a groove; anterior lateral AII moderately long, hooked; posterior lateral PII a barely projecting salient of the valve edge. Pallial sinus unknown.

HOLOTYPE. USNM cat. no. 456073.

PARATYPES. USNM cat. nos. 456074, 456075.

TYPE LOCALITY. USGS loc. M8649c, a clast in conglomerate on north nose of hill 443, elev. 390′ [118.87 m], SW ¼, NE ¼, NW ¼ Sec. 24, T10S, R8E, San Luis Dam Quadrangle, Merced Co., California.

GEOLOGIC AGE. Coniacian, associated with *Meekia louella* Popenoe, 1962.

DISTRIBUTION. Known only from the type locality and vicinity, near San Luis Dam [18], Merced Co., California.

DIMENSIONS. See Table 15.

REMARKS. In outline and inflation *Calva* (*Microcalva*) *elderi* resembles "*Meretrix*" *arata* Gabb, 1864, but "*M.*" *arata* lacks posterior laterals and is sculptured by more closely spaced concentric grooves rather than flatly rounded concentric ribs. *Calva* (*M.*) *elderi* differs from *Calva* (*M.*) *haggarti* in having the anterior end slightly more produced, in being less inflated, and in having the concentric ribs more flattened on their tops and about twice as broad. In *C.* (*M.*) *elderi* both the anterior laterals and especially cardinal 3b are noticeably longer, and cardinal 2a is more anteriorly directed in *C.* (*M.*) *haggarti.*

ETYMOLOGY. The species is named for W. P. Elder who collected the type specimens.

Calva (*Microcalva*) *haggarti,* new species

Figures 262–275

Cytherea (*Callista*) *laciniata* Stoliczka, Whiteaves, 1879, p. 148, pl. 17, figs. 13, 13a; pl. 19, figs. 4, 4a. Not *Cytherea* (*Callista*) *laciniata* Stoliczka, 1871.

Cytherea arata (Gabb) Whiteaves, 1895, p. 125. Not *Meretrix arata* Gabb, 1864.

Meretrix arata Gabb Whiteaves, 1903, p. 378. Not *Meretrix arata* Gabb, 1864.

DIAGNOSIS. A plump *Microcalva* with closely spaced, concentric, round-topped ribs.

DESCRIPTION. Shell small, subtrigonal, roundly inflated medially; beaks prominent, at the anterior third-length of the shell, prosogyrous; lunular

Table 15. Measurements of *Calva* (*Microcalva*) *elderi*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
USNM 456073	18.3	23.8	6.8	11.5	5.6	1.6	115°	1.3	3.5	2.1	2.0	3.5
USNM 456074	21.5	26.3	7.8		6.2	1.9	117°	1.2	3.4	—	—	3.3

margin straight; anterior end well rounded; ventral border roundly arched; posterior end roundly truncated; posterior dorsal slope long, arched; lunule plumply lanceolate, moderately depressed, circumscribed by a line; shell surface ornamented by closely, evenly spaced, round-topped, concentric ribs and irregularly spaced, impressed growth checks.

Ligament groove moderately long, barely arched behind smooth nymphae. Hinge of right valve with cardinals 3a and 1 divergent, beneath the beak, 1 longer than 3a; cardinal 3b twice as long as 1, bifid; anterior laterals elongate enclosing a moderately deep socket for AII, AI rather thick, AIII very slender; posterior lateral PI well developed, bordering an elongate socket. Hinge of left valve with cardinals 2a and 2b sturdy, nearly equal, divergent; cardinal 4b longer, slender, scarely separated from the nymph by a shallow groove; anterior lateral AII short, hooked; posterior lateral PII a barely projecting salient of the valve edge. Pallial sinus linguiform, slightly ascending, extending half of the shell length across the valve; dorsal arm a little convex; ventral arm slightly concave, ascending at nearly 40° to the pallial line. Anterior adductor muscle scar impressed, posterior adductor muscle scar not impressed.

HOLOTYPE. LACMIP cat. no. 8242.

PARATYPES. LACMIP cat. nos. 8243–8248 from LACMIP loc. 10446, Sucia Island [3], San Juan Co., Washington.

TYPE LOCALITY. LACMIP loc. 10446, Sucia Island [3], San Juan Co., Washington.

GEOLOGIC AGE. Campanian.

DISTRIBUTION. Northumberland Formation on Hornby Island (Usher, 1952, p. 27); Cedar District Formation of the Nanaimo Basin [1–2], Vancouver Island, British Columbia; Cedar District Formation, Sucia Island [3], San Juan Co., Washington.

DIMENSIONS. See Table 16.

REMARKS. Whiteaves originally identified this small venerid with the Indian *Cytherea* (*Callista*) *laciniata* Stoliczka (Whiteaves, 1879), but later, in part encouraged by a specimen from Stanton, recognized its similarity to the Californian ?*Meretrix arata* Gabb, 1864 (Whiteaves, 1896, 1903). Whiteaves (1903) noted that Gabb's description of the sculpture as inscribed lines did not fit the ribbing of the specimens from Sucia Island [3], but with Stanton's specimen from Tehama County as a guide, he did not differentiate his specimens from ?*M. arata* on that basis. In addition to the sculptural differences, *Calva* (*Microcalva*) *haggarti* differs from *Aphrodina*? *arata* (Gabb, 1864) in being relatively shorter and higher, having more prominent beaks, having finely striate laterals, and having AII posteriorly hooked and parallel to the lunular margin. The specimen Stanton sent to Whiteaves as an example of "*Meretrix*" *arata* may actually have been a *Microcalva*, although we are unacquainted with occurrences of either "*M.*" *arata* or any *Microcalva* in Tehama County. *Calva* (*M.*) *haggarti* differs from *C.* (*M.*) *elderi* in having a shortened anterior, finer, rounder-topped ribs, shorter anterior laterals, and a shorter cardinal 3b. *Calva* (*M.*) *haggarti* differs from immature *C.* (*E.*) *bowersiana* of comparable size from the Cedar District Formation of the Nanaimo Basin in its overall sculpture, greater inflation, and smaller lunule. *Calva* (*M.*) *haggarti* differs from *Loxo decore* Dailey and Popenoe, 1966, in being ribbed rather than having inscribed concentric lines, being more roundly inflated, and having the hooked anterior lateral of *Calva*.

Whiteaves (1879, 1903) recorded this species from the northwest side of Hornby Island and Texada Island, British Columbia [1], and as most abundant from Sucia Island, Washington [3]. Four incomplete specimens (GSC cat. nos. 5716, a–c) identified by him as *Cytherea* (*Caryatis*) *plana* Sowerby [= *Meretrix nitida* Gabb] from the northwest side of

Table 16. Measurements of *Calva* (*Microcalva*) *haggarti*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8242	18.0	20.9	7.0	10.4	5.5	1.6	109°	1.2	3.0	2.0	1.9	3.4
LACMIP 8243	21.8	27.8	8.4	11.0	6.3	2.0	128°	1.3	3.3	2.5	1.7	3.2
LAMCIP 8244	19.0	22.8	6.0	9.0	6.4	1.8	107°	1.2	3.8	2.5	1.4	3.6
LACMIP 8245	20.2	24.4	8.0	9.6	5.7	2.0	110°	1.2	3.1	2.5	1.7	2.9
LACMIP 8246	19.0	22.6	8.0	10.7	6.4	2.0	112°	1.2	2.8	2.1	1.7	3.2
LACMIP 8247	17.4	21.7	6.0	8.0	6.4	1.6	117°	1.2	3.6	2.7	1.3	4.0


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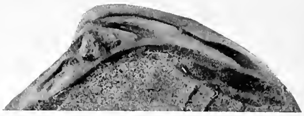
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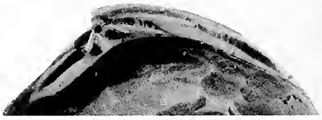
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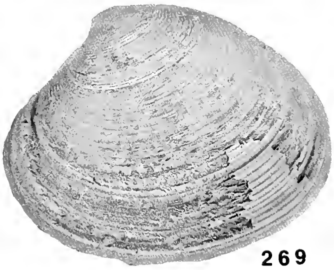
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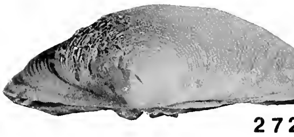
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Figures 262–275. *Calva* (*Microcalva*) *haggarti,* new species. All from LACMIP loc. 10446; all specimens whitened with ammonium chloride. **262, 269,** LACMIP cat. no. 8347, paratype, ×2, **262,** hinge, **269,** exterior. **263, 271, 272,** LACMIP cat. no. 8342, holotype, ×2, **263,** hinge, **271,** exterior, **272,** dorsal view. **264, 265, 270, 273,** LACMIP cat. no. 8345, paratype, ×2, **264,** hinge, **265,** anterior view, **270,** posterior view, **273,** exterior. **266,** LACMIP cat. no. 8346, paratype, ×2, hinge. **267,** LACMIP cat. no. 8343, paratype, ×2, hinge. **268, 275,** LACMIP cat. no. 8344, paratype, ×2, **268,** hinge, **275,** exterior. **274,** LACMIP cat. no. 8348, paratype, ×1, pallial sinus. All photos by De Leon.

Hornby Island may be this species. One specimen, GSC 5716a, clearly displays a pallial line like that of *Calva* (*Microcalva*) *haggarti*; another, GSC 5716c, displays the finely striated anterior lateral typical of *Microcalva.* They differ from Sucia Island specimens in having the concentric sculpture only near the beak, confined to the area circumscribed by the first growth check, and in being relatively shorter. The latter two features make these specimens resemble equivalent sized *C.* (*Egelicalva*) *bowersiana.* Determination of whether these specimens should be placed in *C.* (*M.*) *haggarti,* assigned to a new species of *Microcalva,* or recognized as immature *C.* (*E.*) *bowersiana* awaits more complete specimens. Some specimens of *C.* (*M.*) *haggarti* at the Royal British Columbia Museum that were identified by Whiteaves are also labeled as *C. nitida.* Usher (1952, p. 27) lists *Meretrix arata,* Whiteaves' 1903 name for *C.* (*M.*) *haggarti,* from the Lambert Formation (= Northumberland Formation of Muller and Jeletzky, 1970) but does not specify whether from the lower Lambert on Denman Island or the upper Lambert on Hornby Island. Haggart (1989, p. 184) has placed the Northumberland in the *Pachydiscus suciensis* Zone above that of *Metaplacenticeras pacificum.* The range of *C.* (*M.*) *haggarti* cannot be inferred from these old records; it is known with certainly only from Sucia Island where it is of late early Campanian age. Too few specimens of younger age have been available for this study, but those at hand seem to differ sufficiently from the Sucia Island specimens to constitute a different species.

The *Callista* (?) cf. *arata* (Gabb) of Nagao (1932, p. 39, pl. 6, fig. 6, 6a; *Callista* ? sp. Hayami, 1975, p. 145) from the Coniacian–Santonian upper Yezo Group of Hokkaido, Japan, seems to be too inflated to be "*Meretrix*" *arata* Gabb, and its sculpture is described as conforming to Whiteaves' (1903) description of the specimens from Sucia Island. Its hinge is as yet unknown, however, and it cannot be placed in *Microcalva* solely on the basis of its sculpture.

ETYMOLOGY. The species is named for J. M. Haggart, Geological Survey of Canada, in appreciation of his assistance in loaning specimens from the Nanaimo area.

Subgenus *Penecallista,* new subgenus

TYPE SPECIES. *Calva* (*Penecallista*) *marina,* new species.

DIAGNOSIS. Large veneriform *Calva* with a narrow but well-angled escutcheon. Hinge with short 2b, widely bifid 3b, and relatively short anterior laterals. Nymphaea posteriorly salient and having a groove aligned with the posterior socket.

DISCUSSION. This subgenus is proposed with some reluctance, as only the type species may be assigned to it. However, this species displays several characteristics that distinguish it from other subgenera of *Calva.* Its shape is clearly less trigonal and more ovoid than are species of *Egelicalva* or *Calva* s.s. The combination of relatively short cardinal tooth 2b, widely bifid 3b, and relatively short anterior laterals makes the hinge look less like that of *Calva* s.s. and *Egelicalva* than does the hinge of the much smaller *Microcalva.* In addition, the well-marked groove aligned with the posterior lateral socket on the posterior end of the nymph is not as evident on any other *Calva.*

The shell shape is similar to that of Recent species of *Callista* (*Megapitaria*) Grant and Gale, 1931, from the Panamic faunal province, the hinge plate is of similar width, and the anterior laterals are of similar length. However, *Callista* (*Megapitaria*) lacks posterior laterals, its anterior laterals are at an angle to the valve margin, and anterior lateral AII is not hooked as in *Calva.* In *Callista* (*Megapitaria*), the margin of the right valve is grooved posterior to the ligament to hold a corresponding tongue of the left valve margin. These tongue and groove structures are probably not homologous to the posterior laterals of *Calva,* as the tongue and groove are dorsal to the end of the ligament groove with which the posterior laterals of *Calva* are aligned.

ETYMOLOGY. The subgeneric name is compounded from *pene,* Latin, near, and the venerid genus name *Callista.*

Calva (*Penecallista*) *marina,*
new species

Figures 276–287

Flaventia zeta Popenoe, Sundberg, 1979, p. 176, pl. 1, fig. 8. Not *Flaventia zeta* Popenoe, 1937.

DIAGNOSIS. As for the subgenus.

DESCRIPTION. Shell large, nearly as high as long, moderately inflated, rather thick; beaks prominent, placed anterior to the mid-length of the shell, prosogyrous; anterior dorsal border concave; anterior end rounded; ventral border broadly arched; posterior end truncate vertically; posterior dorsal border arched; lunule relatively small, deep, delimited by an inscribed line; escutcheon narrow, defined by rounded angulation; posterior slope demarked by subangulate change in slope.

Ligament groove long, arched behind strong, posteriorly projecting nymphs. Hinge of right valve with anterior tooth 3a short; 3a and median cardinal tooth 1 narrow, prominent, close together, slightly divergent ventrally, situated directly beneath the beaks; 3a longer than 1, extending from about the hinge plate edge as close to the beak as 3a; right posterior cardinal 3b long, arched, bifid, dorsal arm much the longer, subparallel to nymph; socket for lateral AII moderately elongate, about as long as cardinal 1, narrow, moderately deep, smooth; socket for PII long, deep, bounded below by an elongate tooth. Hinge of left valve with anterior cardinal 2a prominent, slender, gently curved, slightly posteriorly directed; cardinal 2b short, broad based, trigonal, sloping upward to high dorsal side, posteriorly directed; posterior cardinal 4b elongate, twice as long as the anterior teeth, slender; anterior lateral AII elongate, barely longer than cardinal 2b, posteriorly hooked, long arm parallel to lunular

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Figures 276–280. *Calva* (*Penecallista*) *marina,* new species. All ×1; all specimens whitened with ammonium chloride. **276–278,** LACMIP cat. no. 8249, holotype, from UCLA loc. 3796, **276,** hinge, **277,** posterior view, **278,** exterior. **279,** LACMIP cat. no. 8253, paratype, from UCLA loc. 4863, pallial sinus. **280,** LACMIP cat. no. 8252, paratype, from UCLA loc. 4863, dorsal view. All photos by De Leon.

Figures 281–287. *Calva* (*Penecallista*) *marina,* new species. All ×1; all specimens whitened with ammonium chloride. **281,** LACMIP cat. no. 8250, paratype, from UCLA loc. 4863, hinge. **282, 287,** LACMIP cat. no. 8252, paratype, from UCLA loc. 4863, **282,** anterior view, **287,** hinge. **283, 285,** USNM cat. no. 456071, paratype, from USGS loc. M4017, **283,** hinge, and exterior of *Loxo decore* Dailey and Popenoe, 1966, **285,** exterior. **284, 286,** LACMIP cat. no. 8251, paratype, from UCLA loc. 4863, **284,** exterior, **286,** posterior view. All photos by De Leon.

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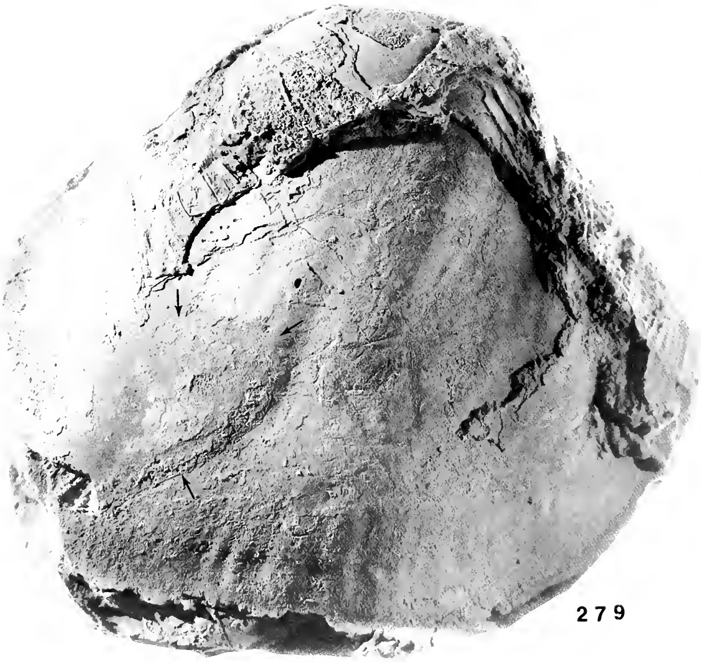

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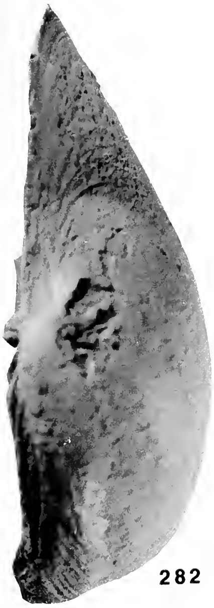

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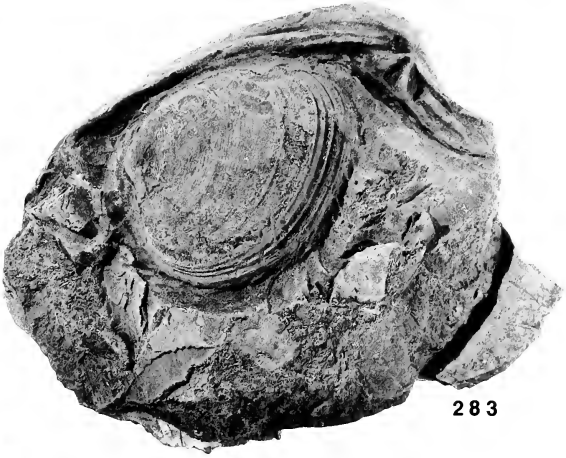

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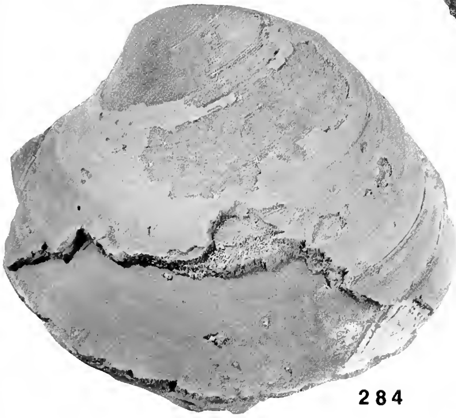

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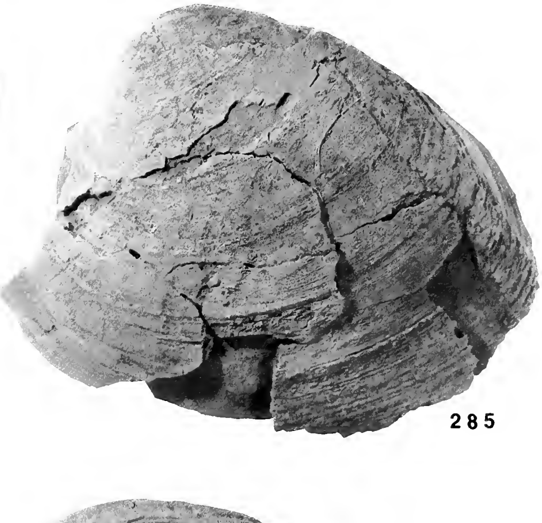

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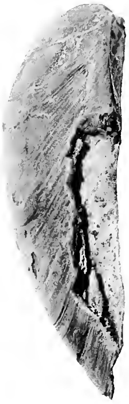

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Table 17. Measurements of *Calva* (*Penecallista*) *marina*. Dimensional abbreviations defined in Figure 4.

	H (mm)	L (mm)	I (mm)	B (mm)	LL (mm)	LW (mm)	LTA	L/H	L/I	L/B	B/LL	LL/ LW
LACMIP 8249	79.0	92.4	25.4	34.8	16.3	4.2	100°	1.2	3.6	2.7	2.1	3.9
LACMIP 8250	90.9	108.0	32	35.5	15.3	4.8	98°	1.2	3.4	3.0	2.3	3.2
LACMIP 8251	53.7	63.0	17.8	24.0	11.5	2.7		1.2	3.5	2.6	2.1	4.3
LACMIP 8252	85.0	108.0	26.7	35.4	15.5	4.8	104°	1.3	5.0	3.0	2.3	3.2

margin, smooth sided; posterior lateral tooth PII, a slightly salient portion of the shell-margin just posterior to the rear end of the nymph. Pallial sinus U-shaped, ascending, extending across one-third of the shell length.

HOLOTYPE. LACMIP cat. no. 8249.

PARATYPES. USNM cat. no. 456071 from USGS loc. M4017, Sisquoc River [22], Santa Barbara Co., California; LACMIP cat. nos. 8250–8253 from UCLA loc. 4863, San Antonio del Mar [30], Baja California, Mexico.

HYPOTYPE. LACMIP cat. no. 7745 (hypotype of *Flaventia zeta* Popenoe of Sundberg, 1979) from LACMIP loc. 11629, La Jolla [28], San Diego Co., California.

TYPE LOCALITY. UCLA loc. 3796, San Antonio del Mar [30], Baja California, Mexico.

GEOLOGIC AGE. ?Latest Campanian and early Maastrichtian.

DISTRIBUTION. Unnamed formation along the Sisquoc River [22], Hurricane Deck Quadrangle, Santa Barbara Co.; Williams Formation along Bee Canyon [26], Orange Co.; ?basal Point Loma Formation at La Jolla [28], San Diego Co., California. Rosario Formation, near San Antonio del Mar [30], Baja California, Mexico.

DIMENSIONS. See Table 17.

REMARKS. The left valve figured as *Flaventia zeta* by Sundberg (1979) was prepared by sawing parallel to the plane of commissure; the saw blade removed most of the hinge teeth. Part of the inscribed lunule yet remains. Bases of some of the hinge teeth and the shape of the hinge plate are also visible. The widening of the hinge plate adjacent to the lunule indicates that an anterior lateral tooth was present; *Flaventia* lacks laterals and does not have an inscribed lunule. The growth line of this specimen and its degree of inflation are most similar to that of *Calva* (*Penecallista*) *marina*. As in *C.* (*P.*) *marina* cardinal tooth 2b is short, extending about halfway across the hinge plate. This specimen is from the basal Point Loma sandstone and from below the early Maastrichtian magnetic reversal 32r (Bannon et al., 1989). It may, therefore, be of late Campanian age.

In addition to several specimens of *Calva* (*Penecallista*) *marina,* USGS loc. M4017 has yielded *Crassatella* (?) *elongata* Anderson, 1958, *Crassatella* (?) *saulae* Dailey and Popenoe, 1966, and *Loxo decore* Dailey and Popenoe, 1966. *Crassatella* (?) *elongata* has previously been found in the late Campanian *Metaplacenticeras pacificum* Zone but not the succeeding *Pachydiscus* (*Neodesmoceras*) *catarinae* Zone; *C.* (?) *saulae* has been recovered from late in the *M. pacificum* Zone and the *P.* (*N.*) *catarinae* Zone, and *Loxo decore* is from the *M. pacificum* Zone and the *P.* (*N.*) *catarinae* Zone. The Sisquoc River [22] specimens are, therefore, probably of very late Campanian age. The sequence at Bee Canyon [26], Orange Co., also yields several late Campanian indicators, among which are *Metaplacenticeras pacificum* and *Perissitys pacificum* Popenoe and Saul, 1987. At its type locality north of San Antonio del Mar, *Calva* (*Penecallista*) *marina* occurs both stratigraphically below and above occurrences of *C.* (*C.*) *peninsularis* and is associated with *Perissitys colocara* Popenoe and Saul, 1987, and *Murphitys madona* Popenoe and Saul, 1987, both of which are considered to be of early Maastrichtian age.

Calva (*Penecallista*) *marina* is a large species comparable in size to *C.* (*Egelicalva*) *crassa,* but *C.* (*P.*) *marina* is more elongate and less inflated than *C.* (*E.*) *crassa.* In shape *C.* (*P.*) *marina* is more like *C.* (*C.*) *peninsularis,* but its posterior angulation is closer to the posterior margin. *Calva* (*P.*) *marina* has a cardinal 3b that is more bent and nymphs that are more strongly projecting posteriorly than any other species herein assigned to *Calva.* It differs from all other *Calva* in the shortness of 2b and in having the posterior end of the nymph noticeably grooved.

In shape *Calva* (*Penecallista*) *marina* resembles the Recent *Callista* (*Megapitaria*) *aurantiaca* (Sowerby, 1831), and *Callista* (*Megapitaria*) *squalida* (Sowerby, 1835), from the Panamic faunal province, and is roughly the same size. These two may be the largest Recent pitarine venerids; *C.* (*M.*) *aurantiaca* is slightly the larger but has a somewhat shorter geographic range and lives from just subtidally to a depth of about 10 m, but *C.* (*M.*) *squalida* inhabits sandy mud flats and has been found offshore down to 160 m (Keen and McLean, 1971, p. 176). *Calva* (*Penecallista*) *marina* may have had a subtidal but shallow water habitat, and as it has not been found north of Santa Barbara County, it may have been a thermophilic species. Its size suggests that by the Late Cretaceous some pitarine venerids had already achieved the upper size range of the group.

ETYMOLOGY. The specific name is from Latin, *marinus,* of the sea, for San Antonio del Mar.

ACKNOWLEDGMENTS

Popenoe pursued species of *Calva* for nearly 50 years. During this time monies of the Penrose Fund, UCLA Academic Senate Research grants, and a National Science Foundation Research Grant were, in part, used to disentangle the species of this genus. Specimens were loaned by the late J. H. Peck, J. W. Durham, and D. R. Lindberg of the University of California, Berkeley, Museum of Paleontology; the late L. G. Hertlein and P. U. Rodda of the California Academy of Sciences; D. L. Jones and W. P. Elder of the U.S. Geological Survey, Menlo Park, California; the late H. G. Richards of the Academy of Natural Sciences of Philadelphia; J. M. Haggart, Geological Survey of Canada; and Richard Hebda and Richard Kools of the Royal British Columbia Museum. We especially thank D. R. Lindberg for his efforts to reorganize and identify specimens collected by the California Geological Survey (Whitney Survey) and deposited in the University of California, Berkeley, Museum of Paleontology.

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LOCALITIES CITED

Geographic areas (bracketed number) of the cited localities are plotted on Figure 1. Type localities of species described in this paper are fully described. Previously published localities are briefly characterized and referenced.

Appendix Text Table

[28]	6	SDSU: See LACMIP loc. 11629 (Sundberg, 1979, p. 173).
[26]	86	CIT: See LACMIP loc. 10120 (Saul, 1974, p. 1093; Saul, 1978, p. 55).
[30]	A-467	UCMP: Cayolitos Creek—name given to small unnamed creek not on map—6 miles [9.654 km] north of San Antonio del Mar, Baja California, Mexico. Coll.: Santillan and Barrera. Rosario Formation. Early Maastrichtian.
[8]	660	USGS: See USGS loc. 21369.
[29]	954	CAS: NE side of Punta Banda, southwest border of Todos Santos Bay, Baja California, Mexico. In beach cliff accessible at low tide, 3 miles [4.827 km] from La Grulla gun club house. Coll.: E. K. Jordan and L. G. Hertelin. Rosario Formation. Early Maastrichtian.
[26]	974	CIT: See LACMIP loc. 10105 (Matsumoto, 1960, p. 99).
[11]	1016	CIT: See LACMIP loc. 10847 (Matsumoto, 1960, p. 101).
[11]	1017	CIT: See LACMIP loc. 10849 (Popenoe and Saul, 1987, p. 34).
[11]	1041	CIT: See LACMIP loc. 10835 (Saul and Popenoe, 1962, p. 328; Popenoe et al., 1987, p. 98).
[9]	1051	USGS: Texas Springs, Shasta Co., California. Budden Canyon Formation. Late early Albian, *Brewericeras hulenense* Zone (Saul, 1978, p. 56).
[24]	1158	CIT: See LACMIP loc. 10710 (Popenoe and Saul, 1987, p. 34).
[24]	1159	CIT: See LACMIP loc. 10715 (Matsumoto, 1960, p. 103).
[26]	1164	CIT: See LACMIP loc. 10079.
[11]	1183	CIT (= UCLA loc. 3648): See LACMIP loc. 10861 (Matsumoto, 1960, pp. 15, 103, 157).
[8]	1232	CIT: See LACMIP loc. 10824 (Saul, 1978, p. 56).
[3]	1400	CIT: See LACMIP loc. 10446 (Matsumoto, 1960, p. 107).

Appendix Text Table. Continued.

[31]	1431	CAS: Cretaceous fossils near mouth of Arroyo Catarina, Baja California, Mexico. Coll.: C. H. Sternberg, 1928. Rosario Formation. Early Maastrichtian.
[26]	2167	UCMP: Williams Canyon, Santa Ana Mts., Orange Co., California. Ladd Formation, Holz Shale Member. Mid-Campanian (Packard, 1922, p. 416).
[26]	2169	UCMP: Santiago-Aliso divide, Santa Ana Mts., Orange Co., California. Williams Formation, Pleasants Sandstone. Late Campanian (Packard, 1922, p. 416).
[26]	2323	UCLA: Sandstone exposed on south end of low hill north of gully, about 2600′ [792.48 m] north of Holz Ranch house, Silverado Canyon, 2100′ [640.08 m] south, 390′ [118.872 m] west of northeast corner Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, 1946. Ladd Formation, Baker Canyon Member. Turonian.
[15]	2359	CAS: Head of Deer Valley, Hooper Ranch, T1N, R2E, MDBM, Contra Costa Co., California. Great Valley Series, Deer Valley Formation of Colburn (1964). Late Maastrichtian.
[26]	2415	UCLA: Bee Canyon, El Toro Quadrangle, Orange Co., California. Williams Formation, ?Pleasants Sandstone. Late Campanian, *Metaplacenticeras pacificum* Zone (Matsumoto, 1960, p. 154; Saul, 1978, p. 56).
[15]	2609	UCMP: Probably loc. 1 of Merriam (1897, p. 768), hills southwest of Martinez, west side Alhambra Valley, Contra Costa Co., California. Coll.: J. C. Merriam. Great Valley Series. Late Maastrichtian.
[31]	2855	LACMIP: West side Arroyo Santa Catarina, Baja California, Mexico. Rosario Formation. Early Maastrichtian (Webster, 1983, pp. 1091, 1096).
[27]	3162A	SDSNH: Carlsbad Research Center, Carlsbad, San Diego Co., California. Point Loma Formation. Early Maastrichtian (Popenoe and Saul, 1987, p. 35).
[31]	3268	UCLA: Olive silts exposed along banks of "Ammonite Ravine," about 3 miles [4.8/8 km] northeast of Santa Catarina Landing and ¼ mile south of channel of Arroyo Santa Catarina, 5.9 km north, 5.9 km east of mouth of Arroyo Santa Catarina, Baja California, Mexico. Coll.: W. P. Popenoe et al., February 1949. Rosario Formation. Early Maastrichtian.
[15]	3313	UCLA: South side of Deer Valley, Contra Costa Co., California. Great Valley Series, Deer Valley Formation of Colburn (1964). Late Maastrichtian (Saul, 1974, p. 1097).
[11]	3623	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Musty Buck Member. Santonian (Matsumoto, 1960, p. 155).
[11]	3625	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Musty Buck Member. Santonian (Saul and Popenoe, 1962, p. 328).
[11]	3627	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Musty Buck Member. Santonian, *Baculites capensis* Zone (Matsumoto, 1960, p. 156).
[11]	3635	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian (Popenoe and Saul, 1987, p. 36).
[11]	3637	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian, *Baculites chicoensis* Zone (Matsumoto, 1960, pp. 15, 156).
[11]	3641	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian, *Baculites chicoensis* Zone (Saul, 1983, p. 121).
[11]	3642	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian, *Baculites chicoensis* Zone (Matsumoto, 1960, p. 156).
[11]	3643	UCLA: Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian, *Bac-*

Appendix Text Table. Continued.

Appendix Text Table. Continued.

		ulites chicoensis Zone (Saul, 1974, p. 1093).
[11]	3648	UCLA: "Fossil Bluff," Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian, *Baculites chicoensis* Zone (Saul, 1988, p. 24).
[30]	3796	UCLA: Boulder at base of seacliff 5600′ [1706.88 m] north of mouth of Arroyo San Antonio del Mar, Johnson's Ranch, about 35 miles [56.21 km] south of Santo Tomás, Baja California, Mexico. Coll.: W. P. Popenoe, 1949. Rosario Formation, Early Maastrichtian.
[9]	3916	UCLA: Texas Springs area, 1000′ [304.8 m] north, 1600′ [487.68 m] west of southeast corner Sec. 29, T31N, R5W, Redding Quadrangle, Shasta Co., California. Coll.: P. U. Rodda. Budden Canyon Formation. Late early Albian, *Brewericeras huelenense* Zone.
[15]	3957	UCLA: South slope of shallow saddle on crest of north-trending spur 2200′ [670.56 m] south, 15° west of northeast corner Sec. 24, T1N, R1E, south side of Deer Valley, Antioch South Quadrangle, Contra Costa Co., California. Coll.: W. P. Popenoe, 1944. Great Valley Series, Deer Valley Formation of Colburn (1964). Late Maastrichtian.
[14]	3976	UCLA: Blocks of coarse sandstone in wheatfield north of P.G. & E. Station, southwest side of 200′ [60.96 m] hill, about 2500′ [762 m] south 70° east of the northwest corner Sec. 33, T3N, R3W, east side of Glenn Cove and west of Southampton Bay, north side Carquinez Strait, Carquinez Quadrangle, Solano Co., California. Coll.: W. P. Popenoe, August 28, 1944. Great Valley series. Late Campanian.
[22]	M4017	USGS: California, Southern Coast Range, Santa Barbara Co., San Rafael Primitive Area. Hurricane Deck 1964 Quadrangle, approx. 12,850′ [3916.68 m] north, 13,200′ [4023.36 m] west of southeast corner. Alt. approx. 2240′ [682.752 m]. On southwest side of Sisquoc River near mouth of Foresters Leap Canyon. About 2¼ miles [3.6135 km] northwest of South Fork Guard Station and 8 miles [12.848 km] eastnortheast from Nira Camp at end of Sunset Valley Road. Coll.: J. G. Vedder, 1965. ?Early Maastrichtian.
[8]	4106	UCLA: North of Clover Creek, Shasta Co., California. Redding Formation, Member VI. Early Santonian (Popenoe, 1983, pp. 760, 765).
[22]	4116	UCLA: Fine grained, gray arkosic sandstone, in bed of Jalama Creek, 1230′ [374.904 m] southwest of corral, 0.79 miles [1.26874 km] south and 2.85 miles [4.5771 km] east of Jalama Ranch Headquarters, 0.31 miles [0.49784 km] north, 1.88 miles [3.01928 km] west of southeast corner of topo sheet, Lompoc Hills Quadrangle, 1947, Santa Barbara Co., California. Coll.: D. H. Dailey, August, 1958. Jalama Formation. Early Maastrichtian.
[22]	4118	UCLA: Medium grained, dark bluish-gray, arkosic sandstone, in bed of Jalama Creek, elev. 350′ [106.68 m], 0.56 miles [0.89936 km] south, 1.85 miles [2.9711 km] east of Jalama Ranch Headquarters, 0.54 miles [0.86724 km] north, 2.81 miles [4.51286 km] west of southeast corner of topo sheet, Lompoc Hills Quadrangle, 1947, Santa Barbara Co., California. Coll.: D. H. Dailey, July, 1958. Jalama Formation, Member V. Early Maastrichtian.
[22]	4120	UCLA: Fine to medium grained, buff, arkosic sandstone, 200′ [60.96 m] north of Jalama Creek, elev. 374′ [113.9952 m], 0.43 miles [0.69058 km] south, 1.75 miles [2.8105 km] east of Jalama Ranch Headquarters, 0.67 miles [1.07602 km] north, 2.9 miles [4.6574 km] west of southeast corner of topo sheet, Lompoc Hills Quadrangle, 1947, Santa Barbara Co., California. Coll.: D. H. Dailey, August, 1958. Jalama Formation, Member V. Early Maastrichtian.
[22]	4131	UCLA: In hard, gray, sandy conglomerate along top of first ridge about 1044′ [318.2112 m] northwest of corral, elev. 750′ [228.6 m], 0.54 miles [0.86724 km] south, 2.93 miles [4.70558 m]

Appendix Text Table. Continued.

		east of Jalama Ranch Headquarters, 0.56 miles [0.89936 km] north, 1.73 miles [2.77838 km] west of southeast corner of topo sheet, Lompoc Hills Quadrangle, 1947, Santa Barbara Co., California. Coll.: D. H. Dailey, July, 1958. Jalama Formation, Member V. Early Maastrichtian.
[22]	4143	UCLA: Top of ridge, 900′ [274.32 m] north of Jalama Creek, elev. 625′ [190.5 m], 0.52 miles [0.83512 km] south, 1.98 miles [3.17988 km] east of Jalama Ranch Headquarters, 0.58 miles [0.93148 km] north, 2.69 miles [4.32014 km] west of southeast corner of topo sheet, Lompoc Hills Quadrangle, 1947, Santa Barbara Co., California. Coll.: W. P. Popenoe, 1938; D. H. Dailey, August, 1958. Jalama Formation, Member III. Early Maastrichtian.
[8]	4209	UCLA: Clover Creek, Millville Quadrangle, Shasta Co., California. Redding Formation, Member IV. Coniacian (Popenoe and Saul, 1987, p. 36).
[8]	4217	UCLA: Clover Creek, Shasta Co., California. Redding Formation, Member VI. Late Santonian (Popenoe, Saul, and Susuki, 1987, p. 100—erroneously as "4127").
[8]	4219	UCLA: Southeast side of Oak Run valley, 1000′ [304.8 m] south, 1900′ [579.12 m] east of northwest corner Sec. 15, T32N, R2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, August 30, 1959. Redding Formation, sandstone interbedded with conglomerate of Member V. Santonian.
[8]	4245	UCLA: South side of Clover Creek valley at center of west line Sec. 33, T32N, R2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe and D. H. Dailey, August 25, 1959. Redding Formation, ?Member IV, sandstone bed 30′ [9.144 m] to 40′ [12.192 m] strat. above conglomerate bed. Late Coniacian.
[7]	4250	UCLA: Young Ranch, Yreka Quadrangle, Siskiyou Co., California. Hornbrook Formation. Late Turonian (Saul and Popenoe, 1962, p. 329).
[7]	4251	UCLA: Sandstone cropping out along ridge by ranch road on Young Ranch, about 2300′ [701.04 m] slightly west of due north of the ranch house, approx. 350′ [106.68 m] west of UCLA 4250, 850′ [259.08 m] south, 3000′ [914.4 m] west of northeast corner Sec. 26, T46N, R6W, Yreka Quadrangle, 9 miles [14.454 km] northeast of Yreka, Siskiyou Co., California. Coll.: M. A. Murphy, W. P. Popenoe, and Takeo Susuki, August 30, 1951. Hornbrook Formation. Turonian.
[13]	4285	UCLA: South slope of hill at about 1000′ [304.8 m] contour, on east side of Antelope Creek valley, from calcareous slump blocks in shale. NW ¼, SW ¼ Sec. 5, T16N, R4W, about 2.8 miles [4.4968 km] due south of Sites, Lodoga 1943, 15′ Quadrangle, Colusa Co., California. Coll.: Todd Harding. Great Valley Series. ?Albian.
[16]	4348	UCLA: Float boulder, shoreline, rocky covelet, south side of elongate seaward pointing rock just south of Bolsa Point, Pigeon Point Quadrangle, San Mateo Co., California. Coll.: L. R. and R. B. Saul, October 11, 1960. Pigeon Point Formation. Mid-Campanian.
[10]	4370	UCLA: See LACMIP loc. 10871.
[5]	4669	UCLA: Sandstone cropping out in field about ¼ mile [0.4015 km] north of road from Suplee to Paulina, and in center of SW ¼ Sec. 23, T17S, R25E, Dayville Quadrangle, Crook Co., Oregon. Coll.: R. W. Imlay and W. P. Popenoe, June 20, 1959. Bernard Formation. Cenomanian.
[30]	4863	UCLA: North side of Arroyo San Antonio del Mar, about 1 mile from coast and north 12° west from "Johnson's Ranch" house, Baja California, Mexico. Coll.: W. P. Popenoe, H. Lusk, and C. Helms, February 3, 1949. Rosario Formation. ?Late Campanian or early Maastrichtian.
[7]	5422	UCLA: Rancheria Gulch, about 1 mile [1.606 km] west of Henley and approx. 400′ [121.92 m] north, 2000′ [609.8 m] west of southeast corner Sec. 19, T47N, R6W, Yreka Quadrangle, Siski-

Appendix Text Table. Continued.

Appendix Text Table. Continued.

		you Co., California. Coll.: W. P. Popenoe, summer 1951. Hornbrook Formation. Osburger Gulch Member. Turonian.
[20]	5522	UCLA: Ridge southeast from Garza Peak, approx. 1 mile [1.606 km] west of Sagaser Ranch house, 2350′ [716.28 m] north, 2300′ [701.04 m] west of southeast corner Sec. 13, T23S, R16E, Garza Peak Quadrangle, Reef Ridge area, Kings Co., California. Coll.: E. V. Tamesis, 1965. Panoche Formation, clast in conglomerate. Turonian.
[31]	5989	LACMIP: South side, north fork of Ammonite Ravine, about 275′ [83.82 m] east of LACMIP 5988. Float fossils collected at elev. 205′ [62.484 m], Arroyo Santa Catarina, Baja California, Mexico. Coll.: M. L. Webster, December 23, 1966. Rosario Formation. Early Maastrichtian.
[24]	6020	UCLA: North bank of Bell Canyon, just east of mouth of large gully and 500′ [152.4 m] south, 9000′ [2743.2 m] west of northeast corner Sec. 4, T1N, R17W, Calabasas Quadrangle, Simi Hills, Ventura Co., California. Coll.: L. R. Saul and F. H. Weber, Jr., June 24, 1971. Chatsworth Formation. Mid-Campanian.
[5]	6165	LACMIP: Andy Bernard Ranch, 2.5 miles north of Suplee, west side of ravine that drains southward into tributary creek to the south fork of Beaver Creek, northeast of the ranch house, SW ¼, SE ¼ Sec. 1, T17S, R25E, Dayville Quadrangle, Crook Co., Oregon. Coll.: Janet Dock, August 27, 1981. Bernard Formation. Cenomanian.
[24]	6232	UCLA: Bell Canyon, very fossiliferous sandstone bed in northwest slope of creek on east slope of north–south spur, 500′ [152.4 m] south, 5800′ [1767.84 m] west of northwest corner Sec. 4 and Ventura Co. line, Calabasas Quadrangle, Simi Hills, Ventura Co., California. Coll.: R. B. Saul, June 24, 1971. Chatsworth Formation. Mid-Campanian.
[18]	6345	UCLA: West side San Joaquin Valley, approx. 2 miles [3.218 km] south of Ortigalita Creek, 3200′ [975.36 m] north, 4650′ [1417.32 m] east of southwest corner Sec. 33, T11S, R10E, Ortigalita Peak Quadrangle, Merced Co., California. Coll.: R. B. Stewart and W. P. Popenoe, 1944. Moreno Formation, Tierra Loma Member. Late early Maastrichtian.
[19]	6370	UCLA: Northeast side of Cooper Canyon, approx. 1350′ [411.48 m] north, 2200′ [670.56 m] west of southeast corner Sec. 2, T21S, R14E, Coalinga Quadrangle, Alcalde Hills, Fresno Co., California. Coll.: John Alderson, June 18, 1977. Panoche Formation, "Alcalde Shale," reworked clast in conglomerate. Turonian.
[21]	6526	UCLA: South side Lake Nacimiento, poorly sorted conglomeratic sandstone east side of narrows of Dip Creek, elev. approx. 740′ [225.552 m], 1500′ [457.2 m] south, 400′ [121.92 m] west of northeast corner Sec. 30, T25S, R10E, Lime Mountain Quadrangle, San Luis Obispo Co., California. Dip Creek Formation of Taliaferro, 1944. Late late Maastrichtian.
[33]	6973	UCLA: Approx. 3.3 km south, 13° west of Campitos, northwest end of Vizcaíno Peninsula, about 21 km east of Punta Eugenia, Baja California Sur, Mexico. Coll.: David Bernal, 1979–1980. Basal upper Valle Formation. ?Cenomanian.
	M6981	USGS: Alaska, Alaska Peninsula, Chignik B-2 Quadrangle. Lat. 56°25′59″N, long. 158°34′20″W Sec. 5. Same locality as M6979 about 2.6 miles [4.1834 km] northeast of house. Massive greenish sandstone several hundred feet higher in section than 41B. Coll.: R. L. Detterman, 1977. Chignik Formation. Early Campanian, *Inoceramus schmidti* Zone.
[17]	7174	UCLA: Orestimba Creek, T7S, R7E, Orestimba Quadrangle, Diablo Range, Stanislaus Co., California. Moreno Formation, Quinto Silt. Late Maastrichtian.
[18]	M8573	USGS: NE ¼, SE ¼, NW ¼ Sec. 20, T23S, R17E, Garza Peak Quadrangle, Kings Co., California. 35°55.38′N, 120°9.38′W. Conglomeratic boulders in float at bottom of gully in conglomer-

Appendix Text Table. Continued.

		ate. Coll.: W. P. Elder, 1989. Panoche Formation. Cenomanian.
[16]	M8601	USGS: In lens in sandstone on beach 0.3 miles [0.4827 km] southeast of Bolsa Point, lat. 37°11.61′N, long. 122°23.94′W, Pigeon Point Quadrangle, San Mateo Co., California. Coll.: W. P. Elder, 1989. Pigeon Point Formation. Campanian
[18]	M8649	USGS: Clasts? (individual clasts lettered) in conglomerate on north nose of hill 443, elev. 390′ [118.872 m], SW ¼, NE ¼, NW ¼ Sec. 24, T10S, R8E, San Luis Dam Quadrangle, Merced Co., California. Coll.: W. P. Elder and A. Benison, 1990. Panoche Formation. Coniacian.
[26]	10079	LACMIP (= CIT loc. 1164): South side Silverado Canyon near mouth of small north-flowing gully, and at top of lower fossiliferous sandstone series, about 400′ [121.92 m] southeast of Holz Ranch house, 1025′ [312.42 m] north, 150′ [45.72 m] east of southwest corner Sec. 8, T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, May 15, 1935. Ladd Formation, Baker Canyon Member. Turonian.
[26]	10096	LACMIP (= CIT loc. 1052): Crest of small spur near head of Alisos Creek drainage about 3750′ [1143 m] east of Pankratz Ranch house, 600′ [182.88 m] south, 175′ [53.34 m] north of northwest corner Sec. 32 and east edge of topo sheet, T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, January, 1933. Williams Formation, Pleasants Sandstone. Late Campanian, *Metaplacenticeras pacificum* Zone.
[26]	10105	LACMIP (= CIT loc. 974): Santiago–Aliso Creek divide, Santa Ana Mts., Orange Co., California. Williams Formation, Pleasants Sandstone. Late Campanian (Matsumoto, 1960, p. 99).
[26]	10120	LACMIP (= CIT loc. 86): Santa Ana Mts., Orange Co., California. Williams Formation, Pleasants Sandstone Member. Late Campanian.
[26]	10135	LACMIP (= CIT loc. 1290): South side of prominent hill west of spring, about 1500′ [457.2 m] north of Holz ranch house, Silverado Canyon, 2600′ [792.48 m] south, 200′ [60.96 m] west of northeast corner Sec. 7, T5S, R7W, Black Star Canyon Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: Popenoe, Henshal, Wells, Church, and Fiedler, April 6, 1937. Ladd Formation, Baker Canyon Member, near top. Turonian.
[3]	10446	LACMIP (= CIT loc. 1400): Sucia Island, San Juan Co., Washington. Cedar District Formation. Mid-Campanian, *Hoplitoplacenticeras vancouverense* Zone (Matsumoto, 1960, p. 107).
[22]	10690	LACMIP (= CIT loc. 590): Jalama Ranch Creek, Lompoc Hills Quadrangle, western Santa Ynez Range, Santa Barbara Co., California. Jalama Formation. Early Maastrichtian (Saul, 1978, p. 55).
[22]	10695	LACMIP (= CIT loc. 602): Float, Jalama Creek, 3.2 miles [5.1488 km] eastsoutheast of Jalama Ranch house, Lompoc Hills Quadrangle, Santa Ynez Mts., Santa Barbara Co., California. Coll.: W. S. W. Kew. Jalama Formation. Early Maastrichtian.
[24]	10709	LACMIP (= CIT loc. 1157): North bank Bell Canyon in shale bluffs above stream channel, about 50′ [15.24 m] below base of heavy Cretaceous sandstone, 1 mile [1.609 km] due west of Los Angeles–Ventura Co. line, on boundry (extended) between T1 and 2N, R27W, Calabasas Quadrangle, southeast slope Simi Hills, Ventura Co., California. Coll.: W. P. Popenoe, June 18, 1935. Chatsworth Formation. Mid-Campanian.
[24]	10710	LACMIP (= CIT loc. 1158): Bell Canyon, Simi Hills, Ventura Co., California. Chatsworth Formation. Mid-Campanian (Popenoe and Saul, 1987, p. 34).
[24]	10715	LACMIP (= CIT loc. 1159): Dayton Canyon, Simi Hills, Calabasas Quadrangle, Los Angeles Co., California. Chatsworth Formation. Late Campanian, *Metaplacenticeras pacificum* Zone (Matsumoto, 1960, p. 103).
[26]	10719	LACMIP (= CIT loc. 1066): Crest

Appendix Text Table. Continued.

Appendix Text Table. Continued.

		of ridge between Baker and Black Star Canyons, about 6600′ [2011.68 m] upstream from mouth of Black Star Canyon along firebreak on Black Star Canyon side of ridge, 2300′ [701.04 m] north, 175′ [53.34 m] east of southwest corner Sec. 31, T4S, R7W, Black Star Canyon Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, June 26, 1934. Williams Formation, basal Schultz Conglomerate Member. Late early Campanian.
[8]	10769	LACMIP (= CIT loc. 1203): Lens in sandstone cropping out in bed of Dry Creek, 700′ [213.36 m] south, 300′ [91.44 m] west of northeast corner Sec. 6, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe and Ahlroth, June 23, 1936. Redding Formation, Bellavista Sandstone. Turonian.
[8]	10782	LACMIP (= CIT loc. 1191): Sandstones about 150 yards [137.16 m] east of Stinking Creek, near base of Cretaceous section, 3530′ [1075.944 m] north 37°30′ west of southeast corner Sec. 6, T32N, R3W, Redding Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe and Ahlroth, June 20, 1936. Redding Formation, Bellavista Sandstone. Turonian.
[8]	10824	LACMIP (= CIT loc. 1232): Price Hollow, Oak Run, Shasta Co., California. Redding Formation, Member V. Early Santonian (Saul, 1978, p. 56).
[11]	10834	LACMIP (= CIT loc. 1040): Limy sandstone beds cropping out along west bank Butte Creek, just under Tertiary gravels, 3.8 miles [6.1142 km] upstream from Honey Run Road covered bridge over Butte Creek, and 10.2 miles [16.4118 km] along Humbug Road from U.S. Hwy 99E, 450′ [137.16 m] north, 600′ [182.88 m] east of southwest corner Sec. 8, T22N, R3E, Paradise Quadrangle, Butte Co., California. Coll.: W. P. Popenoe and W. A. Findlay, September 3, 1933. Chico Formation, Ten Mile Member. Early Campanian, *Baculites chicoensis* Zone.
[11]	10847	LACMIP (= CIT loc. 1016): Chico Creek, Butte Co., California. Chico Formation, Musty Buck Member. Santonian (Matsumoto, 1960, p. 101).
[11]	10849	LACMIP (= CIT loc. 1017): Chico Creek, Butte Co., California. Chico Formation, Musty Buck Member. Santonian (Popenoe and Saul, 1987, p. 34).
[11]	10861	LACMIP (= CIT loc. 1183): "Fossil Bluff," Chico Creek, Paradise Quadrangle, Butte Co., California. Chico Formation, Ten Mile Member. Early Campanian (Matsumoto, 1960, pp. 15, 103, 157).
[10]	10871	LACMIP (= CIT loc. 1020; UCLA loc. 4370): Sandstone boulder in heavy conglomerate, channel of Elder Creek, planetable traverse station S-18, Tehama Co., California. Coll.: W. P. Popenoe and W. A. Findlay, August 18, 1933. Great Valley Series, Budden Canyon Formation. Cenomanian or ?late Albian.
[6]	10903	LACMIP (= CIT loc. 1622): Soft gray sandstone cropping out along irrigation ditch 150′ [45.72 m] to 200′ [60.96 m] above and to southwest of Southern Pacific RR track and about 4 miles [6.436 km] southeast of U.S. hwy bridge over Ashland Creek, Ashland, near midpoint of west boundary Sec. 24, T39S, R1E, Ashland Quadrangle, Jackson Co., Oregon. Coll.: W. P. Popenoe and W. A. Findlay, July 12, 1933. Hornbrook Formation. Turonian.
[28]	11629	LACMIP (= SDSU loc. 6): Top of basal sandstone just below base of mudstone sequence, stratigraphically above LACMIP loc. 11628, west of La Jolla Cove, La Jolla Quadrangle, La Jolla Bay, San Diego Co., California. Coll.: SDSU field classes. Rosario Group, Point Loma Formation. ?latest Campanian–earliest Maastrichtian.
[34]	11944	LACMIP: Approx. 10 km north of Punta Abreojos (southwest of San Ignacio), in first ridges north of arroyo that crosses Punta Abreojos road (dirt) just south of Campo Rene turnoff, approx. 2 km northwest of road and 2–3 km up ravine, Vizcaíno Peninsu-

Appendix Text Table. Continued.

		la, Baja California Sur, Mexico. Coll.: Robert Demetrion, 1987. Valle Formation. Mid-Campanian, *Hoplitoplacenticeras ?* Zone.
[21]	12245	LACMIP: Midway between Pebblestone Shut-In and Grizzly Bend at an elev. of about 750′ [228.6 m], 35°44′28″N, 121°03′01″W, Sec. 19, T25S, R9E, Pebblestone Shut-In Quadrangle, San Luis Obispo Co., California. Coll.: V. M. Seiders, 1985. ?El Piojo Formation, single clast in conglomerate. ?Early Maastrichtian.
[8]	21369	USGS (= USGS loc. 660): "1 mi. [1.609 m] SE of Buckeye," vicinity of Dry Creek, Shasta Co., California. Coll.: J. S. Diller, 1887. Redding Formation. Turonian.
[15]	25707	CAS: East end of Deer Valley, near forks of Brentwood road, SW ¼ Sec. 27, T1N, R2E, Antioch South Quadrangle, Contra Costa Co., California. Coll.: F. M. Anderson and B. L. Clark. Great Valley Series, Deer Valley Formation of Colburn (1964). Maastrichtian.
[11]	27835	CAS: Bluff on southeast side of Chico Creek, 1.3 miles [2.0917 km] by road southwest of bridge across Big Chico Creek at Frank Mickey's place, Sec. 13, T23N, R2E, Paradise Quadrangle, Butte Co., California. Coll.: Taff, Hanna, and Cross, May 3, 1934 and February 16, 1935. Chico Formation, Musty Buck Member. Santonian.
[11]	27836	CAS: Chico Creek, Sec. 1, T23N, R2E, Paradise Quadrangle, Butte Co., California. Coll.: Taff, Hanna, and Cross. Chico Formation, Ponderosa Way Member. ?Coniacian.
[11]	27838	CAS: Southeast bank of Big Chico Creek, 3.6 miles [5.7924 km] by road from 10 Mile House on Humboldt Road, 3.1 miles [4.9879 km] by road south of bridge at Mickey's place, SE ¼ Sec. 23, T23N, R3E, Paradise Quadrangle, Butte Co., California. Coll.: Taff, Hanna, and Cross. Chico Formation, Ten Mile Member. Early Campanian, *Submortoniceras chicoense* Zone.
[17]	27854	CAS: Orestimba Creek, Mt. Boardman Quadrangle, Stanislaus Co., California. Base of Panoche Formation, boulders in conglomerate. Coniacian (Matsumoto, 1960, p. 158).
[15]	28104	CAS: Curry Canyon, Contra Costa Co., California. Great Valley Series. Mid to late Cenomanian (Matsumoto, 1960, p. 84).
[18]	28118	CAS: North bank of Las Baños Creek, Merced Co., California. Quinto Silt. Maastrichtian.
[12]	28766	LACMIP: ¾ mile [1.20675 km] northwest of Stony Creek, SW ¼ Sec. 28, T22N, R5W, Fruto Quadrangle, Glenn Co., California. Coll.: P. W. Reinhart. Great Valley Series. Cenomanian.
[20]	28788	LACMIP: East of Big Tar Canyon Rd., north of Sunflower Valley [McLure Valley, of 1937 Reef Ridge Quadrangle], elev. 1420′ [432.816 m], 1500′ [457.2 m] south, 2700′ [822.96 m] west of northeast corner Sec. 20, T23S, R17E, Reef Ridge Quadrangle, Kings Co., California. Coll.: R. B. Stewart. Panoche Formation, boulder in conglomerate. Cenomanian.
[21]	29217	LACMIP: In creek, on line between Sec. 4 and 5, about 400′ [121.92 m] north of southwest corner Sec. 4, T25S, R9E, Bryson Quadrangle, creek is tributary to Cantinas Creek, northwest of Lake Nacimiento, San Luis Obispo Co., California. Coll.: V. M. Seiders, 1985. El Piojo Formation. Late Maastrichtian.
[9]	29230	LACMIP: Texas Springs area, sandstone cropping out in gully west of first ridge west of road along north–south boundary between Sec. 28 and 29, T31N, R5W, 1000′ [304.8 m] north, 750′ [228.6 m] west of southeast corner of the Redding Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, August 29, 1960. Budden Canyon Formation. Late early Albian, *Brewericeras hulenense* Zone.
[9]	29231	LACMIP: Loose slab on surface of sandstone slope, about ¼ mile [0.40225 km] west of road and ¼ mile [0.40225 km] south of LACMIP loc. 29230, approx. 1 mile [1.609 km] southwest of Texas Springs, SE ¼ Sec. 29, T31N,

Appendix Text Table. Continued.

		R5W, Redding Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, August 29, 1960. Budden Canyon Formation. Late early Albian, *Brewericeras hulenense* Zone.
[17]	29491	CAS: Upper part of Salado Creek, W ½ Sec. 34, T6S, R6E, Mt. Boardman Quadrangle, Stanislaus Co., California. Panoche Formation. Turonian.
[13]	31920	CAS: Thompson Creek, 1200′ [365.76 m] north, 600′ [182.88 m] west of southeast corner Sec. 20, T8N, R2W, Monticello Dam Quadrangle, Yolo Co., California. Coll.: W. E. Kennett, July 26, 1943. Great Valley Series, near base of Yolo Shale. Turonian.
[15]	33706	CAS: Arroyo del Valle, calcareous conglomerate, 1 mile [1.609 m] south of Aqueduct, Tesla Quadrangle, Alameda Co., California. Coll.: A. S. Huey. Panoche Formation. Early Turonian (Matsumoto, 1960, p. 95).
[26]	66028	CAS: Santa Ana Mts., Orange Co., California. Williams Formation, Pleasants Sandstone. Late Campanian.
[15]	66237	CAS (= SU loc. 1825): Alameda Co., ½ mile [0.8045 km] northeast of Niles, in conglomerate along road up south side of Niles Canyon, Niles 7.5 Quadrangle. Coll.: R. Anderson, June 1906. ?Oakland Conglomerate. Turonian.
[31]	66296	CAS (= SU loc. 91): 6 miles [9.654 km] north of Rosario Canyon, Baja California, Mexico. Coll.: B. Hake. "In conglom. in or on Cretac" ?Rosario Formation. ?Late Campanian.
[28]	66512	CAS: Point Loma, San Diego Co., California. Rosario Group. Early Maastrichtian.
[1]	83909	GSC: Southern shore of Denman Island. Collected from interval 150′ [45.72 m] to 250′ [76.2 m] southeast of the lighthouse, halfway between high and low water mark, from a thin conglomerate bed. British Columbia. Coll.: J. A. Jeletzky, July 21, 1969. Upper Trent River Formation.

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Contributions In Science

Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico

Richard L. Squires and Robert A. Demetrion

Natural History Museum of Los Angeles County

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PALEONTOLOGY OF THE EOCENE BATEQUE FORMATION, BAJA CALIFORNIA SUR, MEXICO

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CONTENTS

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ABSTRACT. This study is the first detailed account of marine Eocene macrosized invertebrate fossils from Baja California Sur, Mexico. The fossils, which are locally richly abundant, are from exposures of the middle lower Eocene ("Capay Stage") to upper middle Eocene ("Tejon Stage") Bateque Formation along the Pacific coast from the eastern Laguna San Ignacio area to the San Juanico area about 105 km to the south.

Ninety-nine species were found and are one red alga, one green? alga, five large benthic foraminifers, traces of one demosponge?, one calcareous sponge, one spongiomorph? organism, one helioporid octocoral, one gorgonian, eight colonial corals, four solitary corals, two bryozoans, one polychaete worm, one scaphopod, 37 gastropods, 23 bivalves, two nautiloids, two crabs, and three types of cidaroid echinoids (based on spines), as well as two cassiduloid? and two spatangoid echinoids.

Ten of the macrofossils are new species that have already been named. Eleven other new species are described and named: one gorgonian, *Parisis batequensis* new species; three colonial corals, *Stylosmilia ameliae* new species, *Colpophyllia nicholasi* new species, and *Montastrea laurae* new species; one solitary coral, *Antillia batequensis* new species; one polychaete worm, *Serpula batequensis* new species; one gastropod, *Bernaya* (*Protocypraea*) *grovesi* new species; one bivalve, *Lima kennedyi* new species; two crabs, *Ranina berglundi* new species and *Lophoranina bishopi* new species; and a spatangoid echinoid, *Eupatagus batequensis* new species.

Only 300 m of the formation is exposed, and these deposits grade upward from offshore, to braid delta, to coral reef(?), to shallow marine, and to offshore. Most of the macrofossils are in the shallow-marine deposits in scattered lenses of channel-lag, very short-distance storm accumulations. A large benthic foraminifer-pectinid bivalve-oysterid community is present in a thin muddy interval within quieter water offshore deposits overlying the shallow-marine deposits.

Overlying the Bateque Formation at one locality is a thin interval of diatomite assignable to the late middle Eocene CP14a to CP14b Zones. This diatomite is most likely part of another formation.

The Bateque Formation macrofossil fauna is indicative of warm-water conditions. Many of the taxa show influence of Old World Tethyan warm-water faunal elements. Most of the Bateque Formation macrofossils are known elsewhere in Pacific coast lower Eocene strata, primarily in California. Some Bateque Formation genera are new to the Pacific coast during the early Eocene. A few are Mesozoic relicts. A few other macrofossils have been previously reported from the Pacific coast but have their earliest or their latest occurrence in the Bateque. The Bateque Formation early Eocene occurrence of the gastropod *Platyoptera,* the bivalve *Nayadina* (*Exputens*), and the crab *Ranina* is the earliest anywhere in the world, and the early Eocene occurrence of the gastropod genera *Amauropsis* and *Gyrodes*? is the latest anywhere in the world.

RESUMEN. Este estudio es el primer relato detallado de macrofósiles invertebrados marinos del Eoceno de Baja California Sur, México. Los fósiles, localmente muy abundantes, se hallan en afloramientos ascendiendo del Eoceno inferior medio ("Capay Stage") al Eoceno superior medio ("Tejon Stage") en la Formación Bateque, ubicada por la costa del Pacifico entre la proximidad del lado oriental de la Laguna San Ignacio y la proximidad de San Juanico, cubriendo una distancia de approximadamente 105 km.

Noventa y cinco especies halladas incluyen una alga rhodophyta, una alga? chlorophyta, cinco foraminiferas benthicas grandes, vestigios de una demoporifera, una porifera calcarea, un organismo "spongiomorph?", un octocoral helioporido, un gorgonio, ocho corales coloniales, cuartro corales soliatrios, dos bryozoas, un "polychaete worm," un escafópodo, 37 gasterópodos, 23 pelecípodos, dos cefalópodos, dos cangrejos, tres tipos de "cidaroid" equinoides (basados en espinas), así como dos equinoides "cassiduloid" y dos equinoides "spatangoid."

Diez de los macrofósiles son nuevas especies ya nombradas. Once especies nuevas son describidas y nombradas: un gorgonio, *Parisis batequensis* nueva especie; tres corales coloniales, *Stylosmilia ameliae* nueva especie, *Colpophyllia nicholasi* nueva especie, y *Montastrea laurae* nueva especie; un coral solitario *Antillia batequensis* nueva especie; un "polychaete worm" *Serpula batequensis* nueva especie; un gasterópodo *Bernaya* (*Protocypraea*) *grovesi* nueva especie, un pelecípodo *Lima kennedyi* nueva especie; dos cangrejos *Ranina berglundi* nueva especie y *Lophoranina bishopi* nueva especie, y un equinoide "spatangoid" *Eupatagus batequensis* nueva especie.

Solamente 300 m de la formación está expuesta, y los depósitos se cambian ascendiendo de costafuera a delta a arrecife(?) de coral a marino de poca profundidad a costafuera. Los demás de los macrofósiles se hallan en los depósitos marinos de poca profundidad en bolsas lenticulares dispersas depositadas con poca trasladación durante tormentas y acumuladas en canales. Una comunidad de foraminiferas benthicas grandes, pelecípodos "pectinid," y ostras se halla en un intervalo lodoso delgado dentro los depósitos costafueras que cubren a los depósitos marinos de poca profundidad.

En una localidad la Formación Bateque esta cubierta con un intervalo delgado de tierra diátomacea asignable al Eoceno medio (Zonas CP14a a CP14b). Esta tierra diátomacea es probablemente una parte de otra formación.

La fauna macrofósil el la Formación Bateque es indicativa de condiciónes marinas de aguas cálidas. Mucha de las taxa muestra una influencia de elementos faunales del Mar Tethys con sus aguas cálidas. La mayor parte de los macrofósiles de la Formación Bateque son conocidos en depósitos del Eoceno inferior en otras areas de la costa Pacífica, principalmente en California Alta. Algunos géneros de la Formación Bateque se introducieron a la costa Pacífica durante el Eoceno inferior. Algunos son reliquias del Mesozoico. Algunos otros macrofósiles previamente conocidos en la costa Pacífica aparecen con su primaro o último suceso en la Formación Bateque. Los sucesos del gasterópodo *Platyoptera,* el pelecípodo *Nayadina* (*Exputens*), y el cangrejo *Ranina* son los primeros en el mundo; y los suscesos de los gasterópodos *Amauropsis* y *Gyrodes*? son los últimos en el mundo.

INTRODUCTION

Givens (1974), Givens and Kennedy (1979), and Squires (1984, 1987, 1988b) have provided detailed knowledge of southern California Eocene molluscan faunas. These faunas contain many Old World Tethyan or Tethyan-affinity, warm-water taxa that immigrated to California during the early Eocene (Squires, 1987). A route of migration that paralleled the Pacific coast of Baja California, Mexico, has been implied or suggested by a number of workers, but documentation has been lacking because early Eocene faunas were unknown from this area.

In 1987, while doing reconnaissance field work in Baja California Sur, the junior author discovered some rich deposits of macrofossils near the middle of the Bateque Formation. He shared his find with the senior author who recognized that they were of early Eocene age. Since 1988, we have been making trips into the area to collect these fossils and to search throughout the formation for other localities.

The main purpose of this paper is to document the Eocene macrofossils of the Bateque Formation as well as to describe the stratigraphy, depositional environments, and geologic age of each main part of the formation. Depositional environments will be discussed in a preliminary manner, based on reconnaissance field studies. More detailed work is needed to delineate subenvironments.

This study documents the southern California early Eocene macrofossil fauna in Baja California Sur. Except for a few species that are known only from the Bateque Formation, the geographic distribution of all the molluscan species and a few corals mentioned in this report are extended from southern California to Baja California Sur.

PREVIOUS WORK

Mina (1956, 1957) described and mapped the Bateque Formation. He did not designate a type section. Durham and Allison (1960) mentioned the Bateque Formation in their analysis of the biogeography of peninsular Baja California. Sorensen (1982) worked on the sedimentary petrology and small benthic foraminifers of the formation. McLean et al. (1985) mapped the geology at a scale of 1:125,000. McLean et al. (1987) reported on the distribution and general lithology of the formation, and McLean and Barron (1988) reported the presence of a diatomite. The first macropaleontologic work in the study area was done by Squires and Demetrion (1989, 1990a, 1990b) and Squires (1990a, 1990b, 1990c). Carreño and Cronin (1991) reported on ostracodes from the Bateque Formation.

MACROFOSSILS

Ninety-nine species, 63 percent of which are mollusks and 14 percent are cnidarians, were identified from the Bateque Formation in the study area. The flora and fauna consist of one red alga, one green? alga, five large benthic foraminifers, traces of one demosponge?, one calcareous sponge, one spongiomorph? organism, one helioporid octocoral, one gorgonian, eight colonial corals, four solitary corals, two bryozoans, one polychaete worm, one scaphopod, 37 gastropods, 23 bivalves, two nautiloids, two crabs, and three types of cidaroid echinoids (based on spines) as well as two cassiduloid? and two spatangoid echinoids. Ten of these species are new species that have already been named. They are as follows: one calcareous sponge, *Elasmostoma bajaensis* Squires and Demetrion, 1989; three gastropods, *Velates batequensis* Squires and Demetrion, 1990a, *Tenagodus bajaensis* Squires, 1990a, and *Platyoptera pacifica* Squires and Demetrion, 1990a; and six bivalves, *Batequeus mezquitalensis* Squires and Demetrion, 1990b, *Spondylus batequensis* Squires and Demetrion, 1990b, *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetrion, 1990b, *Pycnodonte* (*Pegma*) *bajaensis* Squires and Demetrion, 1990b, *Cubitostrea mezquitalensis* Squires and Demetrion, 1990b, and *Fimbria pacifica* Squires, 1990c. The bivalve genus *Batequeus* Squires and Demetrion, 1990b, and the bivalve subgenus *Pegma* Squires and Demetrion, 1990b, are also new taxa that have already been named.

Eleven other Bateque Formation species are new and described herein. They are as follows: one gorgonian, *Parisis batequensis* new species; three colonial corals, *Stylosmilia ameliae* new species, *Colpophyllia nicholasi* new species, and *Montastrea laurae* new species; one solitary coral, *Antillia batequensis* new species; one polychaete worm, *Serpula batequensis* new species; one gastropod, *Bernaya* (*Protocypraea*) *grovesi* new species; one bivalve, *Lima kennedyi* new species; two crabs, *Ranina berglundi* new species and *Lophoranina bishopi* new species; and a spatangoid echinoid, *Eupatagus batequensis* new species.

Other macroinvertebrates that are too poorly preserved for generic determination include some solitary corals, some encrusting bryozoans, and crab fragments.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

INTRODUCTION

The Bateque Formation of Mina (1956, 1957) crops out along the Pacific side of Baja California Sur, Mexico, from the north end and east side of Laguna San Ignacio area to the San Juanico area about 105 km to the south (Fig. 1). Isolated outcrops are located in the northern end, whereas continuous exposures are in the cliff faces of large mesas that border the coastal plain on the east side of Laguna San Ignacio to the village of Batequi de San Juan. Although there is extensive slope wash in this area, there are excellent outcrops in a few of the canyons that incise these mesas. Isolated outcrops are in major arroyos between Batequi de San Juan and the San Juanico area. Most of the coastal exposures are difficult to reach because of poor roads that are modified by drifting sands or flooded by maximum

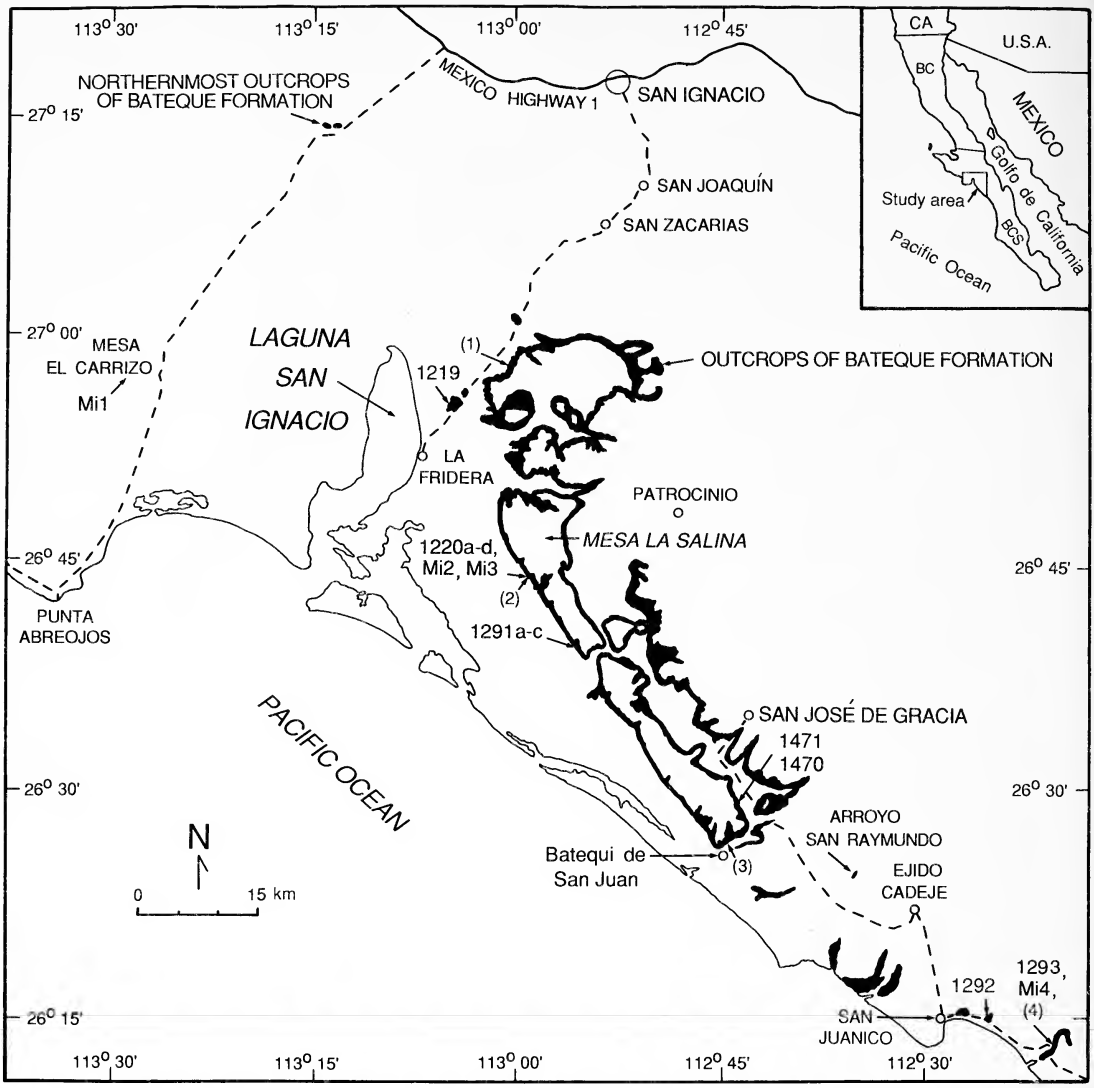

Figure 1. Index map showing the outcrops of the Bateque Formation (from McLean et al., 1985), location of CSUN macrofossil and microfossil (Mi) localities, location of measured sections (1–4), and geographic place names. Dashed lines represent unpaved roads.

spring tides. The Bateque Formation exposures dip northeast at about 3 degrees. They are not exposed east of the coastal mesas.

The base of the Bateque Formation is covered, and the formation is unconformably overlain by sedimentary and volcanic rocks that range in age from late middle Eocene to Holocene. The distribution of these overlying units is discussed in McLean and Barron (1988). Erosion has removed the upper part of the Bateque Formation in the northern part of the area. A combination of the regional dip of the formation and slope wash prevents observation of the lower part of the formation in the southern part of the area. Thus, to the south, higher parts of the formation are exposed. The lowermost 40 m of the formation are exposed only at the north end of Laguna San Ignacio and along its east side. The overlying 200 m are exposed along the coastal cliffs area, and the upper 70 m are exposed in the southern part of the area between the vicinity of Batequi de San Juan and the vicinity of San Juanico (Fig. 1).

The exposed Bateque Formation is 300 m thick, as compiled from four sections measured with a

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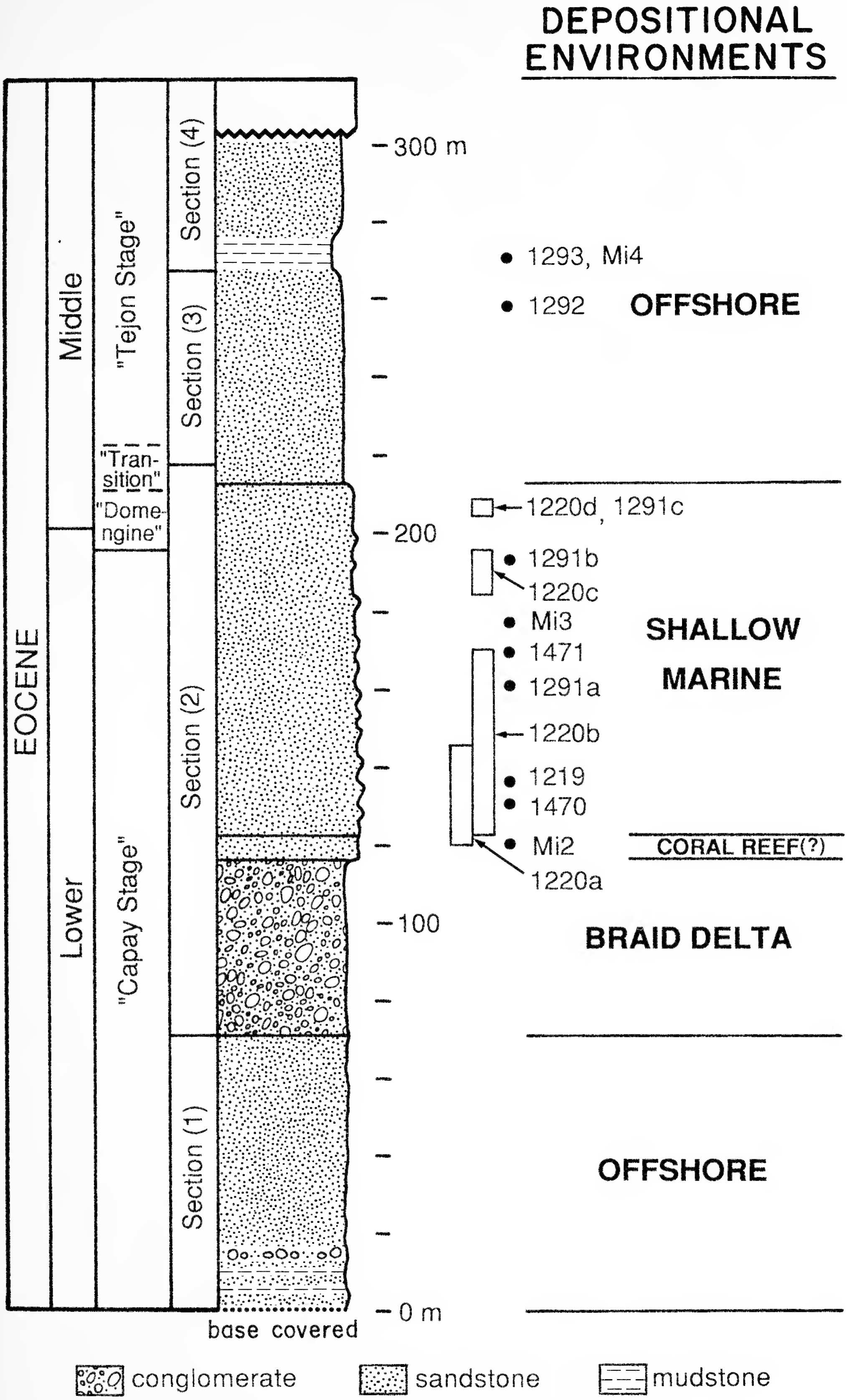
Figure 2. Composite columnar section of the Bateque Formation showing Pacific coast of North America provincial molluscan stages (from Squires, 1987), stratigraphic position of measured sections, position of CSUN macrofossil and microfossil (Mi) localities, and depositional environments.


DEPOSITIONAL ENVIRONMENTS
EOCENE
Middle
Lower
"Tejon Stage"
"Transition"
"Domengine"
"Capay Stage"
Section (4)
Section (3)
Section (2)
Section (1)
base covered
300 m
200
100
0 m
1293, Mi4
1292
OFFSHORE
1220d, 1291c
1291b
1220c
Mi3
1471
1291a
1220b
1219
1470
Mi2
1220a
SHALLOW MARINE
CORAL REEF(?)
BRAID DELTA
OFFSHORE
conglomerate
sandstone
mudstone

Jacob's staff. Locations of sections are shown in Figure 1. A composite columnar section is shown in Figure 2. Rock types are bioturbated, yellow, very fine-grained sandstones (79%), pebble conglomerates (15%), fossil-bearing lenses of sandstone (5%), and mudstones/siltstones (1%). Deposits grade vertically upward from offshore, to braid delta, to coral reef?, to shallow marine, to offshore (Fig. 2).

OFFSHORE DEPOSITS IN LOWER PART OF FORMATION

The offshore deposits in the lower part are 70 m thick. The lowermost 15 m of these deposits consists mostly of silty mudstone interbedded with parallel-laminated, fine-grained sandstone. Rip-up clasts, flame structures, convoluted bedding, and thickening-upward cycles of beds are present as well as a 1-m-thick bed of matrix-supported, disorganized, well-rounded pebble to cobble, volcanic porphyry and quartzite conglomerate. This conglomerate bed crops out in small hills about 17 km south of the junction of Mexico Highway 1 and the dirt road to Punta Abreojos and along the east side of Laguna San Ignacio, about 32 km south of the town of San Ignacio along the main dirt road from the town to La Fridera fish camp (Fig. 1).

Overlying the lowermost 15 m is a 55-m-thick, yellow, bioturbated, very fine-grained sandstone with some intervals of parallel-laminated, very fine-grained sandstone. Locally, there are horizontal burrows of *Thalassinodes*. In the upper half of this section there is only bioturbated sandstone.

The sandstone in the lower 70 m of the Bateque Formation resembles that in the upper part of the informally proposed Ballenas formation (Sorensen, 1982) that reportedly underlies the Bateque Formation. The Ballenas formation crops out in the Punta Abreojos area on the west side of Laguna San Ignacio and is best exposed at Rancho Carrizo Mesa. The Ballenas formation outcrops dip northeast at about 14 degrees, whereas the Bateque Formation outcrops are nearly horizontal. The Ballenas/Bateque formational contact is unconformable. The contact lies below the modern sediments of Laguna San Ignacio.

Sorensen (1982) interpreted the Ballenas formation as inner to mid-bathyal turbidites, approximately correlative to the mid-portion of the continental slope. We interpret the lowermost 15 m of the Bateque Formation as the last turbidite in a basin where shallowing was taking place. The Bateque Formation turbidites were probably deposited in offshore, shelf-like depths rather than bathyal depths, because the overlying, mostly bioturbated sandstone that they grade into resembles deposits described by Reineck and Singh (1980:fig. 566) from the modern offshore zone of Sapelo Island, Georgia.

BRAID-DELTA DEPOSITS

Overlying the offshore deposits in the lower part of the Bateque Formation are braid-delta deposits that are 45 m thick (Fig. 2). Outcrops were found only in the vicinity of localities CSUN 1220a and 1220b and consist of pebble conglomerate with subangular to angular clasts that show fair sorting. Most of the clasts consist of volcanic porphyry, but there are some clasts of granite, quartzite, and fossil wood. Bedding is poorly developed. Locally, there are cross beds and some flat pebbles. There are a few channels that contain a fining-upward sequence of small to large pebble conglomerates. Some of the channels have as much as 2 m of incisement into the underlying deposits. The lower contact of the braid-delta deposits is poorly exposed and appears to be gradational with the underlying offshore sandstone. The upper contact with the shallow-marine unit is erosional. The entire 45-m-thick, pebble-conglomerate unit is interpreted to be a lobe of a gravelly delta that formed where a braided-fluvial system prograded into the marine environment. This type of delta, which has been defined as a braid delta, was previously classified as a fan delta (McPherson et al., 1987).

CORAL REEF(?) DEPOSITS

Overlying the braid-delta lobe in the vicinity of localities CSUN 1220b and 1220c is a very poorly exposed, 7-m-thick interval that consists of laminated?, very fine-grained sandstone containing radially oriented or massive large growths of colonial reef corals. Some of the corals are up to 1 m in height and appear to be in situ. It is interpreted that they grew on the top and/or sides of a shoal caused by the underlying lobe of the braid delta. A similar relationship between a fan delta and a 1.5-m-high coral reef of middle Eocene age in northeastern Spain was described by Taberner and Bosence (1985).

Because of the poor exposures of the coral-reef(?) deposits in the Bateque Formation, positive determination as to whether or not the reef corals actually constructed a coral reef cannot be ascertained. Consequently, the term "coral reef" is queried.

SHALLOW-MARINE DEPOSITS

Overlying the coral-reef(?) deposits are 90-m-thick shallow-marine deposits (Fig. 2) that are extensively exposed along the cliffs facing the Pacific Ocean and consist of bioturbated and parallel-laminated, yellow, very fine-grained sandstone (75%) with many interbedded lenses (25%) filled with abundant macrofossils. Most of the fossils described in this report were collected from this part of the Bateque Formation. The parallel-laminated beds are not as abundant as the bioturbated beds and, locally, the two lithologies alternate. Also, locally, there are fairly high-angle cross beds.

The bioturbated sandstone contains more vertical burrows in the lower half of the shallow-marine deposits. Also, in the lower half near locality CSUN 1220c, an angular unconformity extends for at least 100 m.

The fossiliferous lenses range in thickness from 20 to 50 cm and range in lateral extent from a few meters to several hundred meters. Some show incisement into the underlying bioturbated sandstone. Most lenses are vertically separated by only a few meters of very fine-grained sandstone barren of macrofossils or with only rare fragments. Fossils in the lenses are very abundant and form poorly sorted coquinas. Specimens range in size from 1-mm-diameter benthic miliolid foraminifers to 50-cm-long pieces of colonial corals. Specimens in some of the lenses show normal grading. One lens contains miliolid foraminifers in parallel laminae.

Fossils are fragmental to complete. Fossil-hash concentrations are uncommon. Complete specimens of large benthic foraminifers are abundant. Complete, three-dimensionally preserved specimens of calcareous sponges are common. Complete specimens and growth series of the gastropods *Velates perversus* and *V. batequensis* are common. Growth series of the gastropod *Gyrodes*? sp. are also common. Articulated specimens of the bivalves *Pinna* sp., *Nayadina* (*Exputens*) *batequensis*, *Spondylus batequensis*, and *Lima kennedyi* new species are uncommon. Complete spatangoids are uncommon. Fossils show little or no evidence of abrasion, an indication of minimal post-mortem transport.

Some specimens have delicate parts. Examples are a thin and delicate winged outer lip of the gastropod *Platyoptera pacifica*, patches of small spines adhering to the tests of the spatangoid *Schizaster*, and thin epitheca in all specimens of the solitary coral *Antillia batequensis* new species.

Lenses in the upper half of the shallow-marine deposits are thinner, less laterally extensive, and flat-bottomed or with indistinct tops and bottoms and have fewer fossils and more articulated bivalves. There is also a vertical succession of fossil types within the interval. Those in the lower few meters are characterized by algae and abundant colonial corals. In the overlying 40 m or so, the gastropods *Velates perversus* and *Gyrodes*? sp. are common, as are spatangoid echinoids and the large benthic foraminifer *Pseudophragmina clarki*. Toward the top of the shallow-marine deposits, the bivalve *Pycnodonte* (*Phygraea*) *pacifica* and the gastropod *Turritella andersoni lawsoni* predominate. These *Turritella* commonly show bimodal-preferred orientation, an indication of wave action.

The macrofossils in the lenses are interpreted as storm-bed deposits in channels in a shallow-marine environment adjacent to coral reef(?)-inhabited shoal areas. Each shoal would have been a local source of macrofossils, and distance of post-mortem transport would have been short. This is consistent with the unabraded fossils, the articulated bivalves, the growth series of gastropods, and the retention of delicate parts. It is important to note that certain fossils in the channels would normally occur as fragments because their flexible and erect skeletons were joined by horny connective parts. These are the gorgonian *Parisis* and the cheilostome bryozoan *Cellaria*.

The bioturbated to massive very fine-grained sandstone that surrounds the storm beds is interpreted as fairweather deposits in which much biogenic reworking took place. An environment in which shell-filled storm beds are interbedded with fairweather, bioturbated beds would be between fairweather wave base and maximum storm base. This environment would correlate to the inner shelf zone as defined by Bottjer and Jablonski (1988). The term "shelf" cannot be applied to the Bateque Formation with any degree of certainty because whether or not a true shelf was present is not known. In the case of the Bateque Formation, it would be more appropriate to substitute the term "shelf-like depths" for the term "shelf."

The fossils in the channels also suggest nearby reef conditions, especially the algae and colonial corals. Modern *Archeolithothamnium* red algae live in shallow waters, and modern dasycladacean green algae live just below low tide to about a 30-m depth (Wray, 1977). Species of the colonial coral genera *Stylophora*, *Goniopora*, *Colophyllia*, and *Montastrea* are common as reef builders (Wood, 1983). They are hermatypic corals (Wells, 1956), and these types of corals are restricted to shallow waters by the light requirements of their symbiotic algae (Oliver and Coates, 1987:162) and flourish in depths less than 50 m (Britton and Morton, 1989:275). Many modern octocorals, including *Heliopora*, are also associated with symbiotic algae (Bayer, 1956; Wood, 1983). The gastropod genus *Velates* has been found associated with inner reef facies in middle Eocene strata of northeastern Spain (Taberner and Bosence, 1985). The bivalve *Nayadina* (*Exputens*) *batequensis* was a byssate epifaunal nestler or, possibly, a byssate fissure dweller (Squires, 1990b), and it could have lived in crevices within reefs. The Bateque Formation bivalves *Barbatia* spp., *Spondylus batequensis*, and *Lima kennedyi* new species could also have been reef dwellers. Today, species of these bivalves are part of a reef community in the northern Gulf of Mexico (Britton and Morton, 1989). The crab genus *Ranina* lives today in depths between 20 and 50 m (Sakai, 1976).

Other fossils in the storm beds also indicate shallow-marine depths. Nearly all the mollusks in the storm beds, with the exception of species only found in the Bateque Formation, have been reported as having lived in depths between about 15 and 60 m in other Eocene formations on the Pacific coast of North America (Squires, 1984, 1987, 1988b).

The upper 20 m of the shallow-marine deposits were deposited in slightly deeper waters that were becoming more offshore because the physical sedimentary structures become less pronounced and coral reef(?)-dwelling organisms are replaced by the gastropod *Turritella andersoni lawsoni* and articulated specimens of the bivalve *Pycnodonte* (*Phygraea*) *pacifica*. This particular subspecies of *Turritella* has been reported as an indigenous faunal element of an offshore community in the Eocene

Llajas Formation, Simi Valley, southern California (Squires, 1981, 1984).

OFFSHORE DEPOSITS IN UPPER PART OF FORMATION

Overlying the shallow-marine deposits are offshore deposits that are 90 m thick (Fig. 2). They crop out primarily in the southern part of the area and consist mostly of bioturbated, yellow, very fine-grained sandstone. There are some laminated beds, scattered shell fragments, some oblique burrows, and some low-angle discordances that extend laterally for several hundred meters and may be related to channelling. Locally, at locality CSUN 1293 in the southeasternmost part of the study area (Fig. 1), there is a 9-m-thick interval of reddish gray mudstone with abundant remains of the large benthic foraminifers *Lepidocyclina* sp. and *Pseudophragmina advena* and the bivalves *Batequeus mezquitalensis* and *Cubitostrea mezquitalensis*. The large benthic foraminifers are complete and have growth series. Rare, thin beds of large benthic foraminifer coquina are present. The bivalves are articulated and show growth series.

The 90-m-thick, bioturbated, very fine-grained sandstone upsection from the shallow-marine storm-bed interval is interpreted as having been deposited offshore (Fig. 2) in depths between normal storm wave base and maximum storm base. Biogenic reworking is extensive, and only a few fossil fragments were moved into this environment during maximum storms. This part of the Bateque Formation strongly resembles the offshore strata just below the braid delta and would correlate to the middle "shelf" as defined by Bottjer and Jablonski (1988). This environment prevailed to the top of the Bateque Formation except for the 9-m-thick mudstone at locality CSUN 1293. The large benthic foraminifers, except those in the rare maximum storm-influenced coquinas, and the bivalves are in situ and represent a paleocommunity that lived in fairly quiet waters no deeper than 100 m (Squires and Demetrion, 1990b).

The vertical sequence of offshore, to braid delta, to coral reef(?), to shallow marine, to offshore deposits for the Bateque Formation (Fig. 2) is herein recognized for the first time. Sorensen (1982) reported that the entire formation was massive-bedded and deposited by sheet flow, high-concentration turbidites into bathyal depths. He did find mollusks and echinoids but concluded that they had been transported. Sorensen did not report the braid-delta conglomerate, the overlying coral-reef(?) deposits, and the well-bedded storm beds in the shallow-marine deposits. McLean et al. (1985, 1987) recited Sorensen's (1982) paleoenvironmental interpretations.

DIATOMITE OVERLYING THE BATEQUE FORMATION

In the southeastern part of the study area in Arroyo San Raymundo (Fig. 1), a small exposure of an 8-m-thick sequence grades upward from brown, thin-bedded, well-indurated, fish-scale-bearing mudstone, interbedded with porcellaneous beds, into white unaltered diatomite that strongly resembles the Miocene Monterey Formation of California. The lateral extent of the exposure is only about 50 m because of cover by modern stream alluvium. The base of the sequence is in sharp contact with an underlying 2-m-thick exposure of bioturbated, yellow, very fine-grained sandstone, and the contact between the sandstone and diatomite appears to be an erosional surface with channelling and truncated beds. The lower part of the diatomite sequence also contains two sedimentary dikes consisting of the mudstone and impure diatomite. These dikes extend upward from the contact with the yellow sandstone but they do not pierce the contact. The mudstone and porcellaneous beds are draped over a possible paleo-high in the underlying sandstone. The mudstone and porcellaneous beds on both sides of the paleo-high show pinch outs as they approach it.

McLean and Barron (1988), who did not discuss any field relations regarding the diatomite, included it within the Bateque Formation because the ages are similar. The late middle Eocene CP14a to CP14b age they obtained from diatoms in the unit is about the same to slightly younger than for the mudstone at locality CSUN 1293 in the upper part of the Bateque Formation (see "Age and Correlation"). Diatom samples collected by the authors from the diatomite yielded the same age range (R. Arends, pers. comm., 1990) reported by McLean and Barron (1988).

McLean and Barron (1988) also included the diatomite in the Bateque Formation because they concluded, as did Sorensen (1982), that the entire Bateque Formation was deposited by turbidity currents and sediment-gravity flows in waters between the shelf break and the base of the continental slope.

McLean and Baron (1988) also mentioned another diatomite locality in the northern part of the field area. They included this diatomite within the Bateque Formation, but they lacked an age date for it and did not discuss the field relations.

We are reluctant to include any diatomite beds within the Bateque Formation because a positive relationship to the Bateque Formation cannot be proven at this time. From what was observed at Arroyo San Raymundo, the field relations are ambiguous and more detailed study is needed.

The Arroyo San Raymundo diatomite shares characteristics of the upper Oligocene San Gregorio Formation that McLean et al. (1985, 1987) described, and that McLean and Barron (1988) reported as cropping out in upper Arroyo San Raymundo in an unconformable relationship with the Bateque Formation. The San Gregorio Formation contains brown porcellaneous shale with fish scales, nontectonic folds, and white diatomite that resembles the Miocene Monterey Formation of California. The so-called Bateque Formation diatomite

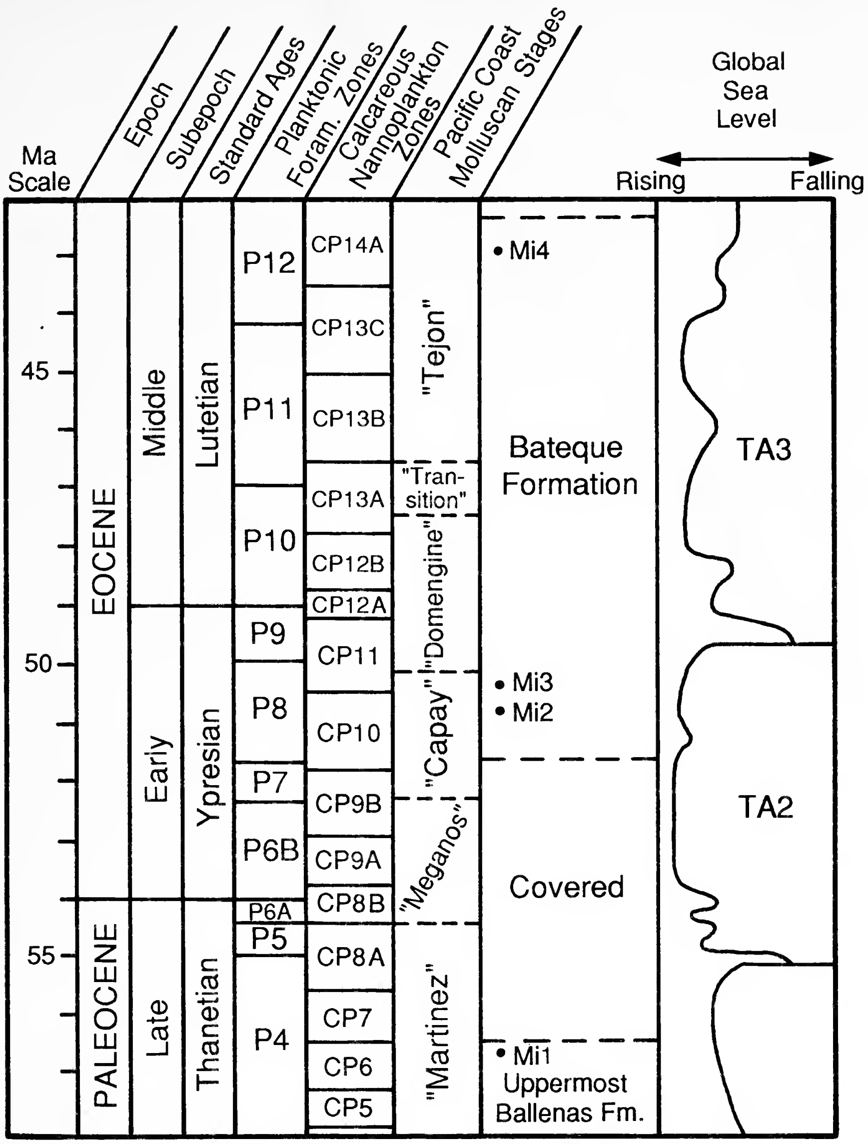


Figure 3. Correlation of the Bateque Formation and uppermost Ballenas formation with millions of year scale (Ma), epochs, subepochs, standard ages, planktonic foraminifera zones, calcareous nannoplankton zones, global sea-level changes (all from Haq et al., 1987), and Pacific coast provincial molluscan stages (from Saul, 1983). Geologic age results of four microfossil (Mi) samples are also plotted.

may be the, heretofore, upper middle Eocene unrecognized basal part of the San Gregorio Formation.

AGE AND CORRELATION

Sorensen (1982) reported that the Bateque Formation overlies the Ballenas formation. Based on small-sized benthic foraminifers, he reported the age of the Ballenas formation to be early to early late Paleocene. A microfossil sample (Mi1) collected by us at the top of the Ballenas formation at Rancho Carrizo Mesa (Figs. 1, 3) yielded the following species of calcareous nannofossils: *Fasciculithus tympaniformis* Hay and Mohler, *Discoaster mohleri* Bukry and Percival, and *Coccolithus pelagicus* (Wallich). M. Filewicz (pers. comm., 1990) assigned them to the upper Paleocene *Discoaster mohleri* (CP6) Zone of Okada and Bukry (1980).

The Bateque Formation ranges in age from middle early Eocene to late middle Eocene (Fig. 3) based on calcareous nannofossils, planktonic foraminifers, and mollusks. An early Eocene age for most of the Bateque Formation ranging into the middle Eocene near the top is also what Sorensen (1982) found using small benthic foraminifers. McLean et al. (1985, 1987) iterated Sorensen (1982).

Macrofossils are lacking in the offshore and braid-delta deposits in the lower 115 m of the Bateque Formation. The only microfossil sin this interval are some rare and poorly preserved calcareous nannofossils that are not zone diagnostic but do indicate an early to early middle Eocene age (M. Filewicz, pers. comm., 1988).

Planktonic foraminifers from microfossil locality Mi2 (Fig. 1) at the base of the shallow-marine deposits (Fig. 2) indicate a middle early Eocene age ("Capay" age) (Figs. 2, 3) based on overlap of *Acarinina nitida* (Martin) and *Morozovella aragonensis* (Nuttall) (equivalent to the *Globorotalia formosa formosa* Zone of Stainforth et al., 1975, and the P8? Zone of Blow, 1979) (R. Fulwider, pers. comm., 1988).

Planktonic foraminifers from microfossil locality Mi3 (Fig. 1) near the middle of the shallow-marine deposits (Fig. 2) also indicate an early Eocene age (Figs. 2, 3) based on the presence of *M. aragonensis* and *M. aragonensis caucasica* (Glaessner) (equivalent to *Globorotalia aragonensis* or *G. pentacamerata* Zones of Stainforth et al., 1975, and the P8 or P9 Zone of Blow, 1979) (R. Fulwider, pers. comm., 1988). The P8 Zone ("Capay" age) interpretation is favored here because of the upsection presence of the gastropod *Turritella andersoni* s.s., which is diagnostic of the "Capay Stage." This gastropod was found at localities CSUN 1291a and 1291b, in the upper part of the shallow-marine deposits. This species is known elsewhere on the Pacific coast only from the middle lower Eocene "Capay Stage" (Givens, 1974; Squires, 1987, 1988b, 1988c).

Turritella andersoni lawsoni was found at localities CSUN 1220c (upper part), 1220d, and 1291c, near the top of the shallow-marine deposits. This subspecies is known elsewhere on the Pacific coast only from the upper lower through lower middle Eocene "Domengine Stage" (Givens, 1974; Squires, 1984).

Most of the other mollusks in the shallow-marine and overlying offshore deposits range from the "Capay Stage" through the "Domengine Stage." Calcareous nannofossils from these deposits are very rare and poorly preserved and generally indicate an undifferentiated Paleogene age (M. Filewicz, pers. comm., 1988).

Calcareous nannofossils from locality CSUN 1293 (= microfossil locality Mi4) (Fig. 1) in the mudstone interval of the offshore deposits near the top of the Bateque Formation (Figs. 2, 3) indicate the middle Eocene *Discoaster bifax* CP14a Subzone of Okada and Bukry (1980) based on the presence of *Reticulofenestra umbilica* (Levin) and *Chiasmolithus solitus* (Bramlette and Sullivan) (M. Filewicz, pers. comm., 1989). Mollusks at this locality are not stage diagnostic. This subzone is equivalent to the middle Eocene part of the molluscan "Tejon Stage."

Beal (1948) assigned all Paleocene and Eocene strata of peninsular Baja California to Heim's (1922) Tepetate Formation, whose type section is about 200 km south of the study area at Rancho Tepetate, east of Bahia Magdalena, Baja California Sur. Mina (1956, 1957) mainly restricted the Tepetate Formation to its type section area but did include the outcrops in the vicinity of locality CSUN 1293 (in the southeasternmost part of the study area) in the Tepetate Formation. McLean et al. (1985) suggested that these particular rocks be included in the Bateque Formation. We concur and restrict the Bateque Formation to the study area (Fig. 1).

PALEOCLIMATE AND PALEOBIOGEOGRAPHY

As reviewed by Squires (1987), the early Eocene was the peak warm interval of the Cenozoic, and tropical conditions were widespread until a worldwide cooling trend began in the late Eocene. Macrofossils within the Bateque Formation strongly support the presence of tropical waters. Living species of *Archaeolithamnium,* a coralline red alga, are restricted to tropical and subtropical marine waters (Wray, 1977:68). Living dasycladacean green algae occur most commonly in tropical and subtropical waters (Wray, 1977:106).

The calcareous nannofossils at locality CSUN 1293 near the top of the Bateque Formation show a greater diversity than that in age-equivalent assemblages in California, which suggests warmer (tropical?) paleotemperatures (M. Filewicz, pers. comm., 1989).

The extinct large benthic foraminifer genus *Pseudophragmina* is indicative of tropical to subtropical waters (Vaughan, 1945:70). Living calcareous sponges, similar to the extinct *Elasmostoma,* are most commonly found in shallow tropical waters (Rigby, 1987). The living octocoral *Heliopora* is associated with coral reefs (Wood, 1983). The living colonial corals *Stylophora, Goniopora, Colpophyllia,* and *Montastrea* are all hermatypic and indicative of tropical waters (Wells, 1956; Wood, 1983). Nearly all the molluscan species have been reported from tropical to subtropical paleoenvironments elsewhere on the Pacific coast of North America (Squires, 1984, 1987, 1988b). Only one species of the crab *Ranina* is now living and is confined to the warm waters of the tropical Indo-Pacific region (Rathbun, 1919). Only five species of *Eupatagus* are known today, and all are in the tropical Indo–West Pacific (Kier, 1984).

The widespread warm-water conditions that prevailed during the Eocene caused latitudinal gradients in the marine faunas to be slight (Addicott, 1970). Paleolatitude determination for Baja California Sur during deposition of the Bateque Formation, therefore, must rely heavily on paleomagnetic data. As reviewed by Flynn et al. (1989), workers have maintained that the Baja California peninsula has been tectonically translated northward by 10–15 degrees since the Late Cretaceous. As to the question of the timing of this northward translation, the paleomagnetic data have been inconsistent and contradictory. For example, Morris et al. (1986) concluded that the translation was entirely post-Miocene, but the work by Flynn et al. (1989) indicated that there has been no significant post–early Eocene northward translation of

Baja California and that the early Eocene paleolatitude of the Baja California peninsula was almost the same as its present latitude.

The early Eocene ("Capay Stage") was a time of major influx of Old World Tethyan macroinvertebrates into the Pacific coast of North America via a seaway through Central America (Clark and Vokes, 1936; Givens, 1979; Squires, 1984, 1987). Arrival of the Tethyan mollusks in California during the early Eocene was also coincident with a major global sea-level rise (Squires, 1987) that is equivalent to the TA2 cycle of Haq et al. (1987) (Fig. 3). Many of the species used to document the timing of this influx of immigrants into California are the same ones present in the lower Eocene ("Capay Stage") part of the Bateque Formation. One of the most important of these is the neretid gastropod *Velates perversus,* which emigrated westwardly from Pakistan into the Pacific coast of North America during the early Eocene (Squires, 1987). Other Bateque Formation mollusk genera that have been recognized as Tethyan or Tethyan affinity (Clark and Vokes, 1936; Squires, 1984, 1987, 1990b; Givens, 1989) and that accompanied *V. perversus* into Pacific coast waters include species of *Paraseraphs, Eocypraea, Ectinochilus, Pachycrommium, Galeodea, Clavilithes, Lyrischapa, Barbatia,* and *Nayadina* (*Exputens*).

Several of the macrofossils from the lower Eocene ("Capay Stage") part of the Bateque Formation are new to the Pacific coast of North America. These include species of the sponge *Elasmostoma,* the cnidarians *Heliopora*?, *Parisis, Heterocoenia*?, *Stylosmilia, Antillia,* and *Montastrea,* the bryozoan *Stomatopora,* the gastropods *Tenagodus, Platyoptera,* and *Cypraedia,* the bivalve *Pycnodonte* (*Phygraea*), the crab *Lophoranina,* possibly the cassiduloid echinoid *Echinolampas,* and possibly the spatangoid echinoid *Eupatagus.* The sponge *Elasmostoma* and the corals *Stylosmilia* and *Heterocoenia*? were previously only known from Mesozoic strata, primarily in western Europe. For the gastropod *Platyoptera* and possibly the gorgonian *Parisis,* this is the earliest occurrence anywhere in the world.

A few of the Bateque Formation macrofossils have been previously reported from the Pacific coast but have their earliest record in the lower Eocene ("Capay Stage") part of the Bateque Formation. These genera are the large benthic foraminifer *Lepidocyclina,* the bryozoan *Cellaria,* the bivalve *Nayadina* (*Exputens*), the crab *Ranina,* and possibly the bivalves *Barbatia* (*Acar*?) and *Lima* as well as possibly the spatangoid echinoid *Eupatagus.* For *Nayadina* (*Exputens*) and *Ranina,* this is the earliest occurrence anywhere in the world.

A few of the Bateque Formation macrofossils have been previously reported from the Pacific coast but have their latest occurrence in the lower Eocene ("Capay Stage") part of the Bateque Formation. These molluscan genera are the gastropods *Bernaya* (*Protocypraea*), *Amauropsis,* and *Gyrodes*?. For the latter two, this is the latest record anywhere in the world.

The bivalve genus *Cubitostrea* appeared on the Pacific coast during the upper middle Eocene ("Tejon Stage") part of the Bateque Formation.

The bivalve genera *Batequeus* and *Pycnodonte* (*Pegma*) are known only from the Bateque Formation.

SYSTEMATIC MATERIALS AND METHODS

Systematic arrangement for the kingdom categories is from Margulis and Schwartz (1982). Systematic arrangement of the generic and higher taxonomic categories follows that of Wray (1977) for the algae, Loeblich and Tappan (1988) for the large benthic foraminifers, Laubenfels (1955) for the sponges, Bayer (1956) for the octocorals, Wells (1956) for the scleractinian corals, Bassler (1953) for the bryozoans, Clark (1969) for the polychaete worm, Palmer (1974) for the scaphopod, generally Wenz (1938–1944) for the gastropods, Bieler (1988) for the gastropod *Architectonica,* Cox et al. (1969) and Vokes (1980) for the bivalves, Kummel (1964) for the cephalopods, Glaessner (1969) for the brachyurans, and Fischer (1966) for the echinoids.

The original reference is given for each species or subspecies. Synonymies and primary type material for most of the positively identified species/subspecies of the Bateque Formation can be found in Squires (1984, 1987, 1988b). For those few taxa that are not included therein, primary type material is given herein, and reference is made to a source in which a synoymy is available.

Molluscan stage range and geographic distribution are given for each positively identified species or subspecies, with most of the data derived from Squires (1984, 1987, 1988b). For those few taxa that are not included herein, literature sources are given under "Remarks" in this present report.

The molluscan stages are those of Clark and Vokes (1936), who informally proposed five molluscan provincial Eocene stages for the Pacific coast of North America: "Meganos," "Capay," "Domengine," "Transition," and "Tejon." They recognized two faunal zones in their "Capay Stage." Givens (1974) showed that the upper faunal zone of the "Capay" should be assigned to the "Domengine Stage," and he restricted the use of "Capay Stage" to the lower faunal zone. The "Capay Stage" is used herein. Saul (1983) and Squires (1984, 1987, 1988b) regarded the restricted "Capay Stage" of Givens (1974) as middle lower Eocene.

Local occurrence and remarks are given for the species. Terms used to denote specimen abundance are defined as follows (number of specimens in parentheses): rare (1–4), uncommon (5–9), common (10–29), and abundant (30 or more).

New stage ranges or new geographic extensions that are the result of this present study also are mentioned under "Remarks."

Abbreviations used for catalog and/or locality numbers are as follows:

CAS: California Academy of Sciences, San Francisco.
CSUN: California State University, Northridge.
IGM: Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City.
LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.
SDNHM: San Diego Natural History Museum.
USNM: United States National Museum of Natural History.

The type specimens are deposited at IGM; plaster casts of the primary type material from the Bateque Formation have also been deposited at LACMIP.

SYSTEMATICS

Kingdom Protoctista

Division Rhodophyta

Class Rhodophyceae

Order Cryptonemiales

Family Corallinaceae (Lamouroux) Harvey, 1849

Genus *Archaeolithothamnium* Rothpletz, 1891

Archaeolithothamnium sp.

Figure 4

LOCAL OCCURRENCE. Localities CSUN 1220 a, 1220b, 1471.

REMARKS. Specimens of this red alga are common at localities 1220a and 1220b. They are rare at locality 1471. Most specimens occur as aggregates (rhodoliths) of crustose lumps up to 5.5 cm across. Some specimens show sporangia arranged in loose rows, a distinctive feature of this genus (Wray, 1977:60). One specimen at locality 1471 encrusts the octocoral *Heliopora*? sp.

Division Chlorophyta

Class Chlorophyceae

Order Dasycladales

Family Dasycladaceae Stizenberger, 1860

Dascyladaceae, indet.

Figure 5

LOCAL OCCURRENCE. Localities CSUN 1220a, 1220b, 1291a, 1470.

REMARKS. Specimens of this green alga are abundant at 1220a, 1220b, and 1291a and form an integral part of the lithology of rocks at these localities. At locality 1470, they are common. All specimens are disarticulated fragments of variable shapes. Lensoidal and polygonal shapes are the most common. Some fragments are up to 4 mm long, and many have closely spaced pits on the exterior. These pits have been subdued by weathering. In some hand specimens, the fragments show concentration and sorting.

Phylum Protista

Class Rhizopodea

Order Foraminiferida

Family Lepidocyclinidae Scheffen, 1932

Genus *Lepidocyclina* Gümbel, 1870

Lepidocyclina sp.

Figures 6, 7

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens are extremely abundant and form a "pavement" on the weathered mudstone outcrops at this locality. Tests show a growth series up to 21 mm in diameter, and many of the tests are of large size. They have a granular exterior, and a few have a small central boss. Internally, they have four-sided to six-sided equatorial chambers. In each chamber, the chamber wall that is nearer the periphery of the test is convex outward.

Unfortunately, the proloculus area in every specimen that was thin-sectioned has been obliterated by diagenesis. Identification as to species is not possible.

Lepidocyclina sp. from the Bateque Formation resembles *L. ocalana* Cushman (1920:71–72, pl. 28, figs. 3, 4; pl. 29, figs. 1–3) from the upper Eocene Ocala Limestone, northern Florida. The Bateque Formation specimens differ in the following features: less inflated central boss area and both sides of test similar rather than dissimilar.

Lepidocyclina has not been reported previously from the Eocene of the Pacific coast of North America any farther north than Chiapas, Mexico, where Vaughan (1924) reported *L.* (*Polylepidina*) *chiapasensis* Vaughan (1924:808–809, pl. 30, figs. 1–3) from Eocene strata and *L.* (*P.*) *adkinsi* Vaughan (1924:809–810, pl. 31, figs. 1–5) from upper Eocene strata. *Lepidocyclina* sp. from the Bateque Formation differs from *L.* (*P.*) *chiapasensis* in having a much larger test and a less inflated central boss area, and the Bateque Formation species differs from *L.* (*P.*) *adkinsi* in having a larger test and a less pronounced granular exterior.

Schenck and Childs (1942) reported *Lepidocyclina* from upper Oligocene deposits in California.

Family Nummulitidae de Blainville, 1827

Genus *Operculina* d'Orbigny, 1826

Operculina sp., aff. *O. cookei* Cushman, 1921a

Figure 8

[*Operculina cookei* Cushman, 1921a:127–128, pl. 18, figs. 1, 2.]

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens are uncommon. The planispiral and flattened tests are up to 9 mm in length. They resemble *O. cookei* Cushman, 1921a, from the upper Eocene Ocala Limestone of Georgia. The Bateque Formation specimens differ in having pustules along the sutures rather than having continuous ridges along the sutures.

There are only a few other Eocene occurrences of *Operculina* from the Pacific coast of North America. *Operculina cushmani* Cole (1927:23, pl. 2, fig. 13) is known from the middle Eocene "Domengine Stage" part of the Llajas Formation, Simi Valley, southern California (Cushman and McMasters, 1936:513, pl. 75, figs. 18–20). *Operculina cushmani* is also known from the lower Paleogene lower Lodo Formation, Media Agua Creek, south-central California (Mallory, 1959:185, pl. 15, fig. 11). The Bateque Formation specimens have less distinct sutures and no raised central boss area. The type locality of *O. cushmani* is on the eastern coast of Mexico at Guayabal (Cole, 1927), which is half way between the cities of Tampico and Veracruz, Mexico.

Operculina sp. is known from the upper Eocene Keasey Formation, southwestern Washington (Durham, 1937:367, fig. 1). The Bateque Formation specimens differ in having pustules along the sutures and fewer sutures.

Givens (1974:table 1) listed *Operculina*? sp. from a locality in middle Eocene "Domengine Stage" strata in the Pine Mountain area, southern California.

Although Woodring (1930) reported *Operculina* cf. *ocalana* Cushman from Eocene limestone deposits, Santa Barbara County, southern California, Cole (1958:411) reassigned these specimens to genus *Operculinoides.*

Family Discocyclinidae Vaughan and Cole, 1940

Genus *Actinocyclina* Gümbel, 1870

Actinocyclina sp., aff. *A. aster* Woodring, 1930

Figure 9

[*Actinocyclina aster* Woodring, 1930:152–155, pl. 14, figs. 3–6; pl. 16, figs. 1–4; pl. 17, figs. 1, 2.]

LOCAL DISTRIBUTION. Locality CSUN 1220b.

REMARKS. Specimens are rare, as much as 4 mm in diameter, and discoidal in outline, and most have seven very narrow rays or ridges emanating from a central raised boss. These rays are papillate and extend to the periphery. One specimen has eight narrow rays because one ray is bifurcated.

The Bateque Formation specimens resemble the narrow-rayed forms of *A. aster* Woodring, 1930, from the lower? Eocene Sierra Blanca Limestone, Santa Barbara County, southern California. Ellis and Messina (1967:unnumbered plates, figs. 1-26) also illustrated *A. aster.* The rays in the Bateque Formation specimens are narrower and show no tendency for having thick rays or as many as 13 rays that can occur in *A. aster.*

Genus *Pseudophragmina* Douvillé, 1923

Pseudophragmina clarki (Cushman, 1920)

Figures 10, 11

Orthophragmina clarki Cushman, 1920:41–42, pl. 7, figs. 4, 5.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Florida, Peru?, Mexico through southwestern Oregon.

LOCAL OCCURRENCE. Localities CSUN 1219, 1220a, 1220b, 1220c, 1291a, 1291b, 1470?, 1471.

REMARKS. Specimens are extremely abundant, especially at localities 1219, 1220a, 1220b, and 1220c. Specimens are up to 7 mm in diameter and have pustules on the exterior, and most show a well-developed central boss.

Cole (1958:419) regarded *Orthophragmina peruviana* Cushman (1922:138–139, pl. 24, fig. 3) to be a synonym of *P. clarki.* If this is correct, then *P. clarki* also occurs in Peru.

Pseudophragmina advena (Cushman, 1921b)

Figures 12, 13

Orthophragmina advena Cushman, 1921b:139, pl. 22, figs. 1–5.

PRIMARY TYPE MATERIAL. Holotype, USNM 328252, from the St. Maurice Formation, Natchitoches, Louisiana, Eocene.

MOLLUSCAN STAGE RANGE. "Capay" through middle Eocene part of "Tejon."

GEOGRAPHIC DISTRIBUTION. Gulf Coast of the United States, Jamaica, Cuba, Baja California Sur, Mexico, through Santa Ynez Range, southern California.

LOCAL OCCURRENCE. Localities CSUN 1293, 1471.

REMARKS. Specimens are abundant, as much as 12 mm in diameter, lensoidal, and smooth exteriorly. Internally, the annuli are much more closely spaced than in *P. clarki,* and the radial walls of the equatorial chambers are not as well developed as those in *P. clarki.*

For the rather involved synonymy and geographic distribution of this species, see Cole (1969:25–26), who regarded *P. perkinsi* (Vaughan, 1928) from Jamaica, *P. compacta* Cole and Gravell, 1952, from Cuba, and *P. cloptoni* (Vaughan, 1929) from Baja California Sur to be synonyms.

The Bateque Formation specimens are like *P. cloptoni* (Vaughan, 1929:14–15, pl. 15, figs. 1–6) from the Tepetate Formation east of Bahia Magdalena, Baja California Sur. Neither the Bateque Formation specimens nor *P. cloptoni* from the Tepetate Formation show the deep umbonal depression than can be associated with *P. advena.* Cole (1969), however, noted that *P. advena* has variable shape and is the same as *P. cloptoni* based on identical internal structures.

Based on its presence in the Bateque Formation, the molluscan stage range of this species can now be reported as "Capay" through the middle Eocene part of the "Tejon."

Kingdom Animalia

Phylum Porifera

Class Demospongea

Order Hadromerida

Family Clionidae Gray, 1867

Clionidae?, indet.

Figure 14

LOCAL OCCURENCE. Localities CSUN 1220b, 1220c, 1471.

REMARKS. Boreholes probably related to the burrowing sponge *Cliona* were found in a few of the larger specimens of *Velates perversus* and *Eocernia hannibali* (Fig. 83) at locality 1220b and on some of the specimens of *Pycnodonte (Phygraea) pacifica* at localities 1220c and 1471.

Class Calcarea

Order Lithonida

Family Elasmostomatidae de Laubenfels, 1955

Genus *Elasmostoma* Fromentel, 1860

Elasmostoma bajaensis Squires and Demetrion, 1989

Figures 15, 16

Elasmostoma bajaensis Squires and Demetrion, 1989:440–442, figs. 1–9.

PRIMARY TYPE MATERIAL. Holotype, LACMIP 7982; paratypes, LACMIP 7983, 7984, and 7985; all from locality CSUN 1220a.

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220a.

REMARKS. Specimens are abundant. They are three-dimensional and many are complete. Others are unabraded fragments formed during weathering of the exposures. Most specimens are ear-shaped, and they form a growth series ranging from 9 to 45 mm in diameter. Three of these specimens have small buds where juveniles are attached. One colonial specimen, consisting of four specimens, is 70 mm in diameter and 20 mm in depth.

Before its discovery in the Bateque Formation, *Elasmostoma* was previously only known from Jurassic and Cretaceous strata of western Europe (Squires and Demetrion, 1989).

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Figures 4–20. Bateque Formation calcareous algae, large benthic foraminifera, sponges, and a spongiomorph? organism. **Figs. 4, 5.** Calcareous algae. **4.** *Archeolithothamnium* sp., ×1.74, width of field 29 mm, hypotype, IGM 5120, loc. CSUN 1220b. **5.** Dasycladaceae, indet., ×3.2, width of field 16 mm, hypotype, IGM 5121, loc. CSUN 1220b. **Figs. 6–13.** Large benthic foraminifera. **6, 7.** *Lepidocyclina* sp., loc. CSUN 1293. **6.** Test exterior, ×1.2, diameter 21 mm, hypotype, IGM 5122. **7.** Part of equatorial section, ×27, width of field 1 mm, hypotype, IGM 5123. **8.** *Operculina* sp., aff. *O. cookei* Cushman, 1921a, test exterior, ×3.1, height 9 mm, width 6 mm, hypotype, IGM 5124, loc. CSUN 1293. **9.** *Actinocyclina* sp., aff. *A. aster* Woodring, 1930, test exterior, ×5.6, diameter 4.5 mm, hypotype, IGM 5125, loc. CSUN 1220b. **10, 11.** *Pseudophragmina clarki* (Cushman, 1920), loc. CSUN 1220b. **10.** Test exterior, ×4.3, diameter 6 mm, hypotype, IGM 5126. **11.** Equatorial section, ×33, width of field 1.5 mm, hypotype, IGM 5127. **12, 13.** *Pseudophragmina advena* (Cushman, 1921b), loc. CSUN 1293. **12.** Test exterior, ×3, diameter 8.3, hypotype, IGM 5128. **13.** Part of equatorial section, ×50, width of field 1 mm, hypotype, IGM 5129. **Figs. 14–16.** Sponges. **14.** Clinoidae?, indet., in left valve of *Pycnodonte (Phygraea) pacifica,* ×0.9, height of valve 67 mm, width 41 mm, hypotype, IGM 5130, loc. CSUN 1471. **15, 16.** *Elasmostoma bajaensis* Squires and Demetrion, 1989, loc. CSUN 1220a. **15.** Side view, ×1.1, height 25 mm, maximum width 31 mm, paratype, LACMIP 7983. **16.** Part of ostia-bearing wall, ×9, width of field 5.8 mm, paratype, LACMIP 7984. **Figs. 17–20.** Spongiomorph organism. Spongiomorphidae?, hypotype, IGM 5131, loc. CSUN 1220a. **17.** Dorsal view of entire colony, ×0.4, length 14 cm. **18.** Part of dorsal surface near center of colony, ×4.3, width of field 11 mm. **19.** Underside of small chip removed from upper right area of colony, ×8.3, width of field 4 mm. **20.** Part of lateral view, ×2, width of field 22 mm.


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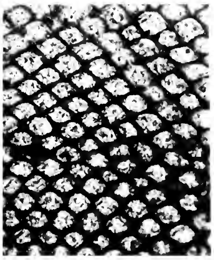
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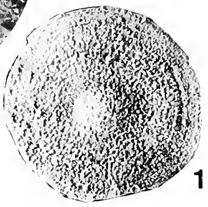
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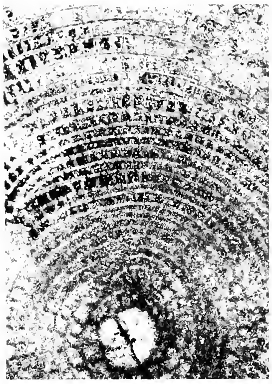
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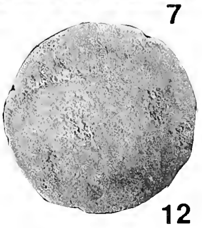
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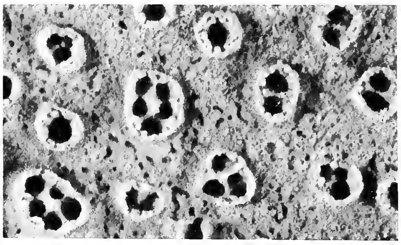
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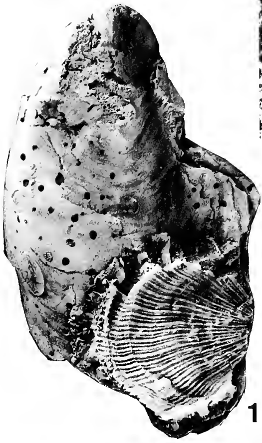
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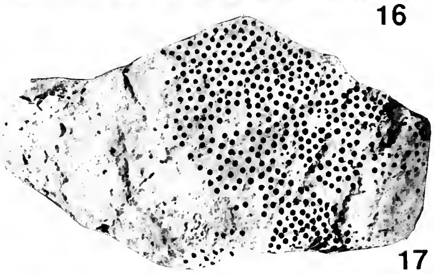
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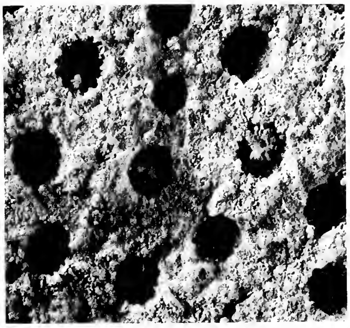
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Phylum Cnidaria

Class Hydrozoa

Order Spongiomorphida

Family Spongiomorphidae Frech, 1890

Spongiomorphidae?, indet.

Figures 17–20

LOCAL OCCURRENCE. Locality CSUN 1220a.

REMARKS. Two specimens were found, one colony about 15 cm in length and 4.5 cm in thickness, and another only a sliver (4 cm thick) of a colony. The larger specimen shows the best preservation. It consists of coenosteum surrounding circular gastropores(?), openings about 1 mm in diameter and spaced about 1.5–2.5 mm apart. The walls of the gastropores(?) consist of 12 stellate columns (pseudosepta). The gastropores(?), which are flush with the external surface, extend vertically all the way through the 4.5-cm-thick colonial structure. They do not vary in diameter throughout their vertical extent. Most of the gastropores(?) are hollow and have a beaded appearance along the walls. This beaded appearance is similar to that of the surrounding coenosteum. About 10 percent of the gastropores(?) are completely filled with calcareous material consisting of six rods grouped starwise as a vertical, tubular structure encircling a central rod. Each of the six rods are bilobate due to a slit that extends toward the central rod. A few structures consist of 10 rods encircling a central one.

In transverse view, the Bateque Formation specimens resemble the spongiomorph *Heptastylis stromatoporoides* [Frech (1890); Hill and Wells, 1956: 88, fig. 74 2a–c; Chudinova, 1962:232, fig. 12a–c] from Triassic strata of Europe. The Bateque Formation specimens differ significantly in lacking the horizontal laminae of *Heptastylis*.

It is interesting to note that the empty, minutely stellate gastropores(?) of the Bateque Formation spongiomorph(?) specimens resemble those seen in the Bateque Formation specimens of the octocoral *Heliopora*? sp.

Class Anthozoa

Order Coenothecalia

Family Heliporidae Moseley, 1876

Genus *Heliopora* de Blainville, 1830

Heliopora? sp.

Figures 21, 22

LOCAL OCCURRENCE. Locality CSUN 1471.

REMARKS. Specimens are rare, and they appear to be distal parts of colonies or incrustations. Specimens consist of finely porous coenosteum surrounding circular autozooid pits about 1.25 mm in diameter and about 1–2 mm apart (measured from wall to wall). The walls of the autozooid pits show about 24 minute columns (pseudosepta). The pits are nearly filled with calcareous sediment.

Heliopora? sp. from the Bateque Formation is only the third occurrence of this genus in North America. *Heliopora mexicanae* Frost and Langenheim (1974:311–312, pl. 123, figs. 1–3; Perrilliat, 1989:93, fig. 32c) is known from middle Eocene strata of Chiapas, Mexico. The Bateque Formation specimens differ in having twice as many pseudosepta per autozooid pit.

Heliopora bennetti Wells (1934:155–156, pl. 2, figs. 1, 2) is known from upper? Eocene strata of Cuba and is more similar to the Bateque Formation species. The Bateque Formation species differs in having pseudosepta that do not project halfway to the center of the autozooids and autozooids that are larger and more widely spaced.

The genus *Heliopora* is queried for the Bateque Formation specimens and also should be queried for the Chiapas and Cuban species, because they do not possess the distinctive tubular openings found within the autozooids of *Heliopora coerulae* (Pallas) (Wood, 1983:214), the type species of *Heliopora*. The Bateque Formation, Chiapas, and Cuban species may belong to a new genus.

Heliopora? sp. from the Bateque Formation closely resembles *H. edwardsana* Stoliczka (1873: 185–186, pl. 11, fig. 11, 11a, 11b) from the Ootatoor Group of southern India. Sastry et al. (1968) assigned the Ootatoor Group to the lower upper Cretaecous (Cenomanian Stage). The Bateque Formation specimens differ in having more pseudosepta (24 rather than 18) and more closely spaced autozooids (1–2 mm apart rather than 4–5 mm apart).

According to Montanaro-Gallitelli (1956), *Heliopora* is confined to the Recent. It is evident, therefore, that all fossil species of *Heliopora* should be reviewed to determine their generic placement. Several Cretaceous specimens have been reported from Europe and southern India (Stoliczka, 1873; Felix, 1914b), and one probable Cretaceous species has been reported from central Texas (Wells, 1932, 1934). A few Eocene species have been reported from Europe (Wells, 1934). Woodring (1957:21) included *Heliopora* sp. in a checklist of corals from the middle to upper Eocene Gatuncillo Formation in the Panama Canal Zone. He did not give any repository numbers nor did he figure or describe the specimen(s).

Order Gorgonacea

Family Parisididae Aurivillius, 1931

Genus *Parisis* Verrill, 1864

***Parisis batequensis* new species**

Figures 23–25

DIAGNOSIS. A *Parisis* with straight-sided internode stems and pointed condyles.

COMPARISON. The geologic record of the gorgonian octocoral *Parisis* is very poorly known, and there is much uncertainty about which fossil species actually belong to the genus. A literature search revealed only one species of fossil gorgonian octocoral that shares many of the characteristics of the new species. It is species *Melitodes*? *hamiltoni* (Thomson, 1908:99, pl. 14, fig. 1) from middle Oligocene strata in New Zealand. Squires (1958:29, pl. 2, figs. 1–7) also discussed *M.*? *hamiltoni.* The new species differs in having more straight-sided stems and a more pointed central apex on the condyles.

According to Bayer (1956), *Melitodes* is now classified as *Melithaea,* a genus characterized by axial internodes that are very porous. The morphology of Thomson's (1908) species from New Zealand is like *Parisis* rather than like *Melithaea,* and we believe that *Melithaea*? *hamiltoni* should be placed in genus *Parisis.*

Parisis batequensis new species resembles *Isis* sp. 1 of Duncan (1880:109, pl. 28, figs. 9, 10) from Miocene strata in western India. The new species differs in having condyles with a central pointed tip (rather than flat-topped) and in the absences of any transverse ribs perpendicular to the radial ribs. Future work may show that *Isis* sp. 1 belongs to family Parisididae.

DESCRIPTION. Solid, nearly circular calcareous internode stems, straight-sided, up to 30 mm long and up to 18 mm in diameter, longitudinally marked by closely spaced single or double ribs that spiral about the axis. Some ribs bifurcate, and some rarely have a single groove that is much wider than the other grooves. Raised condyles branch off from some stems. Condyles with a central small pointed tip, bearing simple or frilled radial ribs that extend to periphery and align with corresponding longitudinal ribs. A few radial ribs bifurcate at the periphery.

PRIMARY TYPE MATERIAL. Holotype, IGM 5133 (= LACMIP plastoholotype 8845); paratypes, IGM 5134–5135 (= LACMIP plastoparatypes 8846–8847); all from locality CSUN 1220b.

TYPE LOCALITY. Locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are common and consist of only the calcareous segments of a colony that had joints (nodes) of spiculiferous horny material. According to Bayer (1956:200), the geologic range of the gorgoian octocoral genus *Parisis* is Tertiary to Recent. The Bateque Formation new species is the first record of *Parisis* from the Pacific coast of North America, and it may be the earliest known species of *Parisis.*

ETYMOLOGY. The new species is named after the Bateque Formation.

Order Scleractinia

Family Astrocoeniidae Koby, 1890

Genus *Astrocoenia* Milne-Edwards and Haime, 1848

Astrocoenia dilloni Durham, 1942

Figure 26

Astrocoenia dilloni Durham, 1942:505, pl. 44, fig. 3.

PRIMARY TYPE MATERIAL. Holotype, CAS 7724, locality CAS 30677A.

MOLLUSCAN STAGE RANGE. "Capay" and "Domengine?."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1471.

REMARKS. Specimens are abundant, well preserved, and fragmentary. Calices are as much as 4 mm in diameter and are much larger than those in the holotype, which has calices as much as 2.5 mm in diameter. Like the holotype, the Bateque Formation specimens have 10 major septa that reach the sunken styliform columella and minor septa that do not reach the columella.

The holotype is from the south side of the headwaters of Media Aqua Creek, Kern County, south-central California. Determination of the formation and geologic age of the Eocene strata at the type locality of *A. dilloni* need refinement. Strata at about the same stratigraphic horizon (Durham, 1942), however, do contain the gastropod *Campanile dilloni* Hanna and Hertlein (1949:393, pl. 77, figs. 2, 4), whose molluscan stage range is "Capay" and possibly "Domengine" (Squires and Advocate, 1986: 853).

The presence of *Astrocoenia dilloni* in the Bateque Formation is the second known occurrence of this species.

Family Pocilloporidae Gray, 1842

Genus *Stylophora* Schweigger, 1819

Stylophora chaneyi Durham, 1942

Figure 27

Stylophora chaneyi Durham, 1942:509, pl. 44, fig. 8.

PRIMARY TYPE MATERIAL. Holotype, CAS 7723, locality CAS 30667.

MOLLUSCAN STAGE RANGE. "Capay" and "Domengine?."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURENCE. Locality CSUN 1220b.

REMARKS. Specimens are abundant and fragmentary, laterally compressed ramose branches. Preservation is fair. Like the holotype, calices are about 0.5 mm in diameter with six major septa that reach the styliform columella and minor septa that do not reach the columella. The calices are 0.2–0.5 mm from each other and separated by solid coenenchymal material.

The holotype is from the same area as the holotype of *Astrocoenia dilloni* and is, therefore, "Capay" and possibly "Domengine."

The presence of *Stylophora chaneyi* in the Bateque Formation is the second known occurrence of this species.

Family Stylinidae d'Orbigny, 1851

Genus *Heterocoenia* *Milne-Edwards, 1848*

Heterocoenia? sp.

Figure 28

LOCAL OCCURRENCE. Locality CSUN 1220a.

REMARKS. Only one specimen was found. It is a poorly preserved fragment that is about 5 cm in height and 4 cm in width. Only the longitudinal view of this plocoid corallum is observable. It shows separate corallites united by dissepiments and coenosteum that resemble *Heterocoenia.*

Wells (1956) reported that *Heterocoenia* is known from Cretaceous strata in Europe, North America, and Japan. If the Bateque Formation specimen is *Heterocoenia,* it would be the first record of the genus from the Pacific coast of North America, and it would extend the geologic range of the genus into the early Eocene.

Genus *Stylosmilia* Milne-Edwards, 1848

Stylosmilia ameliae **new species**

Figures 29, 30

DIAGNOSIS. A *Stylosmilia* with widely spaced, thick-walled corallites having 12 primary septa.

COMPARISON. The new species has been compared with all of the species of *Stylosmilia* listed in Felix (1914a:14–15). Nearly all of these are illustrated in Fromentel (1873). Additional comparisons were made with other species illustrated in Becker (1875), Tomes (1885), Koby (1896), and Geyer (1954). All of the previously described species of *Stylosmilia* are from Europe and occur in strata within the Middle Jurassic to Early Cretaceous age range that has been reported (Geyer, 1954; Wells, 1956) for this genus. Most of the species are not comparable to the new species because they have more septa and/or their corallites are more closely spaced.

The new species is most similar to *S. suevica* Becker (1875:139, pl. 39, fig. 1a, b; Vaughan and Wells, 1943:pl. 9, fig. 5; Wells, 1956:fig. 266, 7a, b) from the Upper Jurassic strata of Germany. The new species differs in having smaller diameter corallites (2–3 mm rather than 3.5–4 mm).

DESCRIPTION. Phaceloid colony, with parallel or nearly parallel laterally free corallites spaced up to 5 mm apart. Corallites about 2–3 mm in diameter, up to 80 mm in length, and with walls up to 0.5 mm thick. Branching common. Exterior finely granulate with numerous very closely spaced ribs. About 12 primary septa, all joining to the strong styliform columella.

PRIMARY TYPE MATERIAL. Holotype, IGM 5139 (= LACMIP plastoholotype 8848).

TYPE LOCALITY. Locality CSUN 1220a.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220a, 1471?.

REMARKS. Only one corallum (holotype, IGM 5139) was found at locality 1220a. This corallum is 120 mm in diameter. At locality 1471, a lens 50 cm thick and 3 m in lateral extent was found to consist of abundant fragments of what appears to be *Stylosmilia ameliae* new species.

The Bateque Formation specimen of *Stylosmilia* extends the geologic range of this genus into the early Eocene and extends the geographic range into North America.

ETYMOLOGY. The new species is named after Amelia Z. Demetrion.

Family Actinacididae Vaughan and Wells, 1943

Genus *Actinacis* d'Orbigny, 1849

Actinacis? sp.

Figures 31, 32

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are common and occur as coralla as much as 30 cm in length and 15 cm in height. In side views of the Bateque Formation specimens, this colonial coral is characterized by massive growth with an extensive and finely laminated coenosteum. The laminae are about 1 mm thick, undulatory, and superficially resemble stromatolites. The coenosteum has a beaded look. Along the dorsal surface of the colony are corallites up to 1.5 mm in diameter, possessing definite calicular margins, and are separated (on the average) by 1 mm of reticulated coenosteum. On unweathered surfaces, the corallites have raised rims and a projecting trabecular columella. There are 24 septa. They are short and their distal ends bifurcate. The septa extend into the spongy columella, which fills most of the corallite interior.

These Bateque Formation colonial corals have the extensive coenosteum and trabecular columella of actinacid corals. They seem to be an intermediate form between the actinacid *Dendraraea,* reported by Wells (1956) from the Jurassic and Cretaceous, Eurasia and South America, and the actinacid *Actinacis,* reported by Wells (1956) from the Middle Cretaceous through Oligocene, Eurasia, Africa, North America, South America, and the West Indies. Future work may show that the Bateque Formation specimens belong to a new genus of actinacids.

Family Poritidae
Gray, 1842

Genus *Goniopora*
Blainville, 1830

Goniopora sp., cf. *G. vaughani* Nomland, 1916

Figures 33–35

[*Goniopora vaughani* Nomland, 1916:68–69, pl. 3, figs. 18, 19.]

LOCAL OCCURRENCE. Locality CSUN 1471.

REMARKS. Specimens are common and each consists of a small mass on a cylindrical stalk with concentric growth layers very obvious on the ventral surface of the corallum. The specimens are badly weathered, and positive specific identification cannot be made. They resemble *Goniopora vaughani* Nomland, 1916, from Eocene strata north of Del Mar, San Diego County, southern California. The holotype is the only known specimen of this species, and it is badly weathered. It is an encrusting form that encompasses both sides of an oyster fragment.

Like the holotype of *G. vaughani,* the Bateque Formation specimens have crowded corallites about 3 mm in diameter with numerous (20–24) septa and a spongy columella that is projecting in some corallites. The septa in the Bateque Formation specimens do not appear to be fused as in *G. vaughani,* but the fusion characteristic in *G. vaughani* may be a function of deep weathering.

Family Faviidae
Gregory, 1900

Genus *Colpophyllia*
Milne-Edwards, 1848

Colpophyllia nicholasi **new species**

Figure 36

DIAGNOSIS. Meandroid colony, fairly deep valleys tend to be short and monocentric, collines moderately continuous to discontinuous.

COMPARISON. The new species has been compared with all the Paleogene species descriptions of *Colpophyllia,* a genus whose geologic range is Eocene to Recent (Wells, 1956). There are only two previously described Eocene species. *Colpophyllia reagani* Durham (1942:96, pl. 16, fig. 5; pl. 17, fig. 2) from the lower Eocene Crescent Formation, northwestern Washington, is the only other species of *Colpophyllia* from the Paleogene of the Pacific coast of North America. The new species differs in the following features: shorter and more circular valleys, more discontinuous collines, about 18–24 septa to the centimeter rather than 12–18, and septal faces not granulate.

The other Eocene species is *C. wellsi* (Durham *in* Clark and Durham, 1946:81, pl. 26, figs. 1, 4–6) from Eocene strata, Columbia. The new species differs in having many more septa per centimeter and shorter valleys.

Woodring (1957:21) included *Colpophyllia* sp. in a checklist of corals from the middle to upper Eocene Gatuncillo Formation in the Panama Canal Zone. He did not give any repository numbers nor did he figure or describe the specimen(s).

The new species somewhat resembles *Colpophyllia willoughbiensis* (Vaughan, 1919:422–423, pl. 104, figs. 2, 2a; pl. 105; Frost and Langenheim, 1974:248–251, pl. 88, figs. 1–6; pl. 89, figs. 1–7) from Oligocene strata, Chiapas, Mexico, as well as Antigua and Puerto Rico. The specimen illustrated by Frost and Langenheim (1974:pl. 89, fig. 2) is most similar to the Bateque Formation specimens. The Bateque Formation specimens differ from *C. willoughbiensis* in the following features: collines more discontinuous, collines tend to be more subcircular, and colline crests more rounded.

DESCRIPTION. Massive corallum, meandroid to submeandroid. Fairly long to short valleys, mostly subcircular, depressions about 2–4 mm deep. Some valleys tend to be monocentric. Collines moderately continuous and sinuous to discontinuous. Colline crests rounded to narrow, some with a deposit formed by fusion of septa. About 18–24 septa to the centimeter. Sides of collines slope from 45 degrees to near vertical. Columella deep in fossa, very small, trabecular, and can be plate-like between corallites. No paliform lobes observed.

PRIMARY TYPE MATERIAL. Holotype, IGM 5143 (= LACMIP plastoholotype 8849).

TYPE LOCALITY. Locality CSUN 1220a.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220a.

REMARKS. Specimens are rare and are as much as 14 cm in diameter and 3 cm thick.

ETYMOLOGY. The new species is named after Nicholas A. Demetrion.

Genus *Montastrea*
Blainville, 1830

Montastrea laurae
new species

Figures 37, 38

DIAGNOSIS. A *Montastrea* with 14 primary septa and with only slightly raised, widely spaced corallites (about 2 mm apart) joined by some prominent distant costae.

COMPARISON. *Montastrea* has very complicated taxonomic history and has been known by at least 13 synonyms (Wells, 1956). Two of the more commonly used names in old literature are *Orbicella* Dana and *Phyllocoenia* Milne-Edwards and Haime. Because the geologic range of *Montastrea* is Late Jurassic to Recent with cosmopolitan distribution (Wells, 1956), there are numerous species. This is a genus that needs to have its species reviewed in a monographic treatment.

We have endeavored to compare *M. laurae* new species with all Western Hemisphere Cretaceous through Eocene species and with many other Cretaceous and early Tertiary species from elsewhere in the world. The reader is referred to Felix (1891), Vaughan (1919), Wells (1933), and Frost and Langenheim (1974) for descriptions and illustrations of many of the Western Hemisphere fossil species. Most of the species are not comparable to the new species because their corallites are more closely spaced than in *M. laurae* new species. Only one species possesses low-relief corallites of the same size and same spacing (with smooth coenosteum in between) as in the new species. It is *Montastrea imperatoris* (Vaughan, 1919:378, pl. 86, figs. 2–5) from the upper Oligocene Emperador Limestone, Panama Canal Zone, Panama. The new species differs in the following features: about 14 primary septa rather than 6, 14 secondary septa rather than 6, no tertiary septa, slightly larger corallites, and no tendency for corallites to project several millimeters upward.

The only other Eocene species of *Montastrea* from the Western Hemisphere is *M. antilliana* Wells (1945:9, pl. 2, fig. 14; Frost and Langenheim, 1974: 261–262, pl. 94, figs. 3–5) from middle Eocene strata in Chiapas, Mexico, and Barbados. Its corallites are smaller and more closely spaced than those of the new species.

DESCRIPTION. Colonial, plocoid, massive, corallites circular in transverse section, 3–4 mm in diameter and about 2–3 mm apart (measured from wall to wall). Corallite wall distinct and slightly raised. Septothecate. Fourteen primary septa and 14 secondary septa. Primary septa reach the columella; secondary septa usually do not. Corallites separated by extensive and smooth coenosteum but joined by some prominent distant costae (1–2 mm in length), which correspond to the primary septa. Some secondary septa project a short distance. Spongy trabecular columella, formed by fusion of inner edges of the primary septa.

PRIMARY TYPE MATERIAL. Holotype, IGM 5144 (= LACMIP plastoholotype 8850); locality CSUN 1220a.

TYPE LOCALITY. Locality CSUN 1220a.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220a, 1220b.

REMARKS. Specimens are common, but not are large-boulder size and could not be collected. One specimen at locality 1220b, for example, measures 1 m in diameter.

The new species is the only early Eocene occurrence of *Montastrea,* and it is the first known occurrence of this genus from the Pacific coast of North America.

ETYMOLOGY. The new species is named after Laura C. Demetrion.

Family Mussidae Ortamnn, 1890

Genus *Antillia*
Duncan, 1863

Antillia batequensis
new species

Figures 39–42

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Figures 21–32. Bateque Formation octocorals and scleractinian corals. **Figs. 21–25.** Octocorals. **21, 22.** *Heliopora*? sp., hypotype, IGM 5132, loc. CSUN 1471. **21.** Lateral view of entire colony, ×0.8, height 60 mm, width 65 mm. **22.** Part of lateral surface along upper right side of colony, ×4.25, width of field 9 mm. **23–25.** *Parisis batequensis* new species, loc. CSUN 1220b. **23.** Lateral view of internode stem, ×1.7, height 24 mm, diameter 6 mm, holotype, IGM 5133. **24.** Lateral view of internode stem, ×2.4, 9.5 mm, maximum diameter 6 mm, paratype, IGM 5134. **25.** Dorsal view of internode stem, ×3.8, diameter 5 mm, paratype, IGM 5135. **Figs. 26–32.** Scleractinian corals. **26.** *Astrocoenia dilloni* Durham, 1942, dorsal view of part of colony, ×2.4, width of field 21 mm, hypotype, IGM 5136, loc. CSUN 1220b. **27.** *Stylophora chaneyi* Durham, 1942, dorsal view of part of colony, ×10, width of field 5 mm, hypotype, IGM 5137, loc. CSUN 1220b. **28.** *Heterocoenia*? sp., lateral view of part of colony, ×2, width of field 20 mm, hypotype, IGM 5138, loc. CSUN 1220a. **29, 30.** *Stylosmilia ameliae* new species, holotype, IGM 5139, loc. CSUN 1220a. **29.** Dorsal view of part of colony, ×1.9, width of field 30 mm. **30.** Lateral view of part of colony, ×1, width of field 64 mm. **31, 32.** *Actinacis*? sp., hypotype, IGM 5140, loc. CSUN 1220b. **31.** Side view of part of colony, ×1, width of field 68 mm. **32.** Dorsal view of upper left center part of colony shown in previous illustration, ×6.4, width of field 10 mm.


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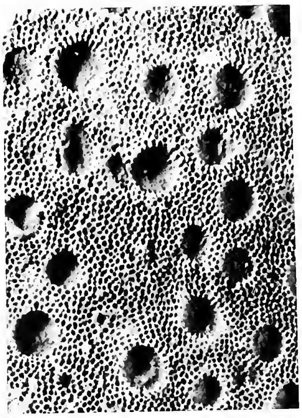
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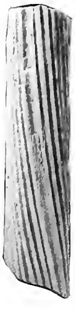
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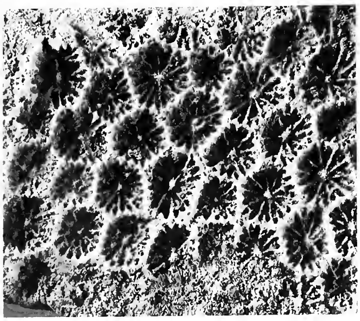
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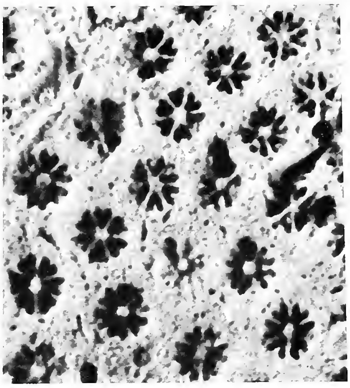
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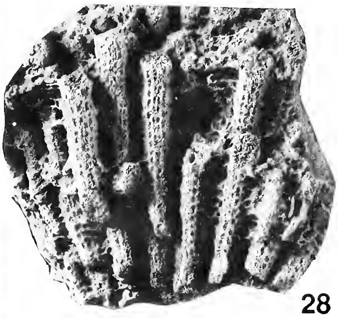
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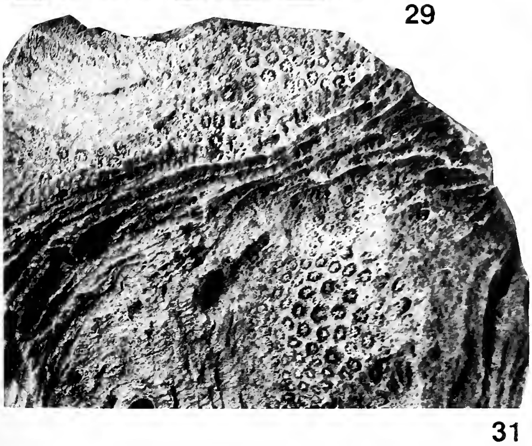
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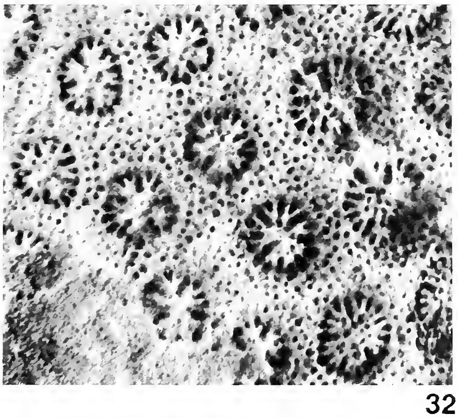
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DIAGNOSIS. A cylindrical-shaped *Antillia* with a flat, wide base.

COMPARISON. The new species has been compared with all the species descriptions of *Antillia,* a genus whose geologic range is Eocene to Miocene (Wells, 1956). There are only two other Eocene species. One is *A. clarki* Durham (*in* Clark and Durham, 1946:74, pl. 25, figs. 4, 6, 7; Frost and Langenheim, 1974:293–294, pl. 113, figs. 1–6, 13–15) from apparently middle Eocene strata in Colombia and lower upper Eocene strata in Chiapas, Mexico (Frost and Langenheim, 1974). The new species differs in having taller sides and a flat base rather than a rounded base.

The other Eocene species is *Antillia hadleyi* (Wells, 1934:153–154, pl. 2, figs. 3, 4) from upper? Eocene strata in Cuba. Woodring (1957:21) also reported *A.* cf. *A. hadleyi* from the middle to upper Eocene Gatuncillo Formation in the Panama Canal Zone. The new species differs in having an epitheca and a cylindrical shape rather than a conical shape.

Nearly all of the younger Tertiary species of *Antillia* are not comparable to the new species because they have a corallum with a rounded or pointed base. Only three specie have a flat base. One is *A. ponderosa* (Milne-Edwards and Haime, 1857–1860) from Miocene strata in the Dominican Republic, West Indies. Duncan (1863:433, 441–442, pl. 161, figs. 6a, b) also discussed this species. The second species is *A. plana* Duncan (1864a:300, pl. 18, fig. 5; 1880:84, pl. 23, fig. 5) from Miocene strata in western India. The third species is *A. granti* (Archiac and Haime, 1853:191, pl. 12, figs. 5a, b), also from Miocene strata in western India. The new species, however, differs from these three Miocene species in having a tall cylindrical shape rather than a short, wide discoidal shape.

Although the corallum of *A. dentata* Duncan (1864b:29–30, pl. 3, fig. 2a–c; Wells, 1956:fig. 318 4a–b) from Miocene strata in the Dominican Republic, West Indies, has a pointed base, it should be mentioned that it does resemble the new species in terms of the tall straight sides of the corallum.

DESCRIPTION. Solitary, cupolate, cylindrical (the walls approach straight-sided), up to 34 mm in height and 30 mm in diameter. Shallow calyx, trabecular columella, 24 primary septa, and 48 secondary septa. Septa thickest at periphery and thinning toward center of calyx. Very thin membraniform epitheca extending only 80–90 percent of the way to the top of the corallite where granulate costae are exposed. Wide, flat base (can be depressed) with a small, pointed apex in center.

PRIMARY TYPE MATERIAL. Holotype, IGM 5145 (= LACMIP plastoholotype 8851); paratypes, IGM 5146–5147 = (LACMIP plastoparatypes 8852–8853); all from locality CSUN 1291a.

TYPE LOCALITY. Locality CSUN 1291a.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, to San Diego County, southern California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1291a.

REMARKS. A single scar of where a corallite base was once attached was found at locality 1220b. Specimens are uncommon at locality 1291a, where they range in height from 20 to 34 mm. This species can be very short or quite tall in the mature stage. Most have a flat base with a central apex, but in one specimen (paratype, IGM 5147) the apex seems to have encrusted an echinoid spine.

Four specimens of the new species were found in the collections of the middle Eocene Ardath Shale (locality SDNHM 3296) in San Diego, southern California. Three are very short (about 10 mm in height and 25 m in diameter), but one is fairly tall (23 mm in height and 29 mm in diameter).

Antillia batequensis new species extends the geographic distribution of this genus into the Pacific coast region of North America. The new species is probably the earliest representative of the genus.

It is pertinent to note, as did Duncan (1864b:28, 1865:186), the remarkable similarity between the predominantly Miocene mussid *Antillia* and the

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Figures 33–52. Bateque Formation scleractinian corals, bryozoans, and polychaete worm. **Figs. 33–48.** Scleractinian corals. **33–35.** *Goniopora* sp., cf. *C. vaughani* Nomland, 1916, loc. CSUN 1471. **33, 34.** Hypotype, IGM 5141. **33.** Lateral view of entire colony, ×1.4, height 25 mm, maximum diameter 31 mm. **34.** Part of lateral surface at center of colony, ×3.1, width of field 15 mm. **35.** Ventral surface, ×1.1, maximum diameter 38 mm, hypotype, IGM 5142. **36.** *Colpophyllia nicholasi* new species, dorsal view of part of colony, ×1.4, width of field 40 mm, holotype, IGM 5143, loc. CSUN 1220a. **37, 38.** *Montastrea laurae* new species, holotype, IGM 5144, loc. CSUN 1220a. **37.** Dorsal view of part of colony, ×2.6, width of field 27 mm. **38.** Lateral view, ×1.3. **39–42.** *Antillia batequensis* new species, loc. CSUN 1291a. **39.** Dorsal view, ×1, diameter 31 mm, holotype, IGM 5145. **40.** Lateral view, ×0.9, height 36 mm, width 30 mm, paratype, IGM 5146. **41, 42.** Paratype, IGM 5147. **41.** Lateral view, ×1.1, height 25 mm, diameter 29 mm. **42.** Ventral view, ×1. **43, 44.** *Stephanocyathus*? sp., hypotype, IGM 5148, loc. CSUN 1220b. **43.** Dorsal view, ×1, diameter 28 mm. **44.** Lateral view, ×1.5, height 12 mm. **45, 46.** *Turbinolia dickersoni* Nomland, 1916, ×5.2, hypotype, IGM 5149, loc. CSUN 1220b. **45.** Dorsal view, diameter 2.8 mm. **46.** Lateral view, height 7 mm. **47, 48.** *Placotrochus*? sp., ×1.4, hypotype, IGM 5150, loc. CSUN 1220b. **47.** Lateral view, height 16 mm, diameter 27 mm. **48.** Ventral view. **Figs. 49, 50.** Polychaete worm. **49.** *Stomatopora* sp., dorsal view, ×4.3, width of field 13 mm, hypotype, IGM 5151, loc. CSUN 1220b. **50.** *Cellaria* sp., lateral view, ×4.6, height 12 mm, hypotype, IGM 5152, loc. CSUN 1220b. **Figs. 51, 52.** *Serpula batequensis* new species. **51.** Lateral view of part of colony, ×3.3, maximum diameter 3 mm, holotype, IGM 5153, loc. CSUN 1470. **52.** Dorsal view, ×1.8, maximum diameter 3 mm, paratype, IGM 5154, loc. CSUN 1470.

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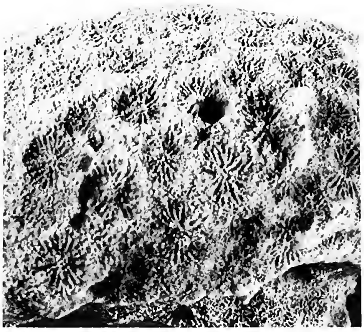

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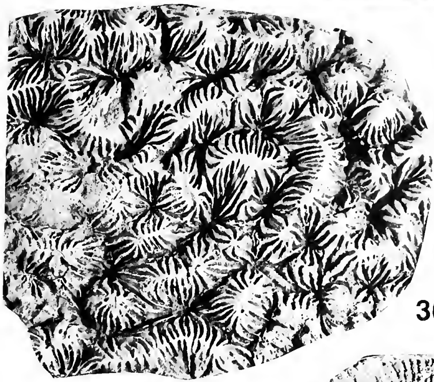

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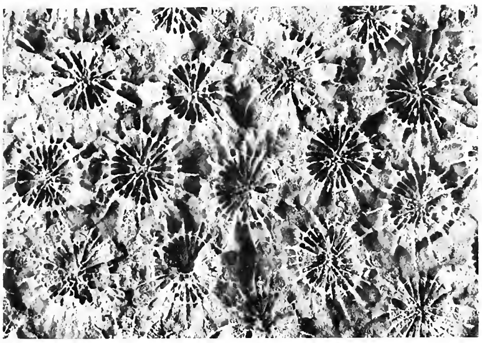

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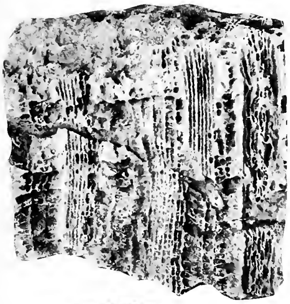

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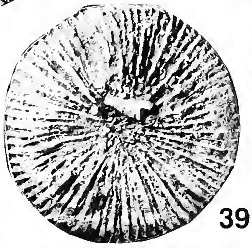

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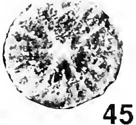

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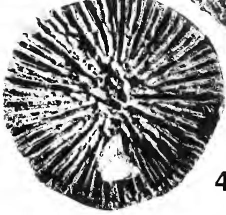

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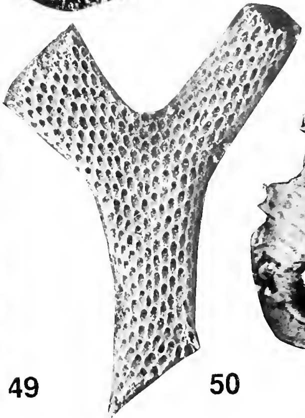

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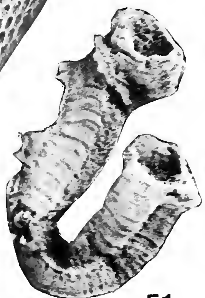

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Mesozoic montlivaltiid *Montlivaltia.* Duncan (1864b:21), in fact, listed *Montlivaltia* as a subgenus of *Antillia.* Prior to Duncan's (1864b) naming of *Antillia,* species of this genus were assigned by earlier workers to *Montlivaltia.* The only distinguishing character is that *Antillia* has a spongy columella, whereas *Montlivaltia* either has no columella or a rudimentary one (Milne-Edwards and Haime, 1850–1854:xxv, 133, pl. 26, figs. 5, 5a, b; Wells, 1956). With future study, it may be found that these two genera are part of an evolutionary sequence.

ETYMOLOGY. The new species is named after the Bateque Formation.

Family Caryophyllidae Gray, 1847

Genus *Stephanocyathus* Seguenza, 1864

Stephanocyathus? sp.

Figures 43, 44

LOCAL OCCURRENCE. Localities CSUN 1220b, 1220c, 1291.

REMARKS. Specimens are common at each locality. Preservation of the free, solitary corallites is as internal molds, and no calices are exposed. Specimens, which are as much as 28 mm in diameter, are patellate and show a trabecular columella. They resemble the genus *Stephanocyathus,* which has a geologic range of Eocene to Recent (Wells, 1956). Better preservation is needed to confirm the generic identification.

Genus *Turbinolia* Lamarck, 1816

Turbinolia dickersoni Nomland, 1916

Figures 45, 46

Turbinolia dickersoni Nomland, 1916:61, pl. 3, figs. 5–8.

MOLLUSCAN STAGE RANGE. Upper Paleocene through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found.

Family Flabellidae Bourne, 1905

Genus *Placotrochus* Milne-Edwards, 1848

Placotrochus? sp.

Figures 47, 48

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found. Preservation of the free, solitary corallite is good except for the calice area, which is mostly covered by well-indurated matrix. The specimen, which is 27 mm in diameter, is compressed flabellate and shows a thin lamellar columella (only exposed at the base of the corallite on the Bateque specimen). The specimen resembles *Placotrochus,* which has a geologic range of Eocene to Recent (Wells, 1956). Better preservation is needed to confirm the generic identification.

Phylum Bryozoa

Order Cyclostomata

Family Diastoporidae Gregory, 1899

Genus *Stomatopora* Bronn, 1825

Stomatopora sp.

Figure 49

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Only a single specimen was found, and it encrusts a valve of the bivalve *Pycnodonte* (*Pegma*) *bajaensis.* The adnate zooarium of this bryozoan is composed of irregularly branching subtubular lines with slightly raised zooecia. The zooarium very closely resembles *Stomatopora granulata* (Milne-Edwards, 1838:205, pl. 16, figs. 3, 3a; Canu, 1909:34–35, pl. 12, fig. 15; Osburn, 1953:619–620, pl. 65, figs. 1, 2) whose geologic range is Early Cretaceous (Gregory, 1896:47; Canu, 1909) through Recent (Osburn, 1953) with fossil occurrences in Europe, Russian and Australia (Canu, 1909). Today, it is widely distributed in the Northern Hemisphere, including southern California (Osburn, 1953).

The Bateque Formation specimen is the first known record of the genus *Stomatopora* in the Paleogene of North America.

Order Cheilostomata

Family Cellaridae Hincks, 1880

Genus *Cellaria* Solander, 1786

Cellaria sp.

Figure 50

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are locally very abundant and constitute the major lithologic component of the rock. They are unworn, hollow, straight, and branching cylindrical segments of zooaria that had chitinous joints. They resemble the posterior view (but not the anterior view) of *Cellaria bifaciata*

Canu and Bassler (1920:274, pl. 40, figs. 14–17) from the upper Eocene Castle Hayne Limestone, North Carolina and South Carolina.

The geologic range of *Cellaria* is Eocene to Recent (Bassler, 1953:177). The Bateque Formation specimens represent the first record of this genus from the Paleogene of North America.

Phylum Annelida

Order Sedentaria

Family Serpulidae Burmeister, 1837

Genus *Serpula* Linné, 1758

***Serpula batequensis* new species**

Figures 51, 52

DIAGNOSIS. Entirely encrusting, calcareous, solitary or colonial, planispiral juvenile tube, irregularly coiled adult tube, tendency for flange to develop along one edge of mature tube. One to three (rarely) longitudinal ribs along length of the tube. Aperture rimmed by thick deposit.

COMPARISON. The geologic range of *Serpula* is Silurian to Recent (Howell, 1962). A review of available literature revealed that the Tertiary fossil record of *Serpula* and other serpulid worm tubes is very poorly known, especially for the Pacific coast of North America. *Serpula batequenesis* new species is the first reported species of this genus from either the Paleocene or Eocene of the Pacific coast of North America. The only other Paleogene species from this area is *Serpula* sp. Clark and Arnold (1923:175, pl. 39, fig. 4), based on a fragmentary specimen from upper Oligocene rocks, Vancouver Island, British Columbia. The new species differs in having much smaller tubes that are not parallel to one another.

The new species most resembles *Serpula (Tetraserpula) quinquangularis* Goldfuss (1831:230, pl. 68, fig. 8b) from Jurassic strata of Germany. Parsch (1956:224, pl. 19, fig. 9; pl. 20, fig. 13; pl. 21, fig. 25) also illustrated this species. The new species differs in the following features: juvenile tube more planispiral, mature tube does not taper, and longitudinal ribs not as prominent.

DESCRIPTION. Encrusting, calcareous tube, solitary or colonial. Juvenile tube of about two tightly coiled planispiral whorls. Mature tube irregularly coiled but usually in loops, tube flat on encrusting side, convex on upper side. Tube always adhering to substrate, tendency for flange to develop along outside edge of the loops. One to three (rare) longitudinal ribs along length of tube. Longitudinal ribs somewhat noded at intersections with prominent growth lines. Tube subrectangular in cross section. Aperture rimmed by thick calcareous deposits. Tubes up to 3 mm in diameter.

PRIMARY TYPE MATERIAL. Holotype, IGM 5153 (= LACMIP plastoholotype 8854), locality CSUN 1470; paratype, IGM 5154 (= LACMIP plastoparatype 8855), locality CSUN 1291a

TYPE LOCALITY. Locality CSUN 1470.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1291a, 1470, 1471.

REMARKS. The holotype, IGM 5153, is one specimen in a colony of about 30 intergrown specimens that measures 50 mm in diameter. One solitary tube (paratype, IGM 5154) (Fig. 52) encrusts a specimen of *Antillia batequensis* new species at locality 1291a.

ETYMOLOGY. The new species is named after the Bateque Formation.

Phylum Mollusca

Class Scaphopoda

Order Dentalioida

Family Dentaliidae Gray, 1834

Genus *Dentalium* Linné, 1758

Dentalium stentor Anderson and Hanna, 1925

Figure 53

Dentalium stentor Anderson and Hanna, 1925:145, pl. 13, fig. 17.

MOLLUSCAN STAGE RANGE. "Domengine" through "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southern San Joaquin Valley, California.

LOCAL OCCURRENCE. Locality CSUN 1291c.

REMARKS. A single, fairly large (45 mm in height) specimen was found. Sculpture consists of longitudinal ribs uniform in size, except near the tapered end where some of the longitudinal ribs alternate with finer ribs. According to Anderson and Hanna (1925), uniform rib size is the norm for this species.

Class Gastropoda

Order Archaeogastropoda

Family Turbinidae Rafinesque, 1815

Genus *Arene* H. and A. Adams, 1854

Arene mcleani Squires, 1988b

Figure 54

Arene mcleani Squires, 1988b:9–10, figs. 9–11.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through northern Lockwood Valley, Los Angeles County, southern California.

LOCAL OCCURRENCE. Locality CSUN 1291a.

REMARKS. Specimens are uncommon, and only one is well preserved. This specimen differs slightly from the published photographs of this species in that it shows one extra costate spiral rib on the shoulder of the body whorl. This variation, which is also present in at least one topotype specimen of *A. mcleani*, corresponds to the case where the rare third spiral rib posterior to the bicostate spiral ribs has become costate itself. The presence of this extra spiral rib was noted in the original description of this species.

Family Neritidae Rafinesque, 1815

Genus *Velates* Montfort, 1810

Velates perversus (Gmelin, 1791)

Figures 55, 56

Nerita perversa Gmelin, 1791:3686.

MOLLUSCAN STAGE RANGE. In Europe and India, Thanetian (upper Paleocene) up to Bartonian (upper middle Eocene). On the Pacific coast of North America, "Capay" and possibly "Domengine."

GEOGRAPHIC DISTRIBUTION. Pakistan, India, Myanmar, Tibet, Middle East, northern Africa, western Europe, Florida, Panama?, and Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1291a, 1470, 1471.

REMARKS. Specimens are abundant, especially at locality 1220b. In one slab of rock that measures 90 mm in diameter, 17 specimens were found. All specimens show fair preservation. At locality 1220b they form a growth series ranging from 4 to 90 mm in height, and at locality 1470 they form a growth series ranging from 6 to 40 mm in height (i.e., height is parallel to axis of coiling).

As discussed in Woods and Saul (1986:648), the age of the only reported "Domengine Stage" beds that *V. perversus* has been found in is not well known. As suggested by them, these beds, which are in Big Tar Canyon, Kings County, central California, may actually belong to the "Capay Stage."

The species was first noted in the Bateque Formation by Squires and Demetrion (1990a). Previously, *V. perversus* had been reported (Beal, 1948: 50) from the Tepetate Formation farther south in Baja California Sur, Mexico.

Velates batequensis Squires and Demetrion, 1990a

Figure 57

Velates batequensis Squires and Demetrion, 1990a: 99–100, figs. 1–5.

PRIMARY TYPE MATERIAL. Holotype, IGM 5051 (= LACMIP plastoholotype 8052); paratypes, IGM 5052–5054 (= LACMIP plastoparatypes 8053–8055); all from locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are abundant and well preserved. They form a growth series ranging from 4 to 48 mm in height.

Order Mesogastropoda

Family Turritellidae Woodward, 1851

Genus *Turritella* Lamarck, 1799

Turritella andersoni s.s. Dickerson, 1916

Figure 58

Turritella andersoni Dickerson, 1916:501–502, pl. 42, fig. 9a, b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Localities CSUN 1291a, 1291b.

REMARKS. Specimens are rare at locality 1291a and common at 1291b. At both localities, most specimens are upper spire fragments and show the diagnostic whorl profile that is broadly concave medially between a pair of broadly spaced primary spiral ribs. The anterior rib is stronger. The posterior rib has small nodes. There are secondary ribs between the two primaries, and there is a secondary rib between the posterior primary and the suture.

At locality 1291b, there are also a few specimens that are intermediate between *T. andersoni* s.s. and *T. andersoni lawsoni*. This locality must be at or very near the boundary between the "Capay Stage" (to which *T. andersoni* s.s. is confined) and the "Domengine Stage" (to which *T. andersoni lawsoni* is confined).

Turritella andersoni lawsoni Dickerson, 1916

Figure 59

Turritella lawsoni Dickerson, 1916:502, pl. 42, fig. 10a, b.

MOLLUSCAN STAGE RANGE. "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Locality CSUN 1220c (uppermost part), 1220d, 1291c.

REMARKS. Specimens are abundant at all localities. At 1220c and 1220d, they form several beds about 15 cm thick that consist of closely packed large individuals showing bimodal preferred orientation. At both localities, many of the specimens are internal molds. Specimens at locality 1291c are the best preserved.

Most specimens are upper spire fragments, but a few are almost complete individuals. All show a whorl profile that has a strong anterior primary spiral rib with many secondary and tertiary spiral ribs posteriorly. The more complete individuals show the gradual weakening of sculpture with increasing whorl size and the incipient development of overhanging of the whorls with increasing whorl size. Both features are diagnostic of this subspecies.

Turritella sp., ? *T. merriami* Dickerson, 1913

Figure 60

[*Turritella merriami* Dickerson, 1913:284–285, pl. 13, fig. 6a–6c.]

LOCAL OCCURRENCE. Locality CSUN 1291b.

REMARKS. Specimens are rare, and they are well-preserved, small fragments of juveniles (15 mm in height or less). They show a posterior tabulation that gradually develops with increasing whorl size.

Two known Paleogene subspecies of *Turritella* from the Pacific coast of North America have a posterior tabulation in the juvenile stage. These are *T. merriami* s.s. and *T. merriami brevitabulata* Merriam and Turner (1937:105, pl. 6, figs. 1, 2). They are virtually indistinguishable as juveniles. In the adult stage, the posterior tabulation develops into a flange on *T. merriami,* whereas in *T. merriami brevitabulata* it does not. The juvenile Bateque Formation specimens are questionably assigned to *T. merriami* because, with increasing whorl size, there is a tendency for the posterior tabulation to develop more strongly.

Turritella merriami is known from the Whitaker Peak area, Los Angeles County, to southwestern Oregon (Squires, 1987). If the Bateque Formation specimens are *T. merriami,* they would extend the geographic distribution of this species southward into the eastern Laguna San Ignacio area, Baja California Sur, Mexico.

Turritella buwaldana Dickerson, 1916

Figure 61

Turritella buwaldana Dickerson, 1916:500–501, pl. 42, fig. 7a, b.

MOLLUSCAN STAGE RANGE. Upper "Meganos?," "Capay" through "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Localities CSUN 1220b?, 1291b.

REMARKS. Specimens are rare. They show the diagnostic flat-sided whorls with three primary spiral ribs (minutely noded) and two slightly weaker posterior spiral ribs (minutely noded). Tertiary ribs are in the interspaces.

Turritella uvasana subsp., ? *T. uvasana applinae* Hanna, 1927

Figure 62

[*Turritella applini* Hanna, 1927:307, pl. 49, figs. 1, 4.]

LOCAL OCCURRENCE. Locality CSUN 1291c.

REMARKS. A single specimen was found. Its fragmentary condition prevents positive identification as to subspecies. *Turritella uvasana applinae* is known from San Diego to the Pine Mountain area, southern California (Squires, 1987). If the Bateque Formation specimen is *T. uvasana applinae,* it would extend the geographic distribution of this species southward into the eastern San Ignacio area, Baja California Sur, Mexico.

Turritella uvasana subsp.

Figure 63

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Several small specimens were found at each locality. They have convex whorls and primary spirals of nearly uniform strength. They probably are apical parts of once larger specimens. Preservation is not good enough to allow subspecific identification.

Family Siliquariidae Anton, 1838

Genus *Tenagodus* Guettard, 1770

Tenagodus bajaensis Squires, 1990a

Figure 64

Tenagodus bajaensis Squires, 1990a:298, figs. 6–8.

PRIMARY TYPE MATERIAL. Holotype, IGM 5102 (= LACMIP plastoholotype 8089); paratype, IGM 5103 (= LACMIP plastoparatype 8090); all from locality CSUN 1291a.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1291a.

REMARKS. Three solitary specimens were found. They show the longitudinal slit that is diagnostic of this genus. The Bateque Formation specimens represent the only known representatives of the genus *Tenagodus* from the Pacific coast of North America (Squires, 1990a).

Family Campanilidae Douvillé, 1904

Genus *Campanile* Fischer, 1884

Campanile sp.

Figure 65

LOCAL OCCURRENCE. Locality CSUN 1220a.

REMARKS. A single poorly preserved specimen was found. Although it is 190 mm in height, it is only the upper spire part of the shell. Shell material is missing from the apertural side, and the abapertural side has been damaged by boring organisms (sponges?). Widely spaced nodes are present just anterior to the suture.

There are only two other reported species of *Campanile* from the Eocene of the Pacific coast of North America. They are *C. dilloni* (Hanna and Hertlein, 1949:392–394, pl. 77, figs. 2, 4) and *Campanile* new species? Squires (1987:31–32, figs. 32, 33) from lower Eocene strata of south-central and southern California. Poor preservation prevents comparison of the Bateque Formation specimen with these two species.

Family Epitoniidae Lamarck, 1822

Genus *Acrilla* H. Adams, 1860

Acrilla new species?

Figure 66

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found. Other than having its abapertural side buried in matrix and its apertural side slightly worn in places, the shell is generally well preserved. There are seven to eight spiral ribs on each whorl, and they are equal in prominence to the axial ribs. Anterior to the prominent basal keel are about five to six weak spiral ribs that become weaker posteriorly.

This species does not match any known Paleogene fossil species from the Pacific coast of North America. It most closely resembles *Acrilla procerus* Zinsmeister (1983:1291, fig. 2G, H) from the upper Paleocene Santa Susana Formation in Simi Valley, Ventura County, southern California, and from the upper Paleocene Sepultura Formation in northern Baja California (Paredes-Mejia, 1989:185–186, pl. 3, figs. 25, 26). The Bateque specimen differs in the

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Figures 53–80. Bateque Formation scaphopod and gastropods. **Fig. 53.** Scaphopod. *Dentalium stentor* Anderson and Hanna, 1925, lateral view, ×1.7, length 48 mm, hypotype, IGM 5155, loc. CSUN 1291c. **Figs. 54–80.** Gastropods. **54.** *Arene mcleani* Squires, 1988, apertural view, ×4.5, height 6.5 mm, width 7 mm, hypotype, IGM 5156, loc. CSUN 1291a. **55, 56.** *Velates perversus* (Gmelin, 1791). **55.** Abapertural view showing spiral surface, ×0.7, height 58 mm, hypotype, IGM 5157, loc. CSUN 1291a. **56.** Apertural view, ×1.8, outer lip missing, height 19 mm, hypotype, IGM 5158, loc. CSUN 1220b. **57.** *Velates batequensis* Squires and Demetrion, 1990a, abapertural view, ×1.7, height 14 mm, width 14.5 mm, holotype, IGM 5051, loc. CSUN 1220b. **58.** *Turritella andersoni* s.s. Dickerson, 1916, apertural view, ×2.5, height 17 mm, width 6 mm, hypotype, IGM 5159, loc. CSUN 1291b. **59.** *Turritella andersoni lawsoni* Dickerson, 1916, abapertural view, ×1.3, height 57 mm, width 10 mm, hypotype, IGM 5160, loc. CSUN 1291c. **60.** *Turritella* sp., ? *T. merriami* Dickerson, 1913, apertural view, ×3.1, height 12 mm, width 5 mm, hypotype, IGM 5161, loc. CSUN 1291b. **61.** *Turritella buwaldana* Dickerson, 1916, apertural view, ×3.9, height 9 mm, width 4.5 mm, hypotype, IGM 5162, loc. CSUN 1291b. **62.** *Turritella uvasana* subsp., ? *T. uvasana applinae* Hanna, 1927, abapertural view, ×3.3, height 9 mm, width 7 mm, hypotype, IGM 5163, loc. CSUN 1291c. **63.** *Turritella uvasana* subsp., apertural view, ×5, height 10 mm, width 4 mm, hypotype, IGM 5164, loc. CSUN 1220b. **64.** *Tenagodus bajaensis* Squires, 1990a, lateral view, ×0.9, height 57 mm, width 27 mm, paratype, IGM 5103, loc. CSUN 1291a. **65.** *Campanile* sp., abapertural view, ×0.2, height 190 mm, width 110 mm, hypotype, IGM 5165, loc. CSUN 1220a. **66.** *Acrilla* n. sp.?, apertural view, ×6.5, height 6.2 mm, width 2.5 mm, hypotype, IGM 5166, loc. CSUN 1220b. **67.** *Epitonium* sp., part of spire, ×5.6, height 5 mm, width 4 mm, hypotype, IGM 5167, loc. CSUN 1220b. **68.** *Xenophora stocki* Dickerson, 1916, lateral view, ×2.8, height 8 mm, width 15 mm, hypotype, IGM 5168, loc. CSUN 1220b. **69.** *Ectinochilus* sp., cf. *E.* (*Macilentos*) *macilentus* (White, 1889), abapertural view, ×2, height 24 mm, width 11 mm, hypotype, IGM 5169, loc. CSUN 1293. **70, 71.** *Ectinochilus* (*Cowlitzia*) sp., aff. *E.* (*C.*) *canalifera* (Gabb, 1864), ×1.5, height 24 mm, width 12 mm, hypotype, IGM 5170, loc. CSUN 1293. **70.** Abapertural view. **71.** Outer lip view. **72.** *Platyoptera pacifica* Squires and Demetrion, 1990a, latex peel of external mold, abapertural view, ×1.1, height 40 mm, width (includes winged outer lip) 33 mm, holotype, IGM 5055, loc. CSUN 1220b. **73.** *Paraseraphs erraticus* (Cooper, 1894), apertural view, anterior area missing, ×1.1, height 36 mm, width 12 mm, hypotype, IGM 5171, loc. CSUN 1220b. **74–76.** *Bernaya* (*Protocypraea*) *grovesi* new species, ×2.1, height 16.5 mm, width 12 mm, holotype, IGM 5172, loc. CSUN 1220b. **74.** Ventral view. **75.** Right lateral view. **76.** Dorsal view, ×2, height 17 mm, width 10 mm, paratype, IGM 5173. **77–79.** *Eocypraea*? sp., ×3.1, height 9.3 mm, width 6.5 mm, hypotype, IGM 5174, loc. CSUN 1220b. **77.** Ventral view. **78.** Right lateral view. **79.** Dorsal view. **80.** *Cypraedia* sp., apertural view, ×1.8, height 20 mm, width 14 mm, hypotype, IGM 5057, loc. CSUN 1220b.


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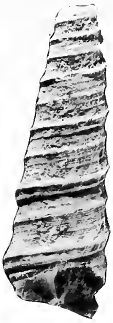
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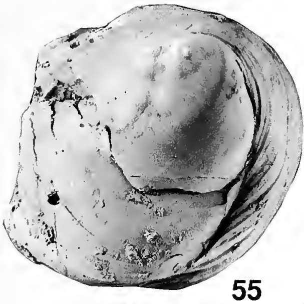
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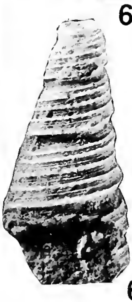
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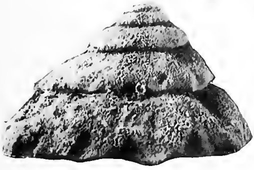
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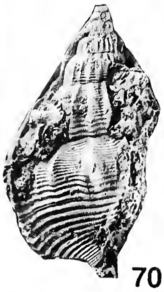
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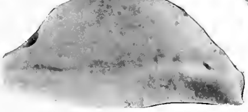
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following features: less elongate, less prominent spiral ribs, and five to six rather than nine spiral ribs anterior to the basal keel. It may be a new species.

Genus *Epitonium*
Röding, 1798

Epitonium sp.
Figure 67

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found. The sculpture is well preserved and shows approximately 20 well-developed lamellar costae (= varices of some authors) and about four to five fairly weak spiral ribs with about three tertiary spiral ribs in the interspaces. Spiral ribbing is obsolete on the whorl posterior. Because the entire anterior portion of the shell is missing, the specimen cannot be assigned to a subgenus.

Family Xenophoridae
Philippi, 1853

Genus *Xenophora*
Fischer von Waldheim, 1807

Xenophora stocki
Dickerson, 1916
Figure 68

Xenophora stocki Dickerson, 1916:502–503, pl. 37, fig. 4a, b.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through northern Lockwood Valley, Ventura County, southern California.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are rare, are internal molds, and range in height from 9 to 45 mm.

Family Strombidae
Rafinesque, 1815

Genus *Ectinochilus*
Cossmann, 1889

Subgenus *Macilentos*
Clark and Palmer, 1923

Ectinochilus sp.,
cf. *E.* (*Macilentos*) *macilentus*
(White, 1889)
Figure 69

[*Rimella macilenta* White, 1889:19, pl. 3, figs. 10–12.]

LOCAL OCCURRENCE. Localities CSUN 1220b, 1293.

REMARKS. Specimens are rare and poorly preserved. *Ectinochilus* (*M.*) *macilentus* is known from San Diego, southern California, to central California (Squires, 1988b). If the Bateque specimens are *E.* (*M.*) *macilentus,* they would extend the geographic distribution of this species southward into Baja California Sur, Mexico.

Subgenus *Cowlitzia*
Clark and Palmer, 1923

Ectinochilus (*Cowlitzia*) sp.,
aff. *E.* (*C.*) *canalifera*
(Gabb, 1864)
Figures 70, 71

[*Rostellaria canalifer* Gabb, 1864:123–124, pl. 29, fig. 228.]

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. Specimens are rare and show good preservation only on their abapertural sides. The specimens have affinity to *E.* (*C.*) *canalifera* known from "Tejon Stage" strata at San Diego, southern California, and the Tehachapi Mountains, Kern County, south-central California (Clark and Palmer, 1923; Hanna, 1927; Givens, 1974). The Bateque Formation specimens differ from *E.* (*C.*) *canalifera* in the following features: spiral ribs not as wide, spiral ribs not as prominent in area of nodes on body whorl, and spiral ribs more closely spaced in area of nodes on body whorl.

Genus *Platyoptera*
Conrad, 1854

Platyoptera pacifica
Squires and Demetrion, 1990a
Figure 72

Platyoptera pacifica Squires and Demetrion, 1990a: 100–102, figs. 2.6, 2.7.

PRIMARY TYPE MATERIAL. Holotype, IGM 5055 (= LACMIP plastoholotype 8056); paratype, IGM 5056 (= LACMIP plastoholotype 8057); all from locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220b, 1470?.

REMARKS. Specimens are uncommon and are internal molds. In one of these (Fig. 72), the associated external mold shows the complete abapertural view of the specimen, including the extended outer lip wing.

This species is the earliest record for the genus anywhere in the world and the first record of this genus from the Pacific coast of North America (Squires and Demetrion, 1990a).

Family Seraphsidae
Jung, 1974

Genus *Paraseraphs*
Jung, 1974

Paraseraphs erraticus
(Cooper, 1894)

Figure 73

Tornatina erratica Cooper, 1894:47, pl. 2, fig. 35.

MOLLUSCAN STAGE RANGE. "Capay" through "Transition."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are uncommon and are internal molds.

Family Cypraeidae Gray, 1824

Genus *Bernaya*
Jousseaume, 1884

Subgenus *Protocypraea*
Schilder, 1927

Bernaya* (*Protocypraea*) *grovesi
new species

Figures 74–76

DIAGNOSIS. Small shell for genus, prominent callus around shell margin, denticulation strong, outer lip with 16 teeth, inner lip with 12 teeth, small pit in spire area.

COMPARISON. Groves (1990) reviewed and illustrated all the North American species of *Bernaya* (*Protocypraea*), a subgenus whose geologic range is Early Cretaceous to Recent. All the previously known North American species are Late Cretaceous in age and are not comparable to the new species because they have much weaker denticulation.

No previously described Cenozoic species of *B.* (*Protocypraea*) are known from the Pacific coast of North America (Groves, 1990). Of the few species of the subgenus known from the Eocene of western Europe, the new species is most similar to *B. malandaini* (Chédeville, 1904:103–104, figs. 3, 3 bis; Cossmann and Pissarro, 1910–1913:pl. 33, fig. 162-22) from middle Eocene (lower Lutetian) strata of the Paris Basin, France. The new species differs from the Paris Basin species in the following features: smaller shell, callosity along margin much better developed, fossula area more separated from inner lip teeth, 17 outer lip teeth rather than 20–21, 12 inner lip teeth rather than about 18, and better development of pit in spire area.

DESCRIPTION. Small shell (17 mm in height), moderately pyriform, maximum diameter in center of shell, base flattened with a small concavity near anterior end. Spire covered, spire area coincident with a small pit. Aperture fairly sinuous, posterior canal curved left, anterior and posterior canals deep, denticulation strong with smooth interstices, outer lip with 16 teeth, inner lip with 12 teeth. Fossula smooth and concave. Outer lip callus prominent and associated with a dorsal ring. Inner lip callus present. Holotype height 17 mm, width 12 mm.

PRIMARY TYPE MATERIAL. Holotype, IGM 5172 (= LACMIP plastoholotype 8856); paratype, IGM 5173 (= LACMIP plastoparatype 8857); all from locality CSUN 1220b.

TYPE LOCALITY. Locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. locality CSUN 1220b.

REMARKS. Two specimens were found. Both are about the same size and are well preserved. The small pit in the spire area is accentuated by weathering.

The new species is the first record of *Bernaya* (*Protocypraea*) in the Cenozoic of the Pacific coast of North America.

ETYMOLOGY. The new species is named after Lindsey T. Groves.

Family Ovulidae Fleming, 1828

Genus *Eocypraea*
Cossmann, 1903

Eocypraea? sp.

Figures 77–79

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single juvenile? specimen (10 mm in height) was found.

Family Pediculariidae
H. and A. Adams, 1854

Genus *Cypraedia*
Swainson, 1840

Cypraedia sp.

Figure 80

Cypraedia sp. Squires and Demetrion, 1990a:102, figs. 2.8–2.10.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single internal mold represents the only record of this genus from the Pacific coast of North America (Squires and Demetrion, 1990a).

Family Naticidae
Forbes, 1838

Genus *Amauropsis*
Mörch *in* Rink, 1857

Amauropsis sp.

Figure 81

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are rare. The best specimen (Fig. 81) shows most of the features that Marincovich (1977) listed as diagnostic of the genus; namely, a distinctly channelled suture, slit-like umbilicus, and elongate proportions. No fine spiral sculpture, however, was seen, but its lack is probably due to poor preservation. The Bateque Formation specimens show variation in relative height of the spire. The figured specimen shows a relatively low-spired example.

The Bateque Formation specimens are the youngest occurrences of *Amauropsis* from the Pacific coast of North America. Previously, the only known Paleogene species of this genus in this area were *A. martinezensis* Dickerson (1914a:142, pl. 13, Fig. 4a, b; Marincovich, 1977:221–222, pl. 17, figs. 5–7, 9–10, not 8 *fide* Zinsmeister, 1983) and *A. meierensis* Zinsmeister (1983:1292–1293, fig. 2L, M) from upper Paleocene strata of California. Paredes-Mejia (1989) also reported *A. martinezensis* from Paleocene strata of northern Baja California.

More Bateque Formation specimens are needed to determine specific identification. It may be that it is a new species.

Genus *Gyrodes* Conrad, 1860

Gyrodes? sp.

Figure 82

LOCAL OCCURRENCE. Localities CSUN 1220b, 1291a, 1470.

REMARKS. Specimens are abundant and are internal molds. Many are large (up to 60 mm in height).

The preservation does not allow for positive generic or specific identification, but the specimens resemble *Gyrodes abyssinus* (Morton, 1834:49, pl. 13, fig. 13) known from Upper Cretaceous (Maastrichtian) strata of the Atlantic and Gulf Coastal Plains (Sohl, 1960:121). Like the Bateque Formation specimens, *G. abyssinus* is medium- to large-sized, has a globular body whorl with a moderately tabular shoulder, and has a wide umbilicus (see Sohl, 1960:pl. 17, figs. 26, 29, 30, 33).

The genus *Gyrodes* is predominantly of later Cretaceous age, but *G.* (*G.* ?) *robustus* Waring, 1917, is known from Paleocene (Selandian) strata of southern California (Popenoe et al., 1987).

Genus *Eocernina* Gardner and Bowles, 1934

Eocernina hannibali (Dickerson, 1914b)

Figure 83

Natica hannibali Dickerson, 1914b:119, pl. 12, fig. 5a, b.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through northwestern Washington.

LOCAL OCCURRENCE. Locality CSUN 1220b, 1291a.

REMARKS. Specimens are common. At locality 1291a, they represent a growth series from 20 to 55 mm in height. At locality 1220b, one of the specimens is very large (90 mm in height).

Genus *Pachycrommium* Woodring, 1928

Pachycrommium clarki (Stewart, 1927)

Figure 84

Amaurellina (*Euspirocrommium*) *clarki* Stewart, 1927:336–339, pl. 26, figs. 8, 9 [new name, in part, for *Amauropsis alveata* (Conrad, 1855), preoccupied and misidentified].

MOLLUSCAN STAGE RANGE. "Capay" through "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through northwestern Washington.

LOCAL OCCURRENCE. Localities CSUN 1229b, 1291a.

REMARKS. Specimens are uncommon. At locality 1220b, they represent a partial growth series from 13 to 45 mm in height.

Family Cassidae Swainson, 1832

Genus *Galeodea* Link, 1807

Galeodea sp.

Figure 85

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are rare and poorly preserved. There are either fragments of the shell or internal molds. All specimens are too fragmentary to allow identification as to species.

Family Bursidae Thiele, 1925

Genus *Olequahia* Stewart, 1927

Olequahia domenginica (Vokes, 1939)

Figure 86

Ranella domenginica Vokes, 1939:147–148, pl. 19, figs. 6, 20.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are rare and are internal molds.

Order Neogastropoda

Family Fasciolariide Gray, 1853

Genus *Clavilithes* Swainson, 1840

Clavilithes tabulatus (Dickerson, 1913)

Figure 87

Clavella tabulata Dickerson, 1913:283, pl. 12, fig. 7.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1291a, 1470.

REMARKS. Specimens are rare and are either partial specimens or internal molds.

Family Olividae Latreille, 1825

Genus *Olivella* Swainson, 1831

? *Olivella mathewsonii* Gabb, 1864

Figure 88

[*Olivella mathewsonii* Gabb, 1864:100, pl. 18, fig. 53.]

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are uncommon, are poorly preserved, and do not clearly show the anterior inner lip area that is necessary for positive identification. *Olivella mathewsonii* is known from Simi Valley, Los Angeles County, southern California, to northwestern Washington (Squires, 1988b). If the Bateque Formation specimens are O. *mathewsonii,* they would extend the geographic distribution of this species southward into Baja California Sur, Mexico.

Family Harpidae Bronn, 1849

Genus *Eocithara* P. Fischer, 1883

Eocithara sp.

Figure 89

LOCAL OCCURRENCE. Locality CSUN 1220c.

REMARKS. A single internal mold was found, but it shows evidence of thin collabral costae on the body whorl.

Family Volutidae Rafinesque, 1815

Genus *Lyria* Gray, 1847

Lyria andersoni Waring, 1917

Figure 90

Lyria andersoni Waring, 1917:97, pl. 15, fig. 12.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Locality CSUN 1291a.

REMARKS. A single specimen was found.

Genus *Lyrischapa* Aldrich, 1911

Lyrischapa lajollaensis (Hanna, 1927)

Figure 91

Pejonia lajollaensis Hanna, 1927:320, pl. 52, figs. 1, 2.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through Pine Mountain area, Ventura County, southern California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are rare and are either fragmentary or internal molds.

Family Conidae Rafinesque, 1815

Genus *Conus* Linné, 1758

Conus caleocius Vokes, 1939

Figure 92

Conus caleocius Vokes, 1939:127–129, pl. 18, figs. 1, 7.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Locality CSUN 1291c.

REMARKS. A single specimen was found.

Subclass Heterobranchia

Order Architectonicoidea

Family Architectonicidae
Gray, 1850

Genus *Architectonica*
Röding, 1798

Subgenus *Stellaxis*
Dall, 1892

Architectonica (*Stellaxis*) *cognata*
Gabb, 1864

Figure 93

Architectonica cognata Gabb, 1864:117, pl. 20, figs. 72, 72a, 72c [not figs. 72d and 72e as stated].

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1291b.

REMARKS. Specimens are rare. They are poorly preserved shells that are smooth except for the prominent keel and a prominent sutural cord. These two cords produce the diagnostic double-keel feature of this species.

Subclass Euthyneura

Order Cephalaspidea

Family Cylichnidae
A. Adams, 1850

Genus *Cylichnina*
Monterosato, 1884

Cylichnina tantilla
(Anderson and Hanna, 1925)

Figure 94

Cylichnella tantilla Anderson and Hanna, 1925: 140, pl. 7, figs. 4, 8, 9.

MOLLUSCAN STAGE RANGE. "Capay" through "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through western Washington.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Specimens are common at locality 1220b. One hand specimen of rock from this locality contained eight specimens. Specimens are rare at locality 1470.

Genus *Scaphander*
Montfort, 1810

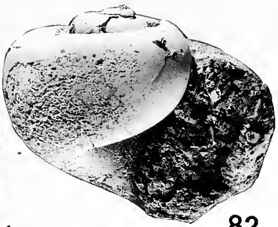
Scaphander? sp.

Figure 95

⟶

Figures 81–105. Bateque Formation gastropods and bivalves. **Figs. 81–96.** Gastropods. **81.** *Amauropsis* sp., apertural view, ×1.7, height 20 mm, width 15 mm, hypotype, IGM 5175, loc. CSUN 1220b. **82.** *Gyrodes*? sp., apertural view, ×0.6, height 45 mm, width 50 mm, hypotype, IGM 5176, loc. CSUN 1220b. **83.** *Eocernina hannibali* (Dickerson, 1914), apertural view, ×0.5, height 85 mm, width 85 mm, hypotype, IGM 5177, loc. CSUN 1220b. **84.** *Pachycrommium clarki* (Stewart, 1927), apertural view, ×1, height 37 mm, width 26.5 mm, hypotype, IGM 5178, loc. CSUN 1291a. **85.** *Galeodea* sp., abapertural view, anterior part missing, ×1.6, height 12 mm, width 15 mm, hypotype, IGM 5179, loc. CSUN 1220b. **86.** *Olequahia domenginica* (Vokes, 1939), internal mold, abapertural view, ×1.2, height 30 mm, width 22 mm, hypotype, IGM 5180, loc. CSUN 1470. **87.** *Clavilithes tabulatus* (Dickerson, 1913), abapertural view, spire area, ×1, height 35 mm, width 30 mm, hypotype, IGM 5181, loc. CSUN 1291a. **88.** ?*Olivella mathewsonii* Gabb, 1864, abapertural view, ×4.4, height 7 mm, width 2.5 mm, hypotype, IGM 5182, loc. CSUN 1470. **89.** *Eocithara* sp., abapertural view, ×1.6, height 21 mm, width 18 mm, hypotype, IGM 5183, loc. CSUN 1220c. **90.** *Lyria andersoni* Waring, 1917, left lateral view, ×3.7, height 10 mm, width 7 mm, hypotype, IGM 5184, loc. CSUN 1291a. **91.** *Lyriscapha lajollaensis* (Hanna, 1927), left lateral view, ×1.3, height 32 mm, width 19.5 mm, hypotype, IGM 5185, loc. CSUN 1220b. **92.** *Conus caleocius* Vokes, 1939, abapertural view, ×4.1, height 9 mm, width 3.5 mm, hypotype, IGM 5186, loc. CSUN 1291c. **93.** *Architectonica* (*Stellaxis*) *cognata* Gabb, 1864, dorsal view, ×4, diameter 7 mm, hypotype, IGM 5187, loc. CSUN 1220b. **94.** *Cylichnina tantilla* (Anderson and Hanna, 1925), apertural view, ×3.2, height 9 mm, width 3.5 mm, hypotype, IGM 5188, loc. CSUN 1220b. **95.** *Scaphander*? sp. abapertural view, ×2.4, height 13 mm, width 10 mm, hypotype, IGM 5189, loc. CSUN 1470. **96.** *Megistostoma gabbianum* (Stoliczka, 1868), internal mold, dorsal view, ×0.7, height 50.5 mm, width 32 mm, hypotype, IGM 5190, loc. CSUN 1293. **Figs. 97–105.** Bivalves. **97, 98.** *Barbatia* (*Barbatia*?) sp., right valve, length 23 mm, height 16 mm, hypotype, IGM 5191, loc. CSUN 1220b. **97.** ×1.7. **98.** ×1.8. **99.** *Barbatia* (*Acar*?) sp., left valve, ×1.3, length 32 mm, height 15 mm, hypotype, IGM 5192, loc. CSUN 1220a. **100, 101.** *Glycymeris* (*Glycymerita*) *sagittata* (Gabb, 1864), right? valve, length 18.5 mm, height 18 mm, hypotype, IGM 5193, loc. CSUN 1220b. **100.** ×1.5. **101.** ×1.8. **102.** *Pinna llajasensis* Squires, 1983, internal mold of right valve of an articulated specimen, anterior end missing, ×0.4, length 130 mm, height 83 mm, hypotype, IGM 5194, loc. CSUN 1220d. **103.** *Nayadina* (*Exputens*) *batequensis* Squires, 1990b, left valve, ×2, length 19 mm, height 11 mm, paratype, IGM 5113, loc. CSUN 1220b. **104, 105.** *Batequeus mezquitalensis* Squires and Demetrion, 1990b, loc. CSUN 1293. **104.** Left valve, ×0.9, length 38 mm, height 36.5 mm, holotype, IGM 5058. **105.** Right valve, ×0.90, length 40 mm, height 38 mm, paratype, IGM 5050.


81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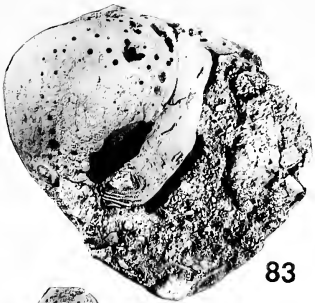
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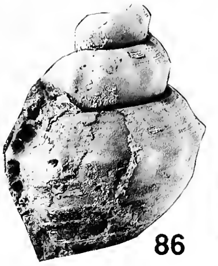
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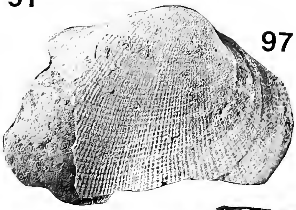
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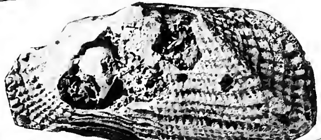
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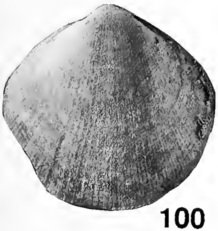
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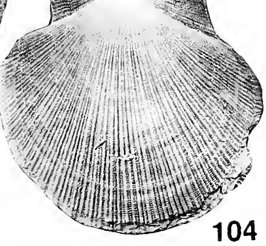
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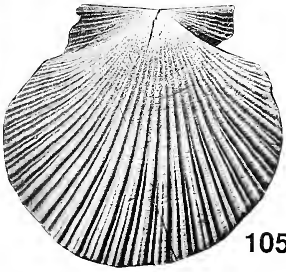
105

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. Only a single poorly preserved specimen was found.

Family Philinidae Gray, 1850

Genus *Megistostoma* Gabb, 1864

Megistostoma gabbianum (Stoliczka, 1868)

Figure 96

Bullaea gabbiana Stoliczka, 1868:434 [new name for *Megistostoma striata* Gabb, 1864, preoccupied.]

MOLLUSCAN STAGE RANGE. "Domengine" through middle part of "Tejon."

GEOGRAPHIC DISTRIBUTION. San Juanico area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. A single internal mold was found. The presence of *M. gabbianum* at locality CSUN 1293 extends the molluscan range of this species into the middle Eocene part of the "Tejon Stage." Previously, the upper range limit had been known to be "Transition Stage" (Squires, 1984).

Class Bivalvia

Order Arcoida

Family Arcidae Lamarck, 1809

Genus *Barbatia* Gray, 1842

Barbatia (*Barbatia*?) sp.

Figures 97, 98

LOCAL OCCURRENCE. Localities CSUN 1220a, 1220b.

REMARKS. Specimens are rare and fragmentary. They have the shape and external ornamentation of *Barbatia* s.s. The best-preserved specimen (Figs. 97, 98) also has the convergent hinge teeth similar to those in *Barbatia* s.s., but the figured specimen has a very narrow cardinal area with only a single ligamental groove. In *Barbatia* s.s., the cardinal area is fairly wide and there are several ligamental grooves.

The steep inclination and narrowness of the cardinal area in the Bateque specimens approach that seen in *B.* (*Acar*), but *Acar* has a different shape, coarser external ornamentation, and a prominent posterior umbonal carina.

More Bateque Formation specimens are needed to resolve the question as to which subgenus this arcid belongs. It may prove to be a new subgenus.

Subgenus *Acar* Gray, 1857

Barbatia (*Acar*?) sp.

Figure 99

LOCAL OCCURRENCE. Localities CSUN 1220a, 1220b.

REMARKS. Specimens are rare and are either fragments of shell or are somewhat weathered. The specimens have the shape and external ornamentation of *Barbatia* (*Acar*). The best-preserved specimen also has hinge teeth (inaccessible for photography) and a fairly narrow cardinal area (with at least two ligamental grooves) that seem to be similar to those in *Acar*. Better preservation is needed to positively assign these specimens to subgenus *Acar*. *Acar* has a geologic range of early Paleocene to Recent (Newell, 1969). If the Bateque specimens do belong to a species of *Acar*, this species would be the earliest one known from the Pacific coast of North America. The only other Paleogene *Acar* species from this area is *B.* (*A.*) *reinharti* Effinger (1938:367, pl. 45, figs. 3, 4; pl. 46, figs. 1, 2) from the upper Eocene Gries Ranch beds, southwestern Washington (Squires, 1989).

The Bateque Formation specimens resemble *B.* (*A.*) *aspera* (Conrad, 1854:pl. 14, fig. 5), the only reported species of *Acar* from the Paleogene of the southeastern United States. This species is from middle through upper Eocene strata in Mississippi and Texas (Palmer and Brann, 1965:44). The Bateque Formation specimens differ from *B.* (*A.*) *aspera* in the following features: anterior end more elongate and umbo more medially located. The Bateque Formation specimens may represent a new species.

Family Glycymerididae Newton, 1922

Genus *Glycymeris* da Costa, 1778

Subgenus *Glycymerita* Finley and Marwick, 1937

Glycymeris (*Glycymerita*) *sagittata* (Gabb, 1864)

Figures 100, 101

Axinaea (*Limopsis*?) *sagittata* Gabb, 1864:197–198, pl. 31, figs. 267, 267a.

MOLLUSCAN STAGE RANGE. "Capay" through "Tejon," Oligocene?.

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through Gulf of Alaska (Marincovich, 1988) and far eastern Soviet Union (Devyatilova and Volobueva, 1981).

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found. Although its exterior is weathered, the interior is excellently preserved and shows the diagnostic 12 well-defined teeth on each side of the hinge. In the medial area, the teeth are smaller. The ligamental area is well defined and contains five inverted V-shaped ridges.

Order Mytiloida

Family Pinnidae Leach, 1819

Genus *Pinna* Linné, 1758

Pinna llajasensis Squires, 1983

Figure 102

Pinna llajasensis Squires, 1983:359–360, fig. 2L.

MOLLUSCAN STAGE RANGE. "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Locality CSUN 1220d and float in vicinity of locality CSUN 1470.

REMARKS. A single large, articulated specimen was found at CSUN locality 1220d. Articulated specimens are common in float in the vicinity of CSUN locality 1470. The float material, which is at the base of the approximately 100-m-high cliff in this area, must have come from higher in the section than at locality 1470. The relatively unfossiliferous very fine-grained sandstone matrix surrounding the specimens is identical to that at locality 1220d.

Order Pterioida

Family Malleidae Lamarck, 1819

Genus *Nayadina* Munier-Chalmas, 1864

Subgenus *Exputens* Clark, 1934

Nayadina (*Exputens*) *batequensis* Squires, 1990b.

Figure 103

Nayadina (*Exputens*) *batequensis* Squires, 1990b: 308–309, figs. 3–25.

PRIMARY TYPE MATERIAL. Holotype, IGM 5108 (= LACMIP plastoholotype 8294); paratypes, IGM 5109–5119 (= LACMIP plastoparatypes 8295–8305); all from locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1471.

REMARKS. Specimens are abundant. There are equal numbers of left and right valves and a few articulated specimens at both localities.

This species is highly variable in shape, and seven variants have been recognized (Squires, 1990b). Specimens at locality 1471 are much larger than those at locality 1220b. With increasing size, the triangular shape that is the most common variant of this species becomes more elongate anteriorly and posteriorly.

Nayadina (*Exputens*) is confined to Eocene deposits of North America, and *N.* (*E.*) *batequensis* is the earliest known species of this subgenus (Squires and Demetrion, 1990b).

Family Pectinidae Rafinesque, 1815

Genus *Batequeus* Squires and Demetrion, 1990b

Batequeus mezquitalensis Squires and Demetrion, 1990b

Figures 104, 105

Batequeus mezquitalensis Squires and Demetrion, 1990b:383, 385, figs. 2.1–2.5.

PRIMARY TYPE MATERIAL. Holotype, IGM 5058 (= LACMIP plastoholotype 8061); paratypes, IGM 5059–5060 (= LACMIP plastoparatypes 8062–8063); all from locality CSUN 1293.

MOLLUSCAN STAGE RANGE. Middle Eocene part of "Tejon."

GEOGRAPHIC DISTRIBUTION. San Juanico area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens are abundant, with about equal numbers of left and right valves. Some are articulated. *Batequeus* is known only from the Bateque Formation.

Family Plicatulidae Watson, 1930

Genus *Plicatula* Lamark, 1801

Plicatula sp., aff. *P. filamentosa* Conrad, 1833

Figures 106, 107

[*Plicatula filamentosa* Conrad, 1833:38; Harris, 1919:18, pl. 2, figs. 3–8.]

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are rare. They closely resemble *P. filamentosa* Conrad, 1833, from middle Eocene strata, southeastern United States. The only difference is that the Bateque specimens show only the faintest hint of any secondary radial ribs. In most specimens of *P. filamentosa,* these secondary ribs are scaly and impart a beaded look. In some slightly weathered? specimens, however, collected by the senior author from the Gosport Sand in Alabama, the scaly ribs are very subdued, and these specimens are virtually indistinguishable from the Bateque specimens. More Bateque material is needed to resolve whether or not the *Plicatula* specimens represent a new species.

Plicatula juncalensis Squires (1987:57–58, figs. 95, 96), the only other reported species of *Plicatula* from the Eocene of the Pacific coast of North America, is from "Capay Stage" strata in the Whitaker Peak area, Los Angeles County, southern California. The Bateque Formation specimens differ from *P. juncalensis* in the following features: fewer, wider, and more lamellose ribs and no secondary radial ribs.

Plicatula sp.

Figure 108

LOCAL OCCURRENCE. Localities CSUN 1291a, 1293, 1471?.

REMARKS. Specimens are uncommon and poorly preserved as fragments, internal molds, and shell interiors. Several are articulated.

Plicatula sp. from the Bateque Formation differs from specimens of *P.* sp., aff. *P. filamentosa* from the formation in the following features: more numerous primary radial ribs (possibly 30 rather than approximately 15) and much narrower radial ribs.

Family Spondylidae
Gray, 1826

Genus *Spondylus*
Linné, 1758

Spondylus batequensis
Squires and Demetrion, 1990b

Figure 109

Spondylus batequensis Squires and Demetrion, 1990b:385–386, figs. 2.6–2.12.

PRIMARY TYPE MATERIAL. Holotype, IGM 5061 (= LACMIP plastoholotype 8064); paratypes, IGM 5062–5066 (= LACMIP plastoparatypes 8065–8069); all from locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220a, 1220b, 1220c, 1471.

REMARKS. Specimens are abundant at localities 1220a and 1220b, and several specimens at these localities were found articulated. A few specimens at locality 1220b are attached to valves of *Pycnodonte* (*Phygraea*) *pacifica.* Specimens are rare at the other localities.

Family Anomiidae
Rafinesque, 1815

Genus *Anomia* Linné, 1758

Anomia? sp.

Figure 110

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single, weathered left valve was found. The interior of the delicate specimen is filled with well-cemented matrix, and it is not possible to positively identify the specimen as to genus.

Family Limidae
Rafinesque, 1815

Genus *Lima* Bruguière

***Lima kennedyi* new species**

Figures 111, 112

DIAGNOSIS. Approximately 47 spinose narrow radial ribs with very closely spaced oblique ribbing in the interspaces; radial ribs become much wider and lamellose in mature individuals.

COMPARISON. A review of fossil *Lima* from the Pacific coast of North America is much needed. *Lima,* whose geologic range is Jurassic to Recent (Cox et al., 1969), may have been present in this area since the Late Cretaceous. A few Late Cretaceous species from southern California (Gabb, 1864, 1869; Packard, 1922; Sundberg, 1979) and a few late middle Eocene or Oligocene species from western Washington and vicinity (Weaver, 1943) have been placed in genus *Lima,* but none of these species has both the relatively well-differentiated auricles and scaly radial ribs diagnostic of *Lima.* A thorough review of these species is needed to understand their proper generic assignments. Until this study is done, it can only be tentatively stated that *Lima kennedyi* new species is the earliest occurrence of *Lima* from the Pacific coast of North America.

In the Paleogene record of the Atlantic and Gulf coasts of North America, only *Lima vicksburgiana* Dall (1898:765, pl. 35, fig. 20) from upper Eocene strata of Florida belongs to *Lima* s.s. (Palmer and Brann, 1965). The new species differs in having 47 rather than 35 primary radial ribs.

Eocene species of *Lima* are best represented in strata of the Paris Basin, France. Comparison with these revealed that the new species is most similar to *Lima rara* Deshayes (1860:pl. 78, figs. 9–11; Cossmann and Pissarro, 1904–1906:pl. 40, fig. 129-2) from middle Eocene (Lutetian) strata of the Paris Basin. The new species differs from *L. rara* in having approximately 47 primary radial ribs rather than about 35, and primary radial ribs more widely spaced and less strongly spinose.

DESCRIPTION. Medium-sized shell for genus, moderately thin, obliquely oval, valves slightly convex. Slight posterior gape adjacent to hinge line. Anterior auricle small. Posterior auricle twice as large, with three or four radial riblets, and a thickened posterior margin that is obliquely truncate. Approximately 47 narrow primary radial ribs, spinose (except in umbo area), with spinosity becoming stronger ventrally. Interspaces about two times as wide as primary radial ribs except anteriorly and posteriorly, where spacing can be variable. Interspaces with closely spaced fine ribs that obliquely intersect the radial ribs; on anterior half of valve these fine ribs point anteriorly and on posterior half of valve they point in the opposite direction. In mature individuals, nearly all primary radial ribs grade into thick lamellose costae that become more strongly spinose (commonly with two rows of spines) near shell venter. Growth lines very closely spaced. Hinge not seen. Holotype height 32 mm, length 25 mm.

PRIMARY TYPE MATERIAL. Holotype, IGM 5198 (= LACMIP plastoholotype 8858); paratype, IGM 5199 (= LACMIP plastoparatype 8859); all from locality CSUN 1220b.

TYPE LOCALITY. Locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Eight specimens were found. They are all single valves except one articulated specimen which is embedded in very hard matrix. They represent a growth series.

Pending a review of Pacific coast of North America fossil *Lima, L. kennedyi* new species is the earliest record of *Lima* from this area.

ETYMOLOGY. The new species is named after George L. Kennedy who has made valuable contributions in the study of Cenozoic mollusks.

Family Gryphaeidae Vyalov, 1936

Genus *Pycnodonte* Fischer de Waladheim, 1835

Subgenus *Phygraea* Vyalov, 1936

Pycnodonte (Phygraea) pacifica Squires and Demetrion, 1990b

Figure 113

Pycnodonte (Phygraea) pacifica Squires and Demetrion, 1990b:386, figs. 3.1–3.4.

PRIMARY TYPE MATERIAL. Holotype, IGM 5067 (= LACMIP plastoholotype 8070); paratype, IGM 5068 (= LACMIP plastoparatype 8071); all from locality CSUN 1220c.

MOLLUSCAN STAGE RANGE. "Capay" through middle Eocene part of "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area through San Juanico area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1220c, 1220d, 1291b, 1293, 1470, 1471.

REMARKS. Specimens are common at locality 1220c, where they occur as large individuals (some articulated) or in concentrations of single valves. At the other localities, specimens are uncommon.

This species is the first report of the subgenus *Phygraea* on the Pacific coast of North America.

Subgenus *Pegma* Squires and Demetrion, 1990b

Pycnodonte (Pegma) bajaensis Squires and Demetrion, 1990b

Figure 114

Pycnodonte (Pegma) bajaensis Squires and Demetrion, 1990b:388, figs. 3.5–3.12.

PRIMARY TYPE MATERIAL. Holotype, IGM 5069 (= LACMIP plastoholotype 8072); paratypes, IGM 5070–5072 (= LACMIP plastoparatypes 8073–8075); all from locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay" through middle Eocene part of "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area through San Juanico area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470, 1471, 1292, 1293.

REMARKS. Specimens are abundant at locality 1220b, where they occur as disarticulated valves that represent a growth series. Most of these valves are unattached right valves. Shell and coral debris commonly form the substrate for attachment of the left valves. A few specimens, however, have a trough-like attachment scar that resembles the outline of a mangrove root (Squires and Demetrion, 1990b:fig. 3.5). At the other localities, specimens are rare to uncommon.

The subgenus *Pegma* is known only from the Bateque Formation.

Family Ostreidae Rafinesque, 1815

Genus *Cubitostrea* Sacco, 1897

Cubitostrea mezquitalensis Squires and Demetrion, 1990b

Figures 115, 116

Cubitostrea mezquitalensis Squires and Demetrion, 1990b:388–390, figs. 4.1–4.9.

PRIMARY TYPE MATERIAL. Holotype, IGM 5073 (= LACMIP plastoholotype 8076); paratypes, IGM 5074–5075 and 5105–5107 (= LACMIP plastoparatypes 8077–8078 and 8276–8278); all from locality CSUN 1293.

MOLLUSCAN STAGE RANGE. Middle Eocene part of "Tejon."

GEOGRAPHIC DISTRIBUTION. San Juanico area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens are very abundant and well preserved with nearly equal numbers of left and right valves. Many specimens are articulated.

Cubitostrea meszquitalensis is the only species of this genus known from the Pacific coast of North America.

Order Veneroida

Family Fimbriidae Nicol, 1950

Genus *Fimbria* Megerle von Mühlfeld, 1811

Fimbria pacifica Squires, 1990c

Figure 117

Fimbria pacifica Squires, 1990c:554–555, figs. 3.1–3.3.

PRIMARY TYPE MATERIAL. Holotype, IGM 5104 (= LACMIP plastoholotype 8097), locality CSUN 1220b; paratype, LACMIP 7519, locality CSUN 830.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southern California.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. This species is known only from single valves, which are rare.

Family Carditidae Fleming, 1820

Genus *Glyptoactis* Stewart, 1930

Subgenus Claibornicardia Stenzel and Krause, 1957

Glyptoactis (*Claibornicardia*) *domenginica* (Vokes, 1939)

Figure 118

Venericardia (*Glyptoactis*?) *domenginica* Vokes, 1939:66, pl. 5, figs. 7–9.

MOLLUSCAN STAGE RANGE. "Capay" through "Transition."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through Mt. Diablo, northern California.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Specimens are uncommon and are single valves.

Family Crassatellidae Férussac

Genus *Crassatella* Lamarck, 1799

Crassatella sp.

Figure 119

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. A single specimen was found, and it is an internal mold of an articulated individual.

→

Figures 106–125. Bateque bivalves. **Figs. 106, 107.** *Plicatula* sp., aff. *P. filamentosa*, Conrad, 1833, ×2.1, length 15 mm, height 16 mm, hypotype, IGM 5195, loc. CSUN 1220b. **106.** Left valve. **107.** Right valve. **Fig. 108.** *Plicatula* sp., interior of left? valve, ×1.8, length 20 mm, height 20 mm, hypotype, IGM 5196, loc. CSUN 1293. **Fig. 109.** *Spondylus batequensis* Squires and Demetrion, 1990b, right valve, ×1.8, length 19 mm, height 21 mm, holotype, IGM 5061, loc. CSUN 1220b. **Fig. 110.** *Anomia*? sp. left valve, ×1.4, length 25.5 mm, height 21 mm, hypotype, IGM 5197, loc. CSUN 1220b. **Figs. 111, 112.** *Lima kennedyi* new species, loc. CSUN 1220b. **111.** Left valve, ×1.2, length 25 mm, height 36 mm, paratype, IGM 5199. **112.** Right valve, ×1.4, length 31 mm, height 33 mm, holotype, IGM 5198. **Fig. 113.** *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetrion, 1990b, left valve, ×0.5, length 72 mm, height 80 mm, holotype, IGM 5067, loc. CSUN 1220c. **Fig. 114.** *Pycnodonte* (*Pegma bajaensis* Squires and Demetrion, 1990b, right valve, ×1.4, length 22 mm, height 26 mm, holotype, IGM 5069, loc. CSUN 1220b. **Figs. 115, 116.** *Cubitostrea mezquitalensis* Squires and Demetrion, 1990b, loc. CSUN 1293. **115.** Left valve, ×0.6, length 79 mm, height 39 mm, holotype, IGM 5073. **116.** Right valve of an articulated specimen, ×0.8, length 39 mm, height 30 mm, paratype, IGM 5075. **Fig. 117.** *Fimbria pacifica* Squires, 1990c, right valve, ×1.1, length 47 mm, height 32 mm, holotype, IGM 5104, loc. CSUN 1220b. **Fig. 118.** *Glyptoactis* (*Claibornicardia*) *domenginica* (Vokes, 1939), left valve, ×2, length 17 mm, height 13 mm, hypotype, IGM 5200, loc. CSUN 1220b. **Fig. 119.** *Crassatella* sp., internal mold of right valve, ×0.7, length 69 mm, height 50 mm, hypotype, IGM 5201, loc. CSUN 1220b. **Fig. 120.** *Acanthocardia* (*Agnocardia*) sp., aff. *A.* (*A.*) *sorrentoensis* (Hanna, 1927), partial left? valve, ×2.6, length 13 mm, height 11 mm, hypotype, IGM 5904, loc. CSUN 1220b. **Fig. 121.** *Nemocardium linteum* (Conrad, 1855), internal mold of left valve, ×1.5, length 22 mm, height 19 mm, hypotype, IGM 5905, loc. CSUN 1293. **Fig. 122.** *Solena* (*Eosolen*) *novacularis* (Anderson and Hanna, 1928), internal mold of left valve of an articulated specimen, ×0.9, length 75 mm, height 18 mm, hypotype, IGM 5906, loc. CSUN 1470. **Fig. 123.** *Pitar* (*Lamelliconcha*) *joaquinensis* Vokes, 1939, left valve, ×1.5, length 20 mm, height 18 mm, hypotype, IGM 5907, loc. CSUN 1470. **Fig. 124.** *Pholadomya* sp., cf. *P.* (*Bucardiomya*) *givensi* Zinsmeister, 1978, internal mold of crushed right valve, ×1.5, length 14 mm, height 28.2 mm, hypotype, IGM 5908, loc. CSUN 1293. **Fig. 125.** Teredinidae, indet., side view of colony, ×1.3, length of colony 40 mm, height of colony 16.5 mm, hypotype, IGM 5909, loc. CSUN 1220b.


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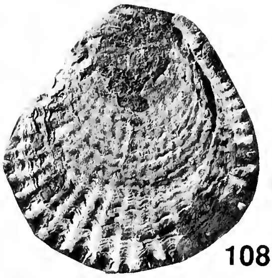
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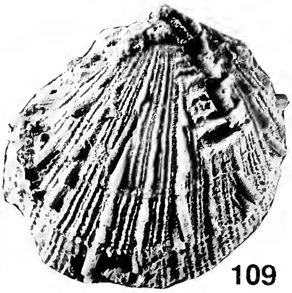
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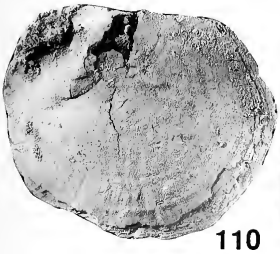
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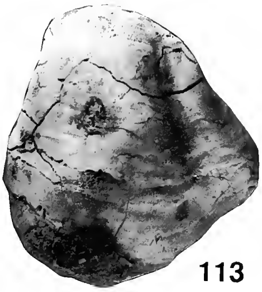
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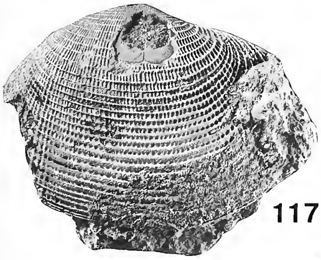
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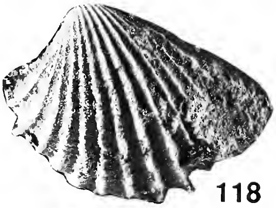
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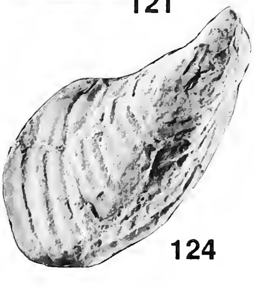
124


125

Family Cardiidae
Lamarck, 1809

Genus *Acanthocardia*
Gray, 1851

Subgenus *Agnocardia*
Stewart, 1930

Acanthocardia (*Agnocardia*) sp.,
Aff. *A.* (*A.*) *sorrentoensis*
(Hanna, 1927)

Figure 120

[*Cardium sorrentoensis* Hanna, 1927:285, pl. 41, figs. 10, 12, 14.]

LOCAL OCCURRENCE. Localities CSUN 1220b, 1293.

REMARKS. Specimens are uncommon at locality 1220b and rare at 1293. Preservation is poor, and a few specimens are internal molds. A few specimens are articulated.

The specimens closely resemble *A.* (*A.*) *sorrentoensis* (Hanna, 1927) from "Domengine Stage" strata, San Diego area, southern California. Stewart (1930:265) assigned Hanna's species to the genus and subgenus *Acanthocardia* (*Agnocardia*). The Bateque Formation specimens, like *A.* (*A.*) *sorrentoensis,* have numerous flat-topped radial ribs with chevron-shaped spines. Ribs with fairly strong chevron-shaped spines usually alternate with ribs that have much weaker chevron-shaped spines. The Bateque Formation specimens differ from *A.* (*A.*) *sorrentoensis* in the following features: more closely spaced ribs and a less inflated umbo area.

Genus *Nemocardium*
Meek, 1876

Nemocardium linteum
(Conrad, 1855)

Figure 121

Cardium linteum Conrad, 1855:3, 9; 1857:pl. 2, fig. 1.

MOLLUSCAN STAGE RANGE. "Martinez" through "Tejon."

GEOGRAPHIC DISTRIBUTION. San Juanico area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. A single internal mold was found.

Family Solenidae
Lamarck, 1809

Genus *Solena* Mörch, 1853

Subgenus *Eosolen*
Stewart, 1930

Solena
(*Eosolen*) *novacularis*
(Anderson and Hanna, 1928)

Figure 122

Solen novacula Anderson and Hanna, 1928:147, pl. 6, fig. 9.

MOLLUSCAN STAGE RANGE. "Capay" through "Tejon."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through southwestern Oregon.

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. Specimens are uncommon and are internal molds of articulated individuals.

Family Veneridae
Rafinesque, 1815

Genus *Pitar* Römer, 1857

Subgenus *Lamelliconcha*
Dall, 1802

Pitar (*Lamelliconcha*)
joaquinensis Vokes, 1939

Figure 123

Pitar (*Lamelliconcha*) *joaquinensis* Vokes, 1939: 85–86, pl. 13, figs. 9–12.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. A single valve was found.

Order Pholadomyoida

Family Pholadomyidae
Gray, 1847

Genus *Pholadomya*
G.B. Sowerby, 1823

Subgenus *Bucardiomya*
Rollier *in* Cossmann, 1912

Figure 124

Pholadomya sp.,
cf. *P.* (*Bucardiomya*) *givensi*
Zinsmeister, 1978

Figure 124

[*Pholadomya* (*Bucardiomya*) *givensi* Zinsmeister, 1978:235, fig. 1.]

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens are uncommon and are crushed internal molds of incomplete individuals.

Poor preservation prevents positive identification as to species.

Pholadomya (*B.*) *givensi* is known only from "Capay Stage" strata in the Whitaker Peak and Pine Mountain areas, southern California (Squires, 1987). If this species is present in the upper part of the Bateque Formation, then the molluscan stage range of the species would be expanded to the middle Eocene part of the "Tejon Stage," and its geographic distribution would be expanded southward to the San Juanico area, Baja California Sur, Mexico.

Order Myoida

Family Teredinidae Rafinesque, 1815

Teredinidae, indet.

Figure 125

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Several clusters and several individuals of calcareous-lined burrows were found. One cluster is in fossil wood.

Class Cephalopoda

Order Nautilida

Family Hercoglossidae Spath, 1927

Genus *Hercoglossa* Conrad, 1866

Hercoglossa? sp.

Figure 126

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Two internal molds were found, one 62 mm in diameter (Fig. 126) and the other, more poorly preserved, is 100 mm in diameter.

The lateral-lobe and lateral-saddle sutural pattern of the Bateque specimens is intermediate between that of the genus *Cimomia* and a primitive *Hercoglossa.* To distinguish these two transitional genera, it is necessary to compare the entire sutural pattern. Unfortunately, the ventral and dorsal parts of the sutural pattern are not well preserved or not observable on the Bateque Formation specimens. In addition, the position of the siphuncle cannot be determined.

The Bateque Formation specimens resemble *Cimomia tenuicosta* Glenister et al. (1956:495–496, pl. 53, figs. 1–9) from uppermost Cretaceous strata in Western Australia. The Bateque specimens also resemble *Hercoglossa peruviana* Berry (1923:427–431, figs. 1, 2) from upper Eocene strata in Peru.

Family Aturiidae Hyatt, 1894

Genus *Aturia* Bronn, 1838

Aturia myrlae Hanna, 1927

Figure 127

Aturia myrli Hanna, 1927:331, pl. 57, figs. 1, 6.

MOLLUSCAN STAGE RANGE. "Capay" through "Domengine."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico, through central California.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470.

REMARKS. Two internal molds of partial specimens were found, both about 70 mm in diameter.

Squires (1988c) summarized published reports that indicated *A. myrlae* may be the same as *A. alabamensis* (Morton, 1834:33, pl. 18, fig. 3), which may have had worldwide distribution during the Eocene.

Phylum Arthropoda

Class Malacostraca

Order Decapoda

Family Raninidae de Haan, 1841

Genus *Ranina* Lamarck, 1801

***Ranina berglundi* new species**

Figures 128, 129

DIAGNOSIS. A *Ranina* s.s. with a wide fronto-orbital margin, two equally spaced wide and strong anterolateral spines (outermost one serrate), and wide spacing between all spines.

COMPARISON. The new species has been compared with all the species descriptions of *Ranina,* a genus whose geologic range is Eocene through Recent with Eocene specimens only known with certainty from North America (Glaessner, 1969).

In the Eocene record of the Atlantic and Gulf coasts of North America, the only two reported species of *Ranina* actually belong to *Lophoranina.* These are *Ranina porifera* Woodward (1866:591–592, pl. 26, fig. 18) and *R. georgiana* Rathbun (1935: 97–98, pl. 21, figs. 7, 8).

In the Eocene record of the Pacific coast of North America, there are only two previously reported species of *Ranina. Ranina americana* Withers (1924:125, pl. 4, figs 1–3) from the upper Eocene Hoko River Formation in northwestern Washington (R. E. Berglund, pers. comm., 1989). Rathbun (1926:91–92, pl 23, figs. 1–4) also discussed this species. The new species differs from *R. americana* in the following features: wider spacing between all spines, wider fronto-orbital margin, stronger and wider anterolateral spines, and outermost anterolateral spine serrate on anterior edge.

The other Pacific coast Eocene species is *R. tejoniana* Rathbun (1926:70–91, pl. 22, figs. 1, 2) from Eocene strata, southern San Joaquin Valley, central California. The new species has a more tapering carapace and more widely spaced spines.

DESCRIPTION. Moderate-sized raninid with ovate, moderately convex carapace, very broad in proportion to its length. Widest along anterior one-fifth at outermost anterolateral spine area. Carapace maximum width (including outermost anterolateral spines) equals total length. Carapace width (excluding outermost anterolateral spines) 80 percent of total length. Lateral borders curve inward, posterior margin very narrow. Surface with small pits, sparse on anterior middle part, closer posteriorly and toward lateral and anterior borders. Posterolaterally, pits in transverse rows of about 10.

Rostrum trifid, small, and pointed. Fronto-orbital margin curved with three spines on each side. First (innermost) fronto-orbital spine small, outward-pointing, and separated from wider second spine by a short furrow. Second fronto-orbital spine separated from forward-pointing and more prominent third spine by a very short and narrow furrow. Length of fronto-orbital area about 60 percent of width of carapace (excluding outermost anterolateral spines). Two anterolateral spines, equally spaced. First anterolateral spine forward-pointing, about equal in size to outermost fronto-orbital spine but more pointed. Second (outermost) anterolateral spine widest and strongest of all spines, extended at a 45-degree angle to a blunt point, with four serrations on anterior edge of spine (the middle two the strongest). Posteriorly to second anterolateral spine, a fine raised rim extends around the carapace. Holotype 39 mm in width (including outermost anterolateral spines), 38 mm in length.

PRIMARY TYPE MATERIAL. Holotype, IGM 5913 (= LACMIP plastoholotype 8860); paratype, IGM 5914 (= LACMIP plastoparatype 8861); all from locality CSUN 1220b.

TYPE LOCALITY. Locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Locality CSUN 1220b.

REMARKS. Four specimens were found, two of which are incomplete. The early Eocene *Ranina berglundi* new species is the earliest report of *Ranina,* not only in North America but in the world.

ETYMOLOGY. The new species is named after Ross E. Berglund who has made valuable contributions in the study of Paleogene decapods from Washington and Oregon.

Genus *Lophoranina*
Fabiani, 1910

Lophoranina bishopi
new species

Figure 130

DIAGNOSIS. A *Lophoranina* with four species in fronto-orbital area and two nonbifurcating anterolateral spines.

COMPARISON. The new species has been compared with all the species descriptions of *Lophoranina,* a genus whose geologic range is Eocene to Oligocene (Glaessner, 1969). These species are described in Vía Boada (1969:119–122). Most of the Eocene species are from the Mediterranean region. Except for one of these, they are not comparable to the new species because their spines are weaker than the new species. The one that is most similiar to the new species is *L. straeleni* Vía Boada (1959: 366–367, text fig. 7; 1969:115–119, text fig. 13, pl. 7, fig. 1a–c; pl. 8, fig. 1) from middle Eocene (Lutetian Stage) strata of Spain and Italy (Vía Boada, 1969). Bishop and Whitmore (1986:fig. 2G, H) also reported *L.* cf. *straeleni* Vía Boada from the middle Eocene Santee Formation in South Carolina. The new species differs from *L. straeleni* in the following features: one extra spine in fronto-orbital area, outermost anterolateral spine not bifurcated, frontal area more distinctly set off from rest of frontal-orbital area, and sides of carapace straighter.

DESCRIPTION. Moderately large-sized lophoraninid with ovate, convex carapace. Widest about halfway between outermost anterolateral spine and posterior margin. Surface with closely spaced parallel transverse granulated ridges. Granules form rows along ridge crests.

Rostrum pointed. Fronto-orbital area with four spines on side. First (innermost) fronto-orbital spine of moderate size, forward-pointing, and separated from about equal-sized second spine by a short but fairly wide furrow. Forward-pointing, second fronto-orbital spine separated from flattish third spine by a very short and narrow furrow. Fourth spine very forward-pointing. Length of fronto-orbital area about 73 percent of width of carapace measured along line connecting outermost anterolateral spines. Two anterolateral spines, approximately equally spaced. Both forward-pointing and about equal in size to outermost, fronto-orbital spine. Posteriorly to outermost anterolateral spine, a fine, raised rim extends around the sides of the carapace. Holotype, 40.5 mm maximum in width, 43 mm in length (incomplete).

PRIMARY TYPE MATERIAL. Holotype, IGM 5915 (= LACMIP plastoholotype 8862).

TYPE LOCALITY. Locality CSUN 1220b.

MOLLUSCAN STAGE RANGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1291b, 1470.

REMARKS. Two partial carapaces were found, one a large fragment (Fig. 130) with the central and left anterior margin areas poorly preserved, the second a small fragment.

Lophoranina bishopi new species is the first occurrence of this genus from the Pacific coast of North America.

ETYMOLOGY. The species is named after Gale A. Bishop, who has made valuable contributions to the study of Cretaceous and early Tertiary crabs.

Phylum Echinodermata

Class Echinoidea

Order Cidaroida

Cidaroida, indet. spine A

Figure 131

LOCAL OCCURRENCE. Localities CSUN 1220b, 1471.

REMARKS. Specimens of these primary spines are common at locality 1220b and uncommon at locality 1471. Some are small fragments, but others are nearly complete and up to 26 mm in length. This type of spine is solid, slightly tapering, and cylindrical, with 9–15 longitudinal rows of spinules. Toward the base of the spine, there is a progressive transition from a smooth neck, to a very finely striated collar, to a milled ring, to a smooth base, and then to a rim that is hollowed out.

Cidaroida, indet. spine B

Figures 132, 133

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens of these primary spines are common. Most are small fragments, but a few are nearly complete and up to 39 mm in length (Fig. 132). None shows the spine tip. This type of spine is solid, flattened throughout its length, very gradually tapering, minutely striated, slightly curved, and elliptical in cross section. Toward the base of the spine there is no neck, but a very minutely striated collar is well developed and passes into a milled ring. The base of the spine has about 10 crenulations at its terminus.

Cidaroida, indet. spine C

Figure 134

LOCAL OCCURRENCE. Locality CSUN 1293.

REMARKS. Specimens of these primary spines are common. Most are small fragments, but a few are up to 28 mm in length. These spines are very similar to cidaroid spine B. The only difference is that cidaroid spine C has fine serrations along the flattened margin. These serrated spines resemble some of the types of primary spines known from the Eocene cidaroid genus *Porocidaris.*

Order Cassiduloida

Family Echinolampadidae
Gray, 1851

Genus *Echinolampas*
Gray, 1825

Echinolampas? sp. A

Figures 135, 136

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. Only one incomplete specimen was found. It shows most of the aboral surface. The posterior region is missing, and the oral surface is mostly obliterated. The specimen has an inflated test with a monobasal apical system, four large genital pores, unequal poriferous zones on the medium-length open petals, wide interporiferous zones, single pores in the ambulacral plates beyond the petals, and numerous inflated small tubercles in deep scrobicules. Preservation of the specimen is too incomplete to allow positive identification as to genus.

The specimen is similar to the *E. oviformis* (Gmelin, 1789:3187; Kier, 1962:107–108, pl. 30, figs. 1–4, text fig. 90; 1966:fig. 393 1a-b). *Echinolampas ociformis,* which is the type species of *Echinolampas,* is found today in the Indian Ocean.

The geologic range of *Echinolampas* is Eocene to Recent (Kier, 1966). If the Bateque specimen does belong to *Echinolampas,* it would be the first report from the Pacific coast of North America.

Echinolampas? sp. B

Figure 137

LOCAL OCCURRENCE. Locality CSUN 1470.

REMARKS. Only a single small-sized, inflated, and circular specimen (maximum diameter 12 mm) was found. The specimen shows most of the aboral surface fairly well, but the oral surface is obliterated. The posterior region is missing. There is a monobasal apical system, a tendency for unequal poriferous zones on the long open petals, wide interporiferous zones, single pores in the ambulacral plates beyond the petals, and numerous small tubercles in deep scrobicules. Preservation of the specimen is too poor, however, to allow positive identification as to genus.

The main part of the test of *Echinolampas?* sp. B generally resembles *E. appendiculata* Emmons (1858:307, figs. 240, 241; Clark and Twitchell, 1915: 149–150, pl. 68, fig. 2a, b; Cooke, 1959:56, pl. 22, figs. 5, 6) from upper Eocene beds in North Carolina (Cooke, 1959). One major difference is that *E.?* sp. B lacks genital pores and *E. appendiculata* has four. The posterior region of *E.?* sp. B is missing so it could not be compared to the distinctly pointed posterior region of *E. appendiculata.*

The geologic range of *Echinolampas* is Eocene to Recent (Kier, 1966). *Echinolampas?* sp. B, along with *Echinolampas?* sp. A, may be the first occurrences of this genus from the Pacific coast of North America.

Order Spatangoida

Family Schizasteridae
Lambert, 1905

Genus *Schizaster*
L. Agassiz, 1836

Subgenus *Paraster* Pomel, 1869

Schizaster (*Paraster*) sp., aff. *S. lecontei* Merriam, 1899

Figures 138–141

[*Schizaster lecontei* Merriam, 1899:164–165, pl. 21, fig. 1, 1a.]

LOCAL OCCURRENCE. Localities CSUN 1220b, 1291a, 1291b, 1470, 1471.

REMARKS. Specimens are common at localities 1220b and 1471 and rare elsewhere. At locality 1220b, specimens range in length from 16.5 mm to 55 mm. A few of these specimens have extensive patches of small spines adhering to the test.

Crushing has affected all of the specimens to varying degrees. Many are incomplete due to crushing and/or weathering. No single specimen is complete, and no specimen shows the ventral surface. One specimen (Fig. 138) shows both the peripetalous fasciole and the lateral fasciole. This same specimen also has the most inflated test, and it seems to be the least affected by crushing. Another specimen (Figs. 139–141) shows a keel extending posteriorly in interambulacrum V from the apical system.

The specimens resemble *S. lecontei* from upper Paleocene strata, northern California. Kew (1920: 151–152, pl. 41, fig. 3a–d) also discussed this species. The Bateque Formation specimens differ in the following features: larger size, more inflated test, narrower? anteriorlateral ambulacra (II and IV), and anterior ambulacrum III does not show distinct ambulacral plates. The differences in test inflatedness may be due to crushing, and the ambulacral differences may be due to weathering or to the fact that most workers previously have only described and figured internal molds of *S. lecontei*.

In terms of test inflatedness, the Bateque Formation specimens resemble *S. diabloensis* Kew (1920:150–151, pl. 41, fig. 5a–c) from upper Paleocene through "Domengine Stage" strata, southern and central California (Squires, 1984).

Only two Bateque Formation specimens show the apical system. One specimen (Fig. 138) has two genital pores that are slightly posterior of the center of the test. The other specimen has four genital pores. The apical system of these two specimens is very similar to that in *S.* (*Paraster*) *tatei* McNamara and Philip (1980:51–52, fig. 2A–E) from lower upper Eocene strata, South Australia. Although Fischer (1966:569) reported that *Paraster* has four genital pores, McNamara and Philip (1980) showed that the number of genital pores is of little taxonomic significance in the Schizasteridae.

Although they could not be photographed effectively, the pore pairs in ambulacrum IV of the the Bateque specimens are oblique and arranged in double rows.

Family Brissidae Gray, 1855

Genus *Eupatagus* L. Agassiz, 1847

Eupatagus batequensis new species

Figures 142–145

DIAGNOSIS. An *Eupatagus* with a circular-shaped aboral surface, elevated posteriorly, greatest height posterior at sharply inflated plastron, anterior ambulacra curved anteriorly, no tubercles on aboral interambulacrum 5.

COMPARISON. *Eupatagus* has complicated

⟶

Figures 126–145. Bateque Formation cephalopods, crabs, and echinoids. **Figs. 126, 127.** Cephalopods. **126.** *Hercoglossa*? sp., internal mold, lateral view, ×0.8, maximum diameter 62 mm, hypotype, IGM 5910, loc. CSUN 1220b. **127.** *Aturia myrlae* Hanna, 1927, internal mold of partial specimen, lateral view, ×1, maximum diameter 29 mm, hypotype, IGM 5911, loc. CSUN 1220b. **Figs. 128–130.** Crabs. **128, 129.** *Ranina berglundi* new species, loc. CSUN 1220b. **128.** Dorsal view, ×1.1, length 37 mm, maximum width (excluding spines) 30 mm, holotype, IGM 5912. **129.** Dorsal view of right anterior area, ×2.1, length 12 mm, width 17.5 mm, paratype, IGM 5913. **130.** *Lophoranina bishopi* new species, dorsal view, posterior area missing, ×1, length 43 mm, width 40 mm, holotype, IGM 5914, loc. CSUN 1291b. **Figs. 131–145.** Echinoids. **131.** Cidaroida, indet. spine A, lateral view, ×1.7, length 24 mm, diameter 3 mm, hypotype, IGM 5915, loc. CSUN 1220b. **132, 133.** Cidaroida, indet. spine B, hypotype, IGM 5916, loc. CSUN 1293. **132.** Lateral view, ×1.2, length 39.5 mm, diameter, 4.5 mm. **133.** Basal view, ×4.4, diameter 4.5 mm. **134.** Cidaroida, indet. spine C, lateral view, ×2.1, length 19 mm, width 3.5 mm, hypotype, IGM 5917, loc. CSUN 1293. **135, 136.** *Echinolampas*? sp. A., hypotype, IGM 5918, loc. CSUN 1470. **135.** Dorsal view, ×1.9, diameter 18 mm. **136.** Right lateral view, ×1.5, height 11 mm. **137.** *Echinolampas*? sp. B, dorsal view, ×2.7, diameter 12 mm, hypotype, IGM 5919, loc. CSUN 1470. **138–141.** *Schizaster* (*Paraster*) sp., aff. *S. lecontei* Merriam, 1899. **138.** Dorsal view, ×1.4, length 26.5 mm, width 25.2 mm, hypotype, IGM 5920, loc. CSUN 1220b. **139–141.** ×1.7, length 22 mm, width 21 mm, height 13 mm, hypotype, IGM 5921, loc. CSUN 1470. **139.** Dorsal view. **140.** Left side. **141.** Posterior view. **142–145.** *Eupatagus batequensis* new species, loc. CSUN 1470. **142–144.** ×1.4, length 29 mm, width 29 mm, height 14.3 mm, holotype, IGM 5922. **142.** Dorsal view. **143.** Ventral view. **144.** Left side. **145.** Dorsal view (lower left area missing), ×1.3, length 30 mm, width 27 mm, paratype, IGM 5923.


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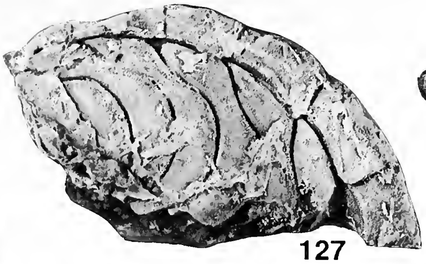
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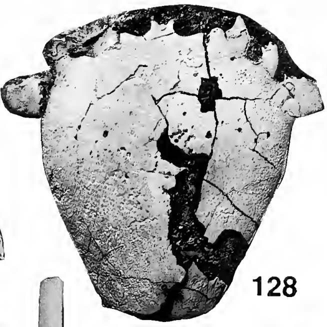
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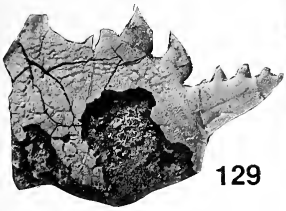
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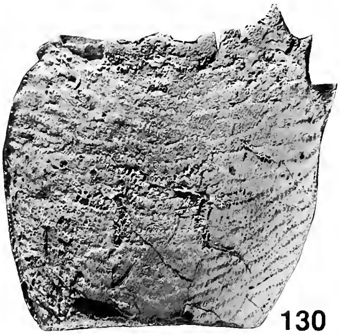
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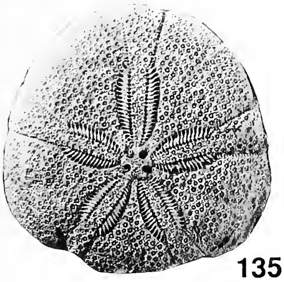
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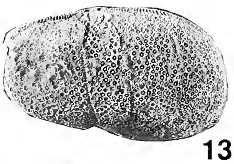
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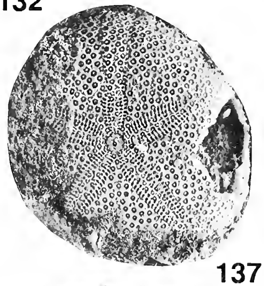
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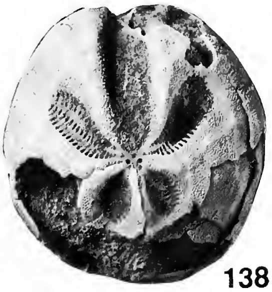
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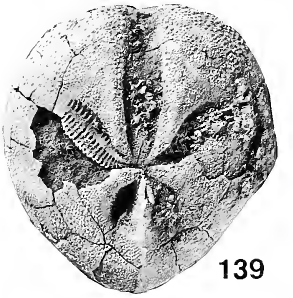
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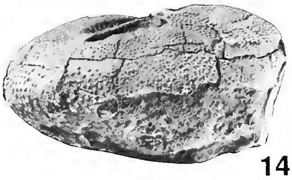
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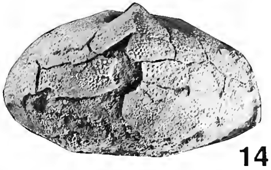
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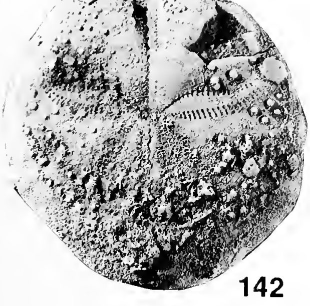
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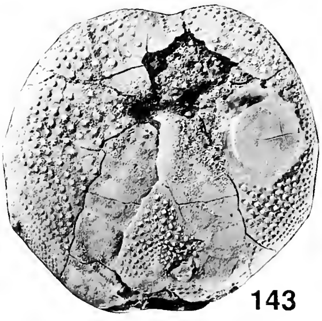
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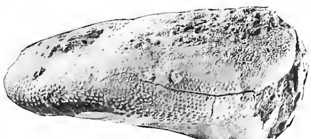
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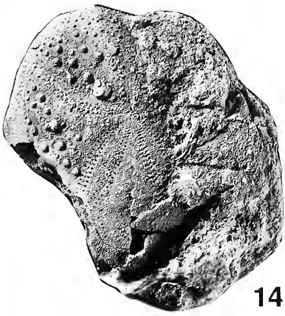
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taxonomic history and has been known by at least eight synonyms (Fischer, 1966). One of the more commonly used names in old literature is *Euspatangus* Cotteau. Although the geologic range of *Eupatagus* is Eocene to Recent (Fischer, 1966), the genus was very common during the Eocene, with many species reported from all over the world (Kier, 1984).

We have endeavored to compare *E. batequensis* new species with all North American and West Indies Eocene species and many other Eocene species from Europe. We also included many Tertiary species from elsewhere in the world. The reader is referred to Cotteau (1889–1891), Clark and Twitchell (1915), Cooke (1942, 1959), and Kier (1984) for descriptions of many of the North American, West Indies, and European Eocene species. Nearly all of the studied species are not comparable to the new species because they do not possess the sharply inflated plastron and depressed anterior ambulacral area.

The new species has the lateral shape of *E. sanchezi* (Lambert *in* Sánchez Roig, 1949:211, pl. 24, figs. 2, 3; Kier, 1984:107–108, pl. 58, figs. 1–3) from Miocene strata in Cuba (Kier, 1984). The new species has the aboral shape of *Maretia arguta* (Clark and Twitchell, 1915:150, pl. 69, fig. 1a–d; Cooke, 1959:81, pl. 34, figs. 1–4) from lower middle Eocene strata in Mississippi (Cooke, 1959). *Maretia* belongs to the family Spatangidae. The new species has the tubercle ornamentation similar to that of *E. curvus* Cooke (1942:56–57, pl. 7, figs. 5–7) from upper Eocene strata in northern Florida.

The new species resembles *E. cordiformes* (Duncan and Sladen, 1884:238–240, pl. 38, fig. 14) from Eocene strata in western India. The new species differs by having a smaller test that is not indented posteriorly.

Previously, only one other species of *Eupatagus* has been reported from the Pacific coast of North America. It is *Eupatagus stevensi* Grant and Hertlein (1938:134–135, text fig. 12) from the middle Eocene part of the Llajas Formation, Simi Valley, southern California, and from upper Eocene beds in upper Cuyama Valley, southern California. The holotype of *E. stevensi* is an internal mold. To confirm that this species actually belongs in *Eupatagus,* it will be necessary to find specimens that show the exterior with the peripetalous and subanal fascioles that are so diagnostic of the genus *Eupatagut.* Until that time, *E. stevensi* can only be tentatively assigned to *Eupatagus.* Even if their species belongs to *Eupatagus,* the Bateque Formation species is the earliest representative of this genus from the Pacific coast of North America.

DESCRIPTION. Medium size (up to 43 mm in length), widest along line drawn laterally through apical system. Circular, truncated posteriorly. Anterior indented, left anterior side may project slightly beyond right side. Test elevated posteriorly and greatest height posterior at sharply inflated plastron. Test slopes downward anteriorly. Apical system slightly in front of the center, four genital pores, the anterior two more closely together. Anterior ambulacral area not petaloid, single pores along sides, ambulacral area slightly depressed with amount of depression increasing anteriorly.

Anterior ambulacra pair slightly depressed, extending four-fifths of the way to the margin, diverging almost directly opposite each other, but curving anteriorly near their extremities. Posterior ambulacra pair flat and approximately same length as anterior ambulacral pair. Interporiferous zones of petals wider than poriferous zones. Peripetalous fasciole without indentations. Paired interambulacral areas with about 6–10 irregularly spaced, large scrobiculated tubercles, confined within the peripetalous fasciole. No tubercles on aboral interambulacrum 5. Subanal fasciole very distinct at posterior end of plastron (elsewhere obliterated).

Peristome slightly farther forward than apical system (peristome details obliterated). Periproct terminal (periproct details obliterated). Plastron inflated with tubercles arranged en chevron. Posterior ambulacral areas smooth. Holotype width 28.7 mm, length 29 mm, greatest height 14.2 mm.

PRIMARY TYPE MATERIAL. Holotype, IGM 5923 (= LACMIP plastoholotype 8863); paratype, IGM 5924 (= LACMIP plastoparatype 8864); all from locality CSUN 1470.

TYPE LOCALITY. Locality CSUN 1470.

MOLLUSCAN STAGE RNAGE. "Capay."

GEOGRAPHIC DISTRIBUTION. Eastern Laguna San Ignacio area, Baja California Sur, Mexico.

LOCAL OCCURRENCE. Localities CSUN 1220b, 1470, 1471.

REMARKS. Specimens are common at locality 1470 and rare at the other localities. Preservation is fair, but well-indurated matrix adheres in places to all specimens. Most are also missing parts of the test due to weathering. Crushing is a minor problem.

Eupatagus batequensis new species may be the first species of this genus from the Pacific coast of North America.

ETYMOLOGY. The new species is named after the Bateque Formation.

LOCALITIES

All localities are in the Bateque Formation. Unless otherwise noted, they are in the Mexican government topographic quadrangle map (scale 1:50,000) of San José de Gracia (number G12A64), Baja California Sur, Mexico, 1982.

CSUN MACROFOSSIL LOCALITIES

1219. Low-relief bluffs along main dirt road from San Ignacio to La Fridera fish camp, at 113°05′W and 26°56′N, Mexican government topographic quadrangle map (scale 1:50,000) of Laguna San Ignacio (number C12A53), Baja California Sur, Mexico, 1982.

1220a. South side of a tributary canyon, at an elevation of 120 m and about 850 m southeast of the mouth of the main canyon, on the west side of Mesa La Salina, 80–104 m above the bottom of the exposures of the Bateque Formation in this area, at 1.25 km southeast of the intersection of 113°00′W and 26°45′N.

1220b. Along a prominent ridge, north side of a minor canyon on the west side of Mesa La Salina, 84–130 m above the bottom of the exposures of the Bateque Formation in this area, approximately 1.25 km southeast of the intersection of 113°00′W and 26°45′N.

1220c. Along the same prominent ridge where locality CSUN 1220b is located, 160–170 m above the bottom on the exposures of the Bateque Formation in this area.

1220d. Along the same prominent ridge where localities CSUN 1220b and 1220c are located, 180–185 m above the bottom of the exposures of the Bateque Formation in this area.

1291a. South side of a minor canyon near the southern end of Mesa La Salina at 120-m elevation, at 112°56′13″W and 26°40′N.

1291b. South side of the same minor canyon where locality CSUN 1291a is located, 32 m stratigraphically above locality 1291a.

1291c. South side of the same minor canyon where localities CSUN 1291a and 1291b are located, 12–16 m stratigraphically above locality 1291b.

1292. Small bluff immediately north of road on east side of El Saucito Arroyo, about 5 km east of San Juanico, Mexican government topographic quadrangle map (scale 1:50,000) San Juanico (number G12A75), Baja California Sur, Mexico, 1983.

1293. West-facing, 40-m-high bluff on east side of Arroyo El Mezquital, 0.5 km east of the northeast-trending part of the prominent loop in the dirt road leading to San Juanico (13.5 km north), Mexican government topographic quadrangle map (scale 1:50,000) of Punta Pequena (number G12A85), Baja California Sur, Mexico, 1983.

1470. At base of canyon wall along west side of Arroyo San Juan de Abajo, about 40-m elevation, about 0.75 km west of dirt road from San José de Gracia to El Datilon, at 112°44′W and 26°29.5′N, Mexican government topographic quadrangle map (scale 1:50,000) of Punta Santo Domingo (number G12A74), Baja California Sur, Mexico, 1982.

1471. Near middle of same canyon wall where locality CSUN 1470 is located, about 80-m elevation, Mexican government topographic quadrangle map (scale 1:50,000) of Punta Santo Domingo (number G12A47), Baja California Sur, Mexico, 1982.

CSUN MICROFOSSIL LOCALITIES

Mi1. At elevation of approximately 225 m, near top of cliff, along south side of Mesa El Carrizo, at 113°30′W and 26°57′N, about 4.5 km due west of main dirt road leading to Punta Abreojos, Mexican government topographic quadrangle map (scale 1:250,000) of San Isidro (number G12-4), Baja California Sur, Mexico, 1981.

Mi2. Approximately same as macrofossil locality CSUN 1220a, at about 80 m above the bottom of the exposures of the Bateque Formation in this area.

Mi3. Along the same prominent ridge where macrofossil localities CSUN 1220b and 1220c are located, about halfway between them, at 138 m above the bottom of the exposures of the Bateque Formation in this area.

Mi4. Same as macrofossil locality CSUN 1293.

CAS LOCALITIES

30667. Southwest corner of section 27 through NE¼ of the SE¼ of section 28, T28S, R19E, south side of headwaters of Media Agua Creek, Kern County, California, Eocene strata.

30677A. From top of ridge, 0.4 km northwest of locality CAS 30667, Eocene strata.

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Charles L. Hogue

Natural History Museum of Los Angeles County

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A NEW GENUS AND SPECIES OF NET-WINGED MIDGE (DIPTERA: BLEPHARICERIDAE) FROM MEXICO, WITH A REDESCRIPTION OF *PALTOSTOMA BELLARDII* BEZZI

CHARLES L. HOGUE[1]

ABSTRACT. The new genus and species, *Aposonalco amoyote* Hogue, are described from central Mexico. The holotype female of *Paltostoma bellardii* Bezzi, 1913, also from Mexico, is redescribed, with notes on the Mexican blephariceridfauna.

INTRODUCTION

On the south slopes of Nevado de Toluca, in April of 1991, only 200 kilometers west of the urban metropolis of Mexico City, I discovered a thriving population of a species of Blephariceridae so distinct morphologically from other known neotropical apistomyiine genera that it requires recognition as a new genus. Aside from this new entity and three additional undescribed *Paltostoma* in my collection, the blepharicerid fauna of Mexico consists only of *P. bellardii* Bezzi, 1913 (locality not given in the original description) and *Philorus vanduzeei* Alexander, 1963 (NEW COUNTRY RECORD) from the San Pedro Mártir Mountains of the peninsula of Baja California. Many new Mexican members of this family certainly await discovery.

The primary purpose of this paper is to describe the new genus and species. I also take the opportunity to redescribe and figure the holotype female of *P. bellardii,* a species known only from this unique specimen heretofore unexamined and unanalyzed by a specialist on the family.

The terminology and format of this paper follow Hogue (1978, 1981) and Hogue and Bedoya Ortiz (1989). A new anatomical term, "vertexal sclerites" (Fig. 13), refers to a pair of small plates separated dorsally from the cephalic sclerite of the pupa in many blepharicerids. For the pupa, "HM/TA" indicates the ratio of the anterior division (length of anterior margin to posterior margin of scutum) compared to the posterior division (remaining length to terminus of abdomen).

Aposonalco Hogue, new genus

TYPE SPECIES. *Aposonalco amoyote* Hogue, new species.

DIAGNOSIS

The new genus is characterized by the following features, which appear to be apomorphic and uniquely combined within the Apistomyiini:

Adults of both sexes are immediately identified by their small, colocephalous heads on which a small, unfacetted region of the eye is set off dorsally from the facetted portion, a condition found in no other apistomyiine. The subanal pouch of the male terminalia is wide and strongly depressed, with lateral barlike armature; the cerci are elongate and without well-defined ventral arms. The spermathecae of the female terminalia are internally setose; specialized sensilla are present to base of dorsal margin as well as apex of cercus.

The pupa is not distinctive. The larva is distinguished by the pair of eye lenses, a feature shared only by *Paltostoma palominoi* Hogue and Garcés, 1990 and related species on the Greater Antilles, but differs from them most obviously in having only six ventral gill filaments per tuft instead of ten on segments I–V and a well-developed rather than vestigial dorsal pseudopod VII.

DESCRIPTION

The genus is monotypic. *Adults.*—Medium-sized blepharicerids. Head small, colocephalous, lacking

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mandibles and hypopharynx, palpus small, with a single segment. Wing venation as in most Apistomyiini: Rs forked, M2 missing, 1A present, terminating short of wing margin. Tibial spurs 0-0-1. *Male terminalia.*—Genital capsule short and wide; inner dististyle a simple porrect digit; outer dististyle simple, subtriangular; subanal pouch strongly depressed with narrowed opening; aedeagal filaments long and slender with simple apices; cerci elongate, divergent, without well-defined sclerotizations marking ventral arms. *Female terminalia.*—Spermathecae without necks, internally setate. Tubular setae present dorsally on cercus basally as well as apicad. *Pupa.*—Ovate in outline; moderately convex, scutum evenly rounded. Integument dorsally papillose. Branchiae of four erect plates, inner plates narrower and more flexible than wider, rigid outer plates; primary atrial pore of branchia on base of operculum (Zwick, 1977:18). Three adhesive organs, on segments IV–VI. *Fourth instar larva.*—Body lobiform; without dorsal, sclerotized tubercles or plates; weak circumlateral series of specialized setae present. Two antennal segments. Dorsal pseudopod VII small with plantar sole. Six ventral gill filaments per tuft.

ETYMOLOGY

Aposonalco is from Nahuatl ["atl" (combining form "a") = water + "pozonalli" = foam]; its gender is declared feminine.

AFFINITIES

The genus exhibits many of the plesiomorphic character states seen in the tribe Apistomyiini and is only related to other genera by the presence of the double eye lens of the larva, a feature also present in Greater Antillean species (*Paltostoma argyrocincta* Curran, 1927 and relatives). The reduced colocephalic head is a homoplasous derivation from the complete head and does not indicate relationship with the many species of *Paltostoma* and *Limonicola* which also possess this condition. The genus represents a stem group that probably dispersed to Mexico early in tribal history from the South American portion of Gondwanaland. Other American members of this group appear to be *Kelloggina* and an undescribed genus from southern Chile and Argentina, all of which display many plesiomorphies, including three adhesive discs in the pupa. Derivatives of the line are species groups of *Paltostoma*. For a more thorough discussion of the placement of the genus relative to other groups of Apistomyiini, see Hogue (in prep.).

Aposonalco amoyote Hogue, new species

DIAGNOSIS

No other species of *Aposonalco* are known. The species is isolated by the generic characteristics listed above.

DESCRIPTION

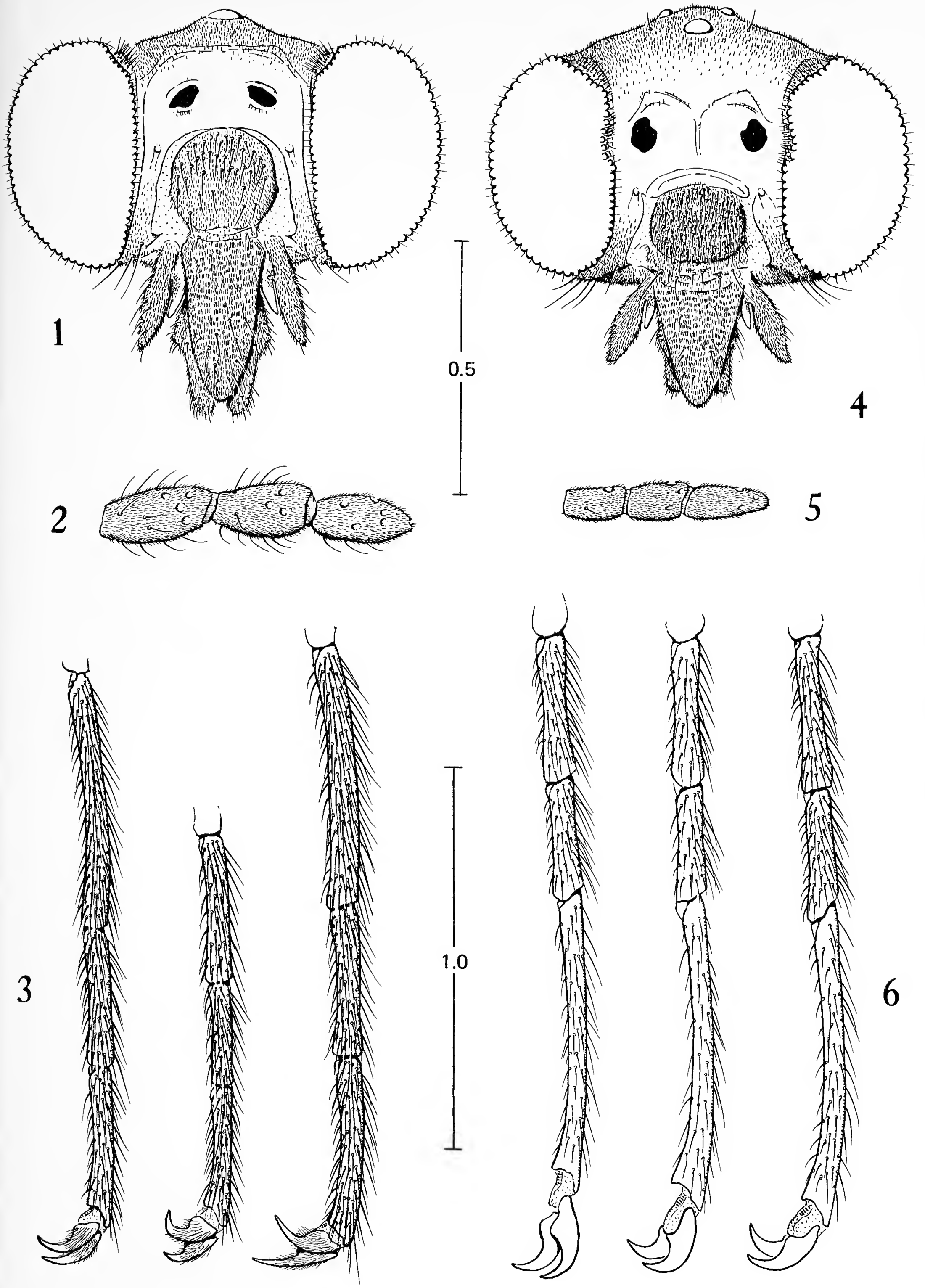
MALE (Figs. 1, 2, 5–8). A composite description from all available material, including holotype. **Coloration.** Wings lightly infuscate. Body generally plumbeus, without silvery pollinosity or opalescent reflections seen in other Apistomyiini; humeral area of thorax light brown; head, antennae, and terminalia near black; abdominal tergites mostly black, darkbrown basad. Legs blackish-brown, femora lighter basad.

Size. A medium-sized blephariceid. Measurements (lengths in mm), from fully mature specimens:

			N	mean	min.	max.
wing			10	7.1	6.8	7.6
fore	femur		10	2.8	2.6	3.0
	tibia		10	3.6	3.3	4.1
	tarsus	1	10	2.5	2.2	2.7
		2	10	1.13	1.03	1.23
		3	10	0.60	0.54	0.63
		4	10	0.33	0.32	0.38
		5	10	0.41	0.38	0.44
mid	femur		10	2.3	2.2	2.4
	tibia		10	2.3	2.2	2.5
	tarsus	1	10	1.2	1.1	1.3
		2	10	0.57	0.52	0.63
		3	10	0.38	0.34	0.43
		4	10	0.26	0.25	0.28
		5	10	0.41	0.38	0.47
hind	femur		10	5.2	4.7	5.5
	tibia		10	5.3	4.8	5.8
	tarsus	1	10	2.6	2.4	2.8
		2	10	1.14	1.03	1.21
		3	10	0.65	0.55	0.72
		4	10	0.39	0.34	0.44
		5	10	0.48	0.42	0.50
Total lengths of legs				41.65	38.60	45.06

Head (Fig. 1). Colocephalous type, dichoptic. Eyes undivided, a narrow, unfacetted region set off dorsally from main facetted portion (possible vestigium of dorsal division?); eyes disjunct, interocular distance equal to 0.4 head width. Ocellar triangle sessile, barely raised. Mouthparts poorly developed: proboscis very short, labium length about 0.4 head width; hypopharynx absent; labella short, lobulate; palpus a single, fusiform segment without sensory pit; galea small, broad with acute apex. Antenna 13-segmented, flagellar segments elongate, ultimate segment slightly shorter than penultimate (Fig. 2), proportions of segments 1.0–1.0–1.5–1.0–0.7–0.7–0.7–0.7–0.7–0.7–0.66–0.66–0.66.

Sensilla. Setiform groups on head capsule and mouthparts as follows: clypeals short and very numerous, forming a moderately dense mat over entire sclerite (less dense than in female); genals few (5–6); medio-occipitals numerous (21); occipitals



Figures 1–6. *Aposonalco amoyote.* **1.** Male head (frontal aspect). **2.** Terminal antennal segments of male. **3.** Terminal tarsal segments of male (fore leg, left; mid leg, center; hind leg, right); lateral aspect. **4.** Female head (frontal aspect). **5.** Terminal antennal segments of female. **6.** Terminal tarsal segments of female (arrangement and aspect as in male). Note: Numerical values on scale bars in figures are in millimeters.

very numerous, generally dispersed, and confluent with postgenals; labials few (5), subapical; facials absent.

Thorax and Appendages (Fig. 3). Anal angle of wing not produced. Venation as typical for Apistomyiini; 1A present and terminating short of wing margin; dense microtrichia throughout membrane. Mid legs much shorter than others, hind legs stoutest; all femora incrassate. Tibial spurs 0-0-1. Progressive leg segment proportions: fore leg 1.0–1.3–0.7–0.5–0.5–0.6–1.2; mid leg 1.0–1.0–0.5–0.5–0.7–0.7–1.6; hind leg 1.0–1.0–0.5–0.4–0.6–0.6–1.2. Tarsomeres 5 similar on all legs, slender, simple (without pollex of heavy setae), only slightly longer than tarsomeres 4; claws similar on all legs, uncinate, simple (without subbasal tooth); microtrichia present over basal half.

Sensilla. Setiform groups on thoracic segments as follows: acrostichals and supraalars apparently absent; preepisternals few (3–4); dorsocentral series complete; prescutellars few; scutellars numerous, generally dispersed (not concentrated in a dense lateral group); episternals few (3–4); metapleurals numerous (13–14); suprametapleurals few (3); a few (3) setae also in membrane anterior to metapleuron. Legs densely setate.

Abdomen. Elongate, almost as long as wings.

Terminalia (Figs. 7–10). Epandrium simple, broad. Genital capsule slightly longer than broad. Genital capsule broad with large aedeagal guide. Cerci moderately long, divergent; interlobular depression deep, widely V-shaped; individual cercus elongate, with rounded apex. Inner arm indistinct, undeveloped, evident only by setae. Subanal pouch complex: somewhat depressed, anterior portion membranous (with minute elongate spiculae), lateral walls modified into elongate arms articulating posteriorly with gonite and continuous mediad with a heavily sclerotized, transverse strap; dorsal wall modified into a flat plate with divergent anterior arms and articulating posteriorly with base of cercal complex. Gonite elongate, angulate, posterior arm narrowed. Tegmen membranous, smooth and evenly rounded apically, without dorsal keel. Outer gonostylus moderately large (length 0.5 midlength of genital capsule), subtriangular, slightly lobulate apically. Inner gonostylus an elongate, smooth, porrect finger with rounded apex. Sperm sac boxlike, with three posterior chambers communicating with aedeagal filaments, chambers long spiculate internally. Piston confluent with sac, poorly developed, apodeme small, fan-shaped, horizontal; vasa deferentia joining to form a single entry to sac via a single, broad, heart-shaped aperture. Neither ventral plate nor lateral tines present. Aedeagal rods long, simple, slightly broader basad, of equal diameter and length.

Sensilla. Epandrium with numerous medium setiforms centrally, extending laterad to margin. Cercus with moderately long setiforms over most of posterior and terminal portions. Setae of inner arm numerous, moderately long setiforms along entire length and directed proximad. Outer gonostylus with medium setiforms general on outer surface, an elongate group of heavier and longer setiforms along middle portion of inner surface. Proctiger with two to four dorsal setiforms medially; four to five small setiforms on undersurface of proctiger lateral to anus.

FEMALE (Figs. 4–6, 11). **Coloration.** Presumably as in male, no eclosed specimens available.

Size. A medium-sized blephariceriid. Measurements (lengths in mm; values from pharate specimens within their pupal cases and therefore insufficient as absolutes, given for relative comparison only):

		N	mean	min.	max.
fore tarsus	2	10	0.56	0.52	0.63
	3	10	0.36	0.28	0.48
	4	10	0.29	0.26	0.38
	5	10	0.74	0.64	0.79
mid tarsus	2	10	0.53	0.48	0.58
	3	10	0.33	0.28	0.37
	4	10	0.27	0.26	0.30
	5	10	0.76	0.69	0.82
hind tarsus	2	10	0.65	0.60	0.72
	3	10	0.39	0.37	0.42
	4	10	0.34	0.32	0.38
	5	10	0.79	0.72	0.84

Head (Fig. 4). Colocephalous and otherwise as in male; mandibles absent. Interocular distance equal to 0.4 head width. Antenna 13-segmented, flagellar segments elongate, ultimate segment slightly longer than penultimate (Fig. 5); proportions of segments 1.0–1.0–1.3–0.7–0.6–0.6–0.6–0.6–0.6–0.6–0.57–0.57–0.6.

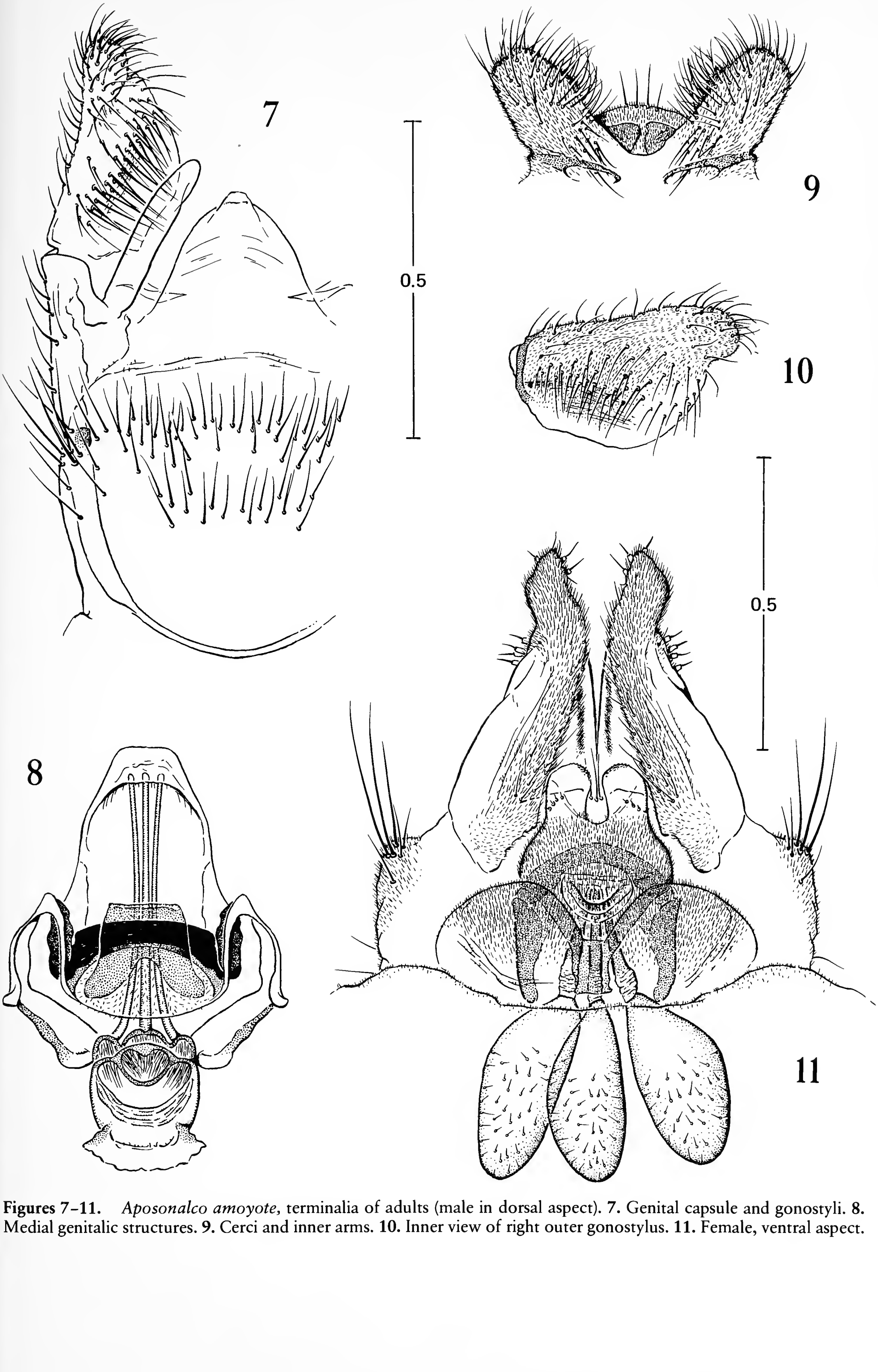
Sensilla. Setiform groups on head capsule and mouthparts as in male; clypeals forming a dense mat.

Thorax and Appendages (Fig. 6). Wing as in male. Legs shorter than in male and not incrassate; tibiae heavy, those of hind legs stoutest. Tibial spurs 0-0-1. Progressive leg segment proportions (tarsomeres 2–5 only): fore leg 1.0–0.64–0.61–2.54; mid leg 1.0–0.64–0.64–2.76; hind leg 1.0–0.60–0.65–2.38. Tarsomeres 5 very long in proportion to segment 4, slender, simple (without pollex of heavy setae); claws similar on all legs, uncinate, simple (without subbasal tooth); microtrichia absent (claw completely nude).

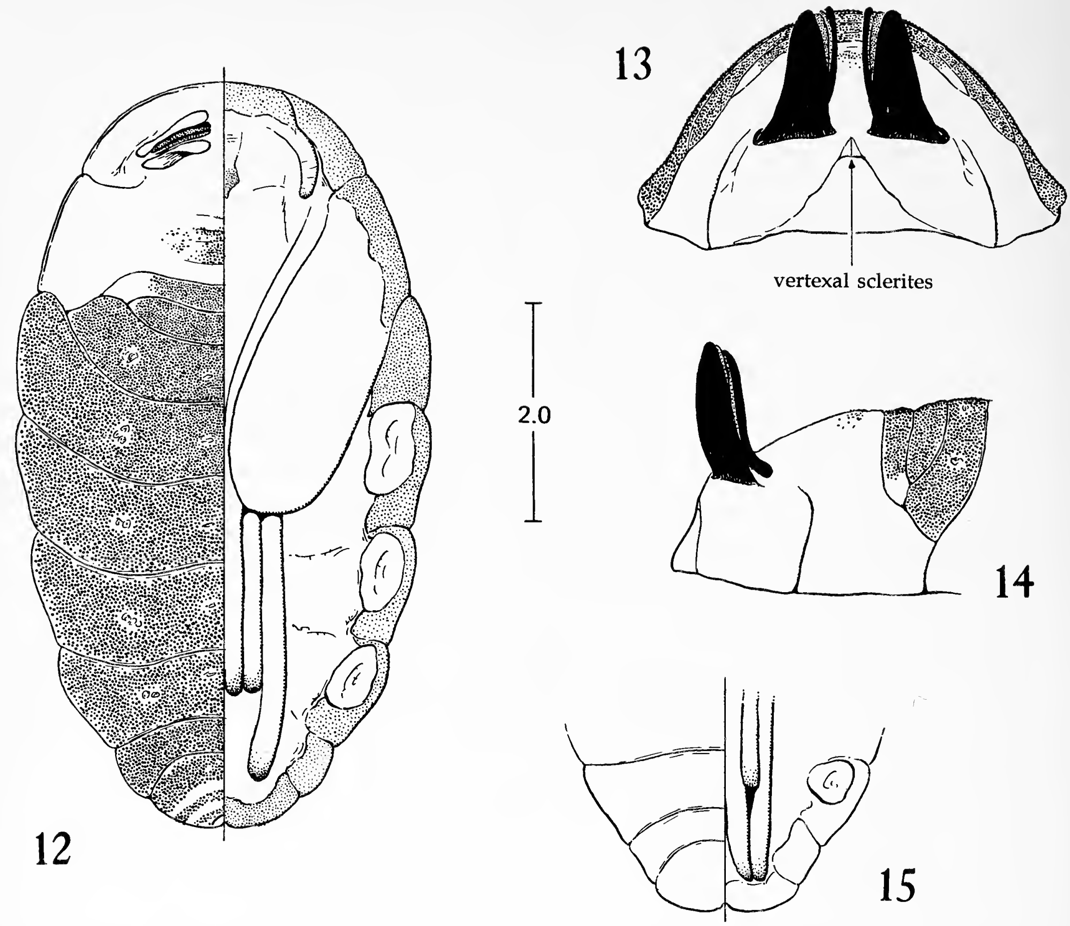
Sensilla. Setiform groups on thoracic segments as follows: acrostichals and supraalars apparently absent; preepisternals few (2–5); dorsocentral series complete; prescutellars few; scutellars numerous, general (not concentrated in a dense lateral group); a single episternal; metapleurals numerous (13–16); suprametapleurals few (4); a single seta also in membrane anterior to metapleuron. Legs generally lightly setate; a dense setal mat on inner surface of mid trochanter (not present in male).

Abdomen. Elongate, as in male.

Terminalia (Fig. 11). Sternite VIII lightly scler-



Figures 7–11. *Aposonalco amoyote,* terminalia of adults (male in dorsal aspect). **7.** Genital capsule and gonostyli. **8.** Medial genitalic structures. **9.** Cerci and inner arms. **10.** Inner view of right outer gonostylus. **11.** Female, ventral aspect.



Figures 12–15. *Aposonalco amoyote,* pupa. **12.** Entire female (dorsal left, ventral right). **13.** Anterior portion, frontal aspect. **14.** Anterior portion, lateral aspect. **15.** Posterior portion of male.

otized throughout, anterior portion a bow-shaped, ligulate piece, broadly lobate posteriorly; medial depression deep, widely V-shaped; internal sclerotization rectangular; VIIIth sternite lobe rounded. Hypogynial plate internally complex, with median folds, base slightly wider than lobes; lobes simple, elongate, with a few minute microtrichia apically, ventral division undeveloped. Anterior margin of gonotreme ribbed. Stirrup-shaped plate present. Spermathecae three, equal in size and shape, asymmetrically elongate ovoid; necks absent, duct membranous for a short distance from corpus, thence a smooth, straight, sclerotized tube.

Sensilla. Sternite VIII with medium to long setiforms laterally. Hypogynial plate and lobes of sternite VIII non-setate. Tergite X with two to three long setiforms apically. Sternite X with four small, short setiforms submedially. Distal two-thirds of corpora of spermathecae set internally with short, straight setae with well-developed alveoli. Tubular sensilla present over entire dorsal portion of cercus, from apical lobes to base.

PUPA (Figs. 12–15). **Integument.** Border terminate, sharply underfolded and ventrally sclerotized narrowly on entire periphery. Papillose dorsally; absent from thorax except for small field medioposteriad on scutum, medial only on metathoracic tergite; abdominal papillae evenly spaced, close set. Individual papillae small, subequal in diameter throughout, slightly oval in outline shape (approximately 16 × 20 micra), non-spiculate.

Size. Medium for family. Measurements, male (N = 10): body length 6.0 (5.7–6.4), width 3.4 (3.0–3.6); female (N = 10): body length 6.6 (6.3–7.0), width 3.6 (3.4–3.9). Male slightly smaller (0.85) than female.

General. Outline shape oviform, L/W both sexes = 1.8. Margin of thorax smoothly continuous with abdomen (not abruptly narrowed). Anterior division small in relation to posterior (HM/TA male and female = 0.3). Dorsum of abdomen convexly rounded, cross section hemiovate; sides slightly inclined. Dorsal sclerites: cephalic sclerite an equilateral triangle, dorsal portion divided into two small vertexal sclerites; margin slightly reflexed. Branchial sclerite broad, evenly rounded. Anterior margin and sides of scutum steeply inclined, former in line with anterior branchial plates. Suture separating meta-

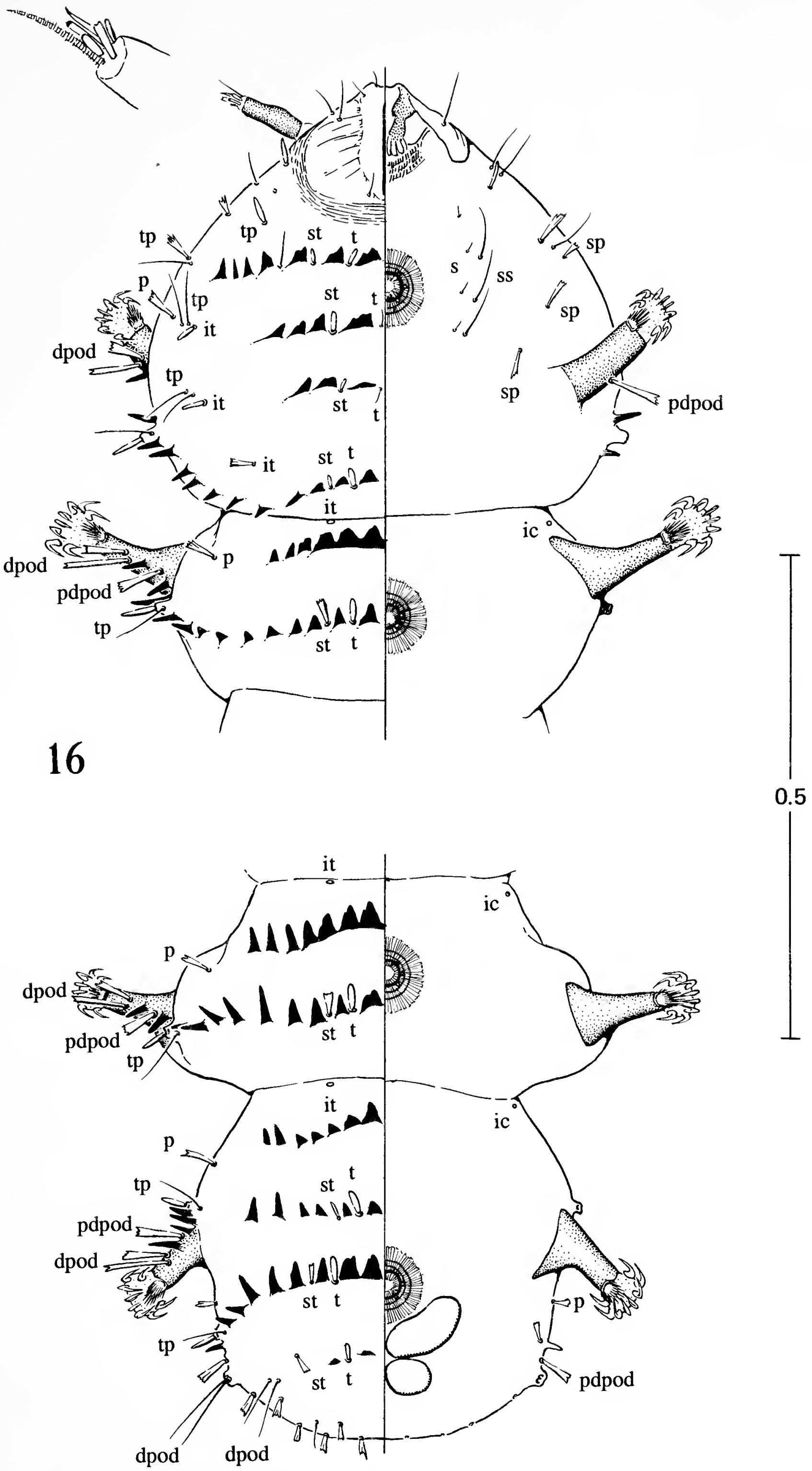


Figure 16. *Aposonalco amoyote,* first instar larva (dorsal left, ventral right). Significant primary setae labeled: it—intertergal, ic—intercalary, t—tergal, st—subtergal, tp—tergopleural, pdpod—pre-dorso-pseudopodal, dpod—dorso-pseudopodal ("geminate"), p—pleural, sp—sternopleural, ss—substernal, s—sternal.

thoracic from abdominal tergite I smoothly curved at midline. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

Branchiae. Erect; outer plates rigid and heavily sclerotized; inner plates narrower, thinner and flexible. Plates compact; in frontal aspect all plates slightly convergent. Bases of outer plates slightly expanded, lateral expansions the more extensive and converging around bases of inner plates. Outer plates elongate, with acute apices, somewhat curved; inner plates also elongate, similar to outer in shape.

Ventral Sclerites. Antennal cases short, slightly exceeding base of wing pad, other cases of head appendages obscure; leg cases of both sexes unequal in length: in male fore and hind leg long, coterminate, mid leg shorter; in female hind leg long, mid and fore legs short and coterminate. Three adhesive discs (on abdominal segments IV–VI).

FIRST INSTAR LARVA (Fig. 16). Based on two specimens mounted on slides in Hoyer's medium (CLH 91-52, 91-53). Body form cylindrical. Outline shape of anterior division ovate.

Integument. Dorsum poorly sclerotized. Corrugations distinct, mostly irregular. Venter uncorrugated; pseudopods sclerotized.

Size. Large for the family. Measurements of two available specimens: body length 1.6 and 1.4, head capsule length 0.17, antenna 0.06.

Head. Dorsal sclerites weakly developed laterally, bounded posteriorly by series of concentric corrugations. Egg burster distinct. A single, short segment in antenna.

Trunk. Two transverse rows of flattened, slightly irregular denticles on segments II–VI, a single row on segments I and VII–VIII, of VIII weakly developed; otherwise without convexities, projections, tubercles, or large plates. Pseudopods and dorsal pseudopods combined into single conical structure; apices of each with small plate with radiating spines and eversible membrane bearing eight small sclerotized hooks. Lateral gills absent.

Anal Division. Dorsal pseudopod of segment VII undeveloped, a small tubercle. No terminal incision. Terminal lobe broadly and smoothly arcuate throughout.

Primary Sensilla. Medium setiform, elongate oviform, and narrow foliose forms with irregular apices; arranged as figured (Fig. 16). Head and antennal setae as figured, the latter a group of six varied types, longest setiform. Trunk sensilla as follows: tP submedial; stP mediolateral, slightly laterad of stM–T; tpM–T paired, equal long slender setiforms; tpI–VII unequal (inner setiform at base of tubercle, outer elongate oviform on apex of tubercle); tpI–VI distant from stI–VI; tI–VII larger than stI–VII; dpodI–VI foliose (inner shorter and wider) on distal third of combined dorsal pseudopod-pseudopod; dpodVII on small tubercle; itI–VI obscure, faintly visible alveoliforms without setae; icI–VI far laterad, alveoliform; isI–VI indiscernible. Terminal setae few, short.

FOURTH INSTAR LARVA (Fig. 17). **General.** Body form lobiform. Outline shape of anterior division subhexagonal.

Integument. Dorsum moderately well sclerotized. Corrugations distinct, mostly irregular. Small (segment I) to extensive denticulate areas at bases of pseudopods ventrally; entire terminal border extensively denticulate ventrally.

Coloration. Trunk pigmentation even, light-brown; sclerotized portions pale brown, terminal border lightly pigmented.

Size. Medium for the family. Measurements (N = 10; prepupal larvae with branchiae visible): body length 7.3 (6.9–8.0), head capsule width 1.9 (1.8–2.0), antennal segment lengths, basal 0.13 (0.11–0.14), apical 0.15 (0.14–0.17).

Head. Two distinctly separated lenses in eye. Antenna short, two-segmented, segment proportions 1.0–1.2.

Trunk. Dorsum of abdominal segments I–VI smoothly rounded, without convexities, projections, tubercles, or large plates; numerous small platelets in positions as figured. Pseudopods short, broad, truncate. Ventral gills with six filaments (sometimes five on segment VI).

Anal Division. Dorsal pseudopod small, directed obliquely posterolaterad; plantar surface present. Terminal incision small. Terminal lobe short, posterior margin broadly and smoothly arcuate throughout.

Primary Sensilla (medium setiforms unless otherwise described). tM–T in line, very close to midline. tpM present. tpI–VI distant from stI–VI, tI–VII setiform. stM–T weak to absent. Inner tpII–VI set well anteriad. Terminal setae few and short, ventral.

Dorsal Modified Sensilla. Minute oviforms dorsad, becoming gradually larger and more falciform laterad on trunk segments. All elongate oviform and small on head capsule, generally and evenly spaced in positions as figured. Circumlateral series poorly developed, of elongate falciforms. Sensilla of pseudopods all setiform and generally dispersed dorsally, none ventrally. Background field of fine setiforms absent.

SPECIMENS EXAMINED

TYPES. HOLOTYPE MALE (point mounted on pin), ALLOTYPE female (pharate, ex associated pupal skin, dissected and mounted whole on slides Nos. CLH 91-45H, 91-45W, 91-45B, 91-45F; 25 MALE PARATYPES (point mounted): MEXICO, State of Mexico, southeast slope Nevado de Toluca, Río Temascaltepec, Temascaltepec, 1650 meters, 5 April 1991, C.L. and J.N. Hogue and S. Ibáñez-Bernal. Type specimens deposited as follows: Holotype and allotype in the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM); one male paratype each in National Museum of Natural History, Washington, D.C. (USNM), American Museum of Natural History, New York (AMNH); 22 paratypes in Natural History Museum of Los Angeles County (LACM).

OTHER MATERIAL. Same data as types [238 pupae and pupal skins, 229 larvae]. Deposited as follows: all in

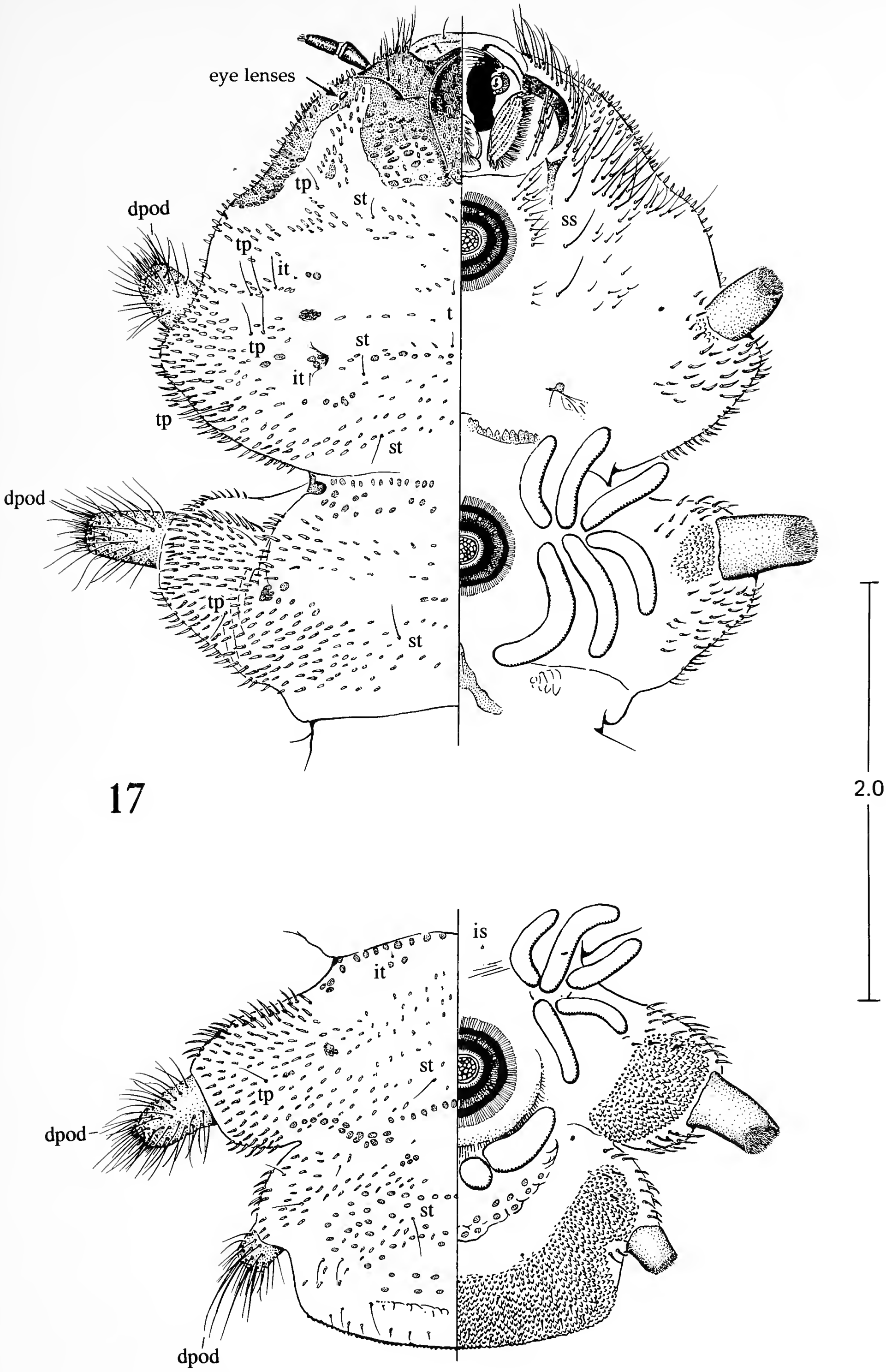


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Figure 17. *Aposonalco amoyote*, fourth instar larva (dorsal left, ventral right). Significant primary setae labeled as in Figure 16; is—intersternal.

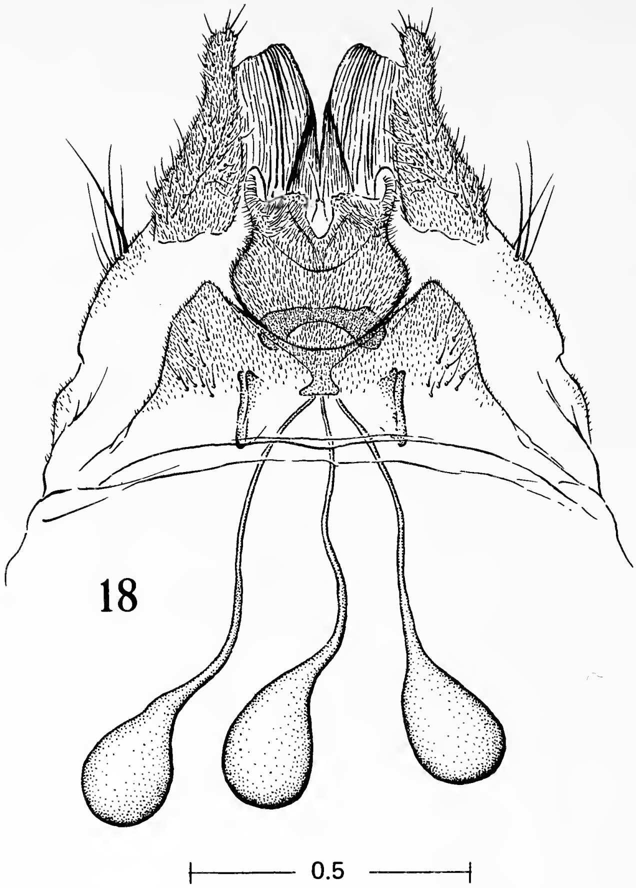

Figure 18. *Paltostoma bellardii* Bezzi. Female holotype, ventral view of terminalia.

LACM except one larva and one pupa each in USNM, AMNH, and UNAM. Same locale as types, 11 May 1991, S. Ibáñez-Bernal, C. Martínez-Campos, and H. Huerta [1 pupa, 39 larvae, LACM]. MEXICO, State of Veracruz, 3 km from Xico, between Municipios of Xico and Teocelo, Cascada de Texolo, Río de La Antigua, 25 May 1991, S. Ibáñez-Bernal [78 larvae, LACM].

ETYMOLOGY

The species name is from Nahuatl ["atl" (combining form "a") = water + "moyotl" = midge (Hispanicized for euphony)].

DISTRIBUTION

The species is apparently widespread, at least through the eastern portion of the transverse volcanic belt of central Mexico, as indicated by the disjunct collections at the type locality (State of Mexico) and one site in central Veracruz State.

REMARKS

At 1650 meters the Río Temascaltepec is a permanent, 6–7th order stream flowing southwest from the peak of Nevado de Toluca through the small town of Temascaltepec. The type material was collected from the main flow at a point immediately above the bridge on the road entering the town to the south. At this point the stream forms a series of rapids with a stony bottom and emergent boulders. In spite of considerable recreational and power use of its waters, the stream remains clear and unpolluted. Temperature of the water at the time of collection was 18° C.

Collections were made between 1300 and 1430 hours on a clear, hot day. Adult males were very numerous, flying with their heads facing upstream in front of the downstream faces of emergent boulders, often in heavy spray. Immature individuals were extremely abundant on the upper surfaces of a gray, slatelike rock in whitewater areas. Associated with the new species were abundant larvae of an undescribed species of *Paltostoma* and the psychodid genus *Maruina*.

Paltostoma bellardii Bezzi

Paltostoma superbiens ? Osten Sacken, 1878a:17, 218.

"unbeschriebene Gattung und Art . . . aus Mexico" Osten Sacken, 1878b:411.

"mexican *Paltostoma*" Osten Sacken, 1895:166.

Paltostoma bellardii Bezzi, 1913:63. Edwards, 1929: 68. Alexander, 1958:824. Hogue, 1971:8.7. Type locality: "Mexique."

REDESCRIPTION OF HOLOTYPE

FEMALE (Fig. 18). Incomplete, specimen missing some leg segments. **Coloration.** All surfaces yellowish-brown with silvery pollinosity, forming irregular patches which appear and disappear as specimen is rotated in front of light source; antenna blackish-brown.

Size. A medium-sized blephariceríd. Measurements (lengths in mm): wing 8.5; fore leg missing; mid femur 6.6, mid tibia 6.7; hind femur 7.8, hind tibia 7.1.

Head. Normal type, dichoptic. Eyes undivided, disjunct dorsally, interocular distance 0.3 width of head capsule. Ocellar triangle sessile, slightly raised. Mouthparts well developed: proboscis moderately long, 1.1 head width; mandibles present; palpus with three segments, sensory pit present at apex of last segment, segments 2–3 elongate, approximately equal in length; galea long and curved. Antenna 15-segmented, flagellar segments barrel-shaped, ultimate segment subequal to penultimate.

Sensilla. Setiform groups on head and mouthparts indeterminable.

Thorax and Appendages. Anal angle of wing not produced. Venation as typical for Apistomyiini; 1A short, terminating short of wing margin; membrane hyaline and without evident microtrichia. Leg characters mostly indeterminable, hind tibia with a single long spur (although a space next to its base may be occupied by a second spur in complete specimens).

Sensilla. Setiform groups on thoracic segments indeterminable.

Terminalia (Fig. 18). Sternite VIII narrowly lobate posteriorly, medial depression shallow, widely U-shaped; internal sclerotization hour-glass-shaped; VIIIth sternite lobe acute. Hypogynial plate quadrate, base slightly wider than lobes; lobes with finger-like ventral division densely set with long microtrichia apicad. Stirrup-shaped plate present. Spermathecae three, equal in size and shape, flask-shaped with long, gradually tapering necks leading directly to membranous ducts.

Sensilla. Sternite VIII with short, fine setiforms on lateral portion of lobe only (14–15). Hypogynial plate non-setate. Tergite X with two long setiforms apically. Sternite X with four small short setiforms submedially.

TAXONOMY

The exact locality and other information concerning the collection of the holotype are unknown. The specimen in the Torino Museum is in fair condition, although lacking several leg segments; one wing is separate from the thorax and glued to a celluloid slip. The specimen bears the following original labels: "181." "Mexique" to which I have added two labels as follows: "♂ genitalia/on slide no:/CLH 91-82" and "HOLOTYPE"/Paltostoma/bellardii/Bezzi 1913/affix by/C.L. Hogue '91."

DISTRIBUTION

The species is known only from the type locality which, unfortunately, is not specified in the original description.

ACKNOWLEDGMENTS

The trip on which the new genus was found was financed by grants from the Ralph J. Weiler Foundation and Taylor Science Fund of the Life Sciences Division of the Natural History Museum of Los Angeles County. I am grateful to Dr. José G. Palacios Vargas and Biol. Sergio Ibáñez-Bernal of Mexico City, and my son James N. Hogue, for their company in the field and logistical assistance on that trip and to Ibáñez for providing additional material. I also greatly appreciate the cooperation of Dr. Antonio Rolando for the loan of the holotype of *P. bellardii* which is in the Museo di Zoologia, Dipartimento di Biologia Animale, Universita di Torino, Italy.

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A Review of *Perdita*, Subgenus *Macrotera* (Hymenoptera: Andrenidae)

Roy R. Snelling and Bryan H. Danforth

Natural History Museum of Los Angeles County

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A REVIEW OF *PERDITA*, SUBGENUS *MACROTERA* (HYMENOPTERA: ANDRENIDAE)

ROY R. SNELLING[1] AND BRYAN H. DANFORTH[2]

ABSTRACT. The taxonomy of the species comprising *Perdita,* subgenus *Macrotera* is reviewed; these bees are oligoleges on *Opuntia* (Cactaceae). A key to the species is given; two new species are described from Mexico: *P. pipiyolin* from Jalisco and *P. nahua* from Michoacan; new synonymy is proposed: *P. secunda* Cockerell, 1904, and *P. texana ablusa* Timberlake, 1958 = *P. texana* (Cresson, 1878). Appropriate morphological features are illustrated for all species and the known distributions are mapped.

INTRODUCTION

Macrotera, although originally described as a genus by F. Smith (1853), has long been treated as a subgenus of *Perdita* F. Smith (1853) (e.g., Timberlake, 1954). The few species occur in Mexico and in Texas and New Mexico in the United States. All are presumed oligoleges on *Opuntia* and possibly other Cactaceae. The species were treated by Timberlake (1954, 1958). With the discovery of two additional Mexican species, we deem it appropriate to review the previously described species in addition to describing the new ones.

Species of *Macrotera* are relatively large for *Perdita* (body length up to 10 mm); males have heads that are conspicuously broader than long, with the inner eye margins somewhat divergent below. Although the head is broader than long in females, the disparity is less extreme than in the males. Other features characteristic of *Macrotera* include: glossa of both sexes 2–3 times length of prementum and extending between metacoxae; second segment of maxillary palpus longer than first or any of the following segments; both sexes with well developed facial foveae; marginal cell of forewing large, at least subequal to first submarginal; stigma slender and tapering; metatibia and basitarsus of male with long, flattened, scale-like hairs; both sexes with basitibial plate on metatibia; tibial spurs stout and abruptly hooked at apex in both sexes; metasoma of male flattened and broader than mesosoma.

MATERIALS AND METHODS

INSTITUTIONAL COLLECTIONS

During the course of this review we have studied material from the following collections: Bee Biology and Systematics Laboratory, USDA, Logan, Utah (BBSL); Natural History Museum, London (BMNH); California Academy of Sciences (CAS); Central Texas Melittological Institute, Austin, Texas (CTMI); Natural History Museum of Los Angeles County (LACM); United States National Museum of Natural History (USNM); Universidad Autónoma de México (UNAM); University of California, Berkeley (UCB) and University of California, Riverside (UCR); University of Kansas (UKAN).

TERMINOLOGY

In general, the terminology employed here is standard among bee systematists. For a description of puncture sizes and spacing, see Snelling (1985). The following abbreviations are used in the descriptions.

HL—head length: in frontal view, the midline distance between the lower clypeal margin and the summit of the vertex.

HW—head width: in frontal view, the maximum distance across the eyes.

IOD—interocellar distance: the minimum distance between the posterior ocelli.

LID—lower interocular distance: the distance between the inner eye margins at the level of the lateral angle of the clypeus.

OD—ocellus diameter: the transverse diameter of the anterior ocellus.

OOD—ocellocular distance: the minimum distance between either posterior ocellus and the adjacent inner eye margin.

OVD—ocellovertexal distance: with head in frontal view, the minimum distance between either posterior ocellus and the dorsal margin of the vertex.

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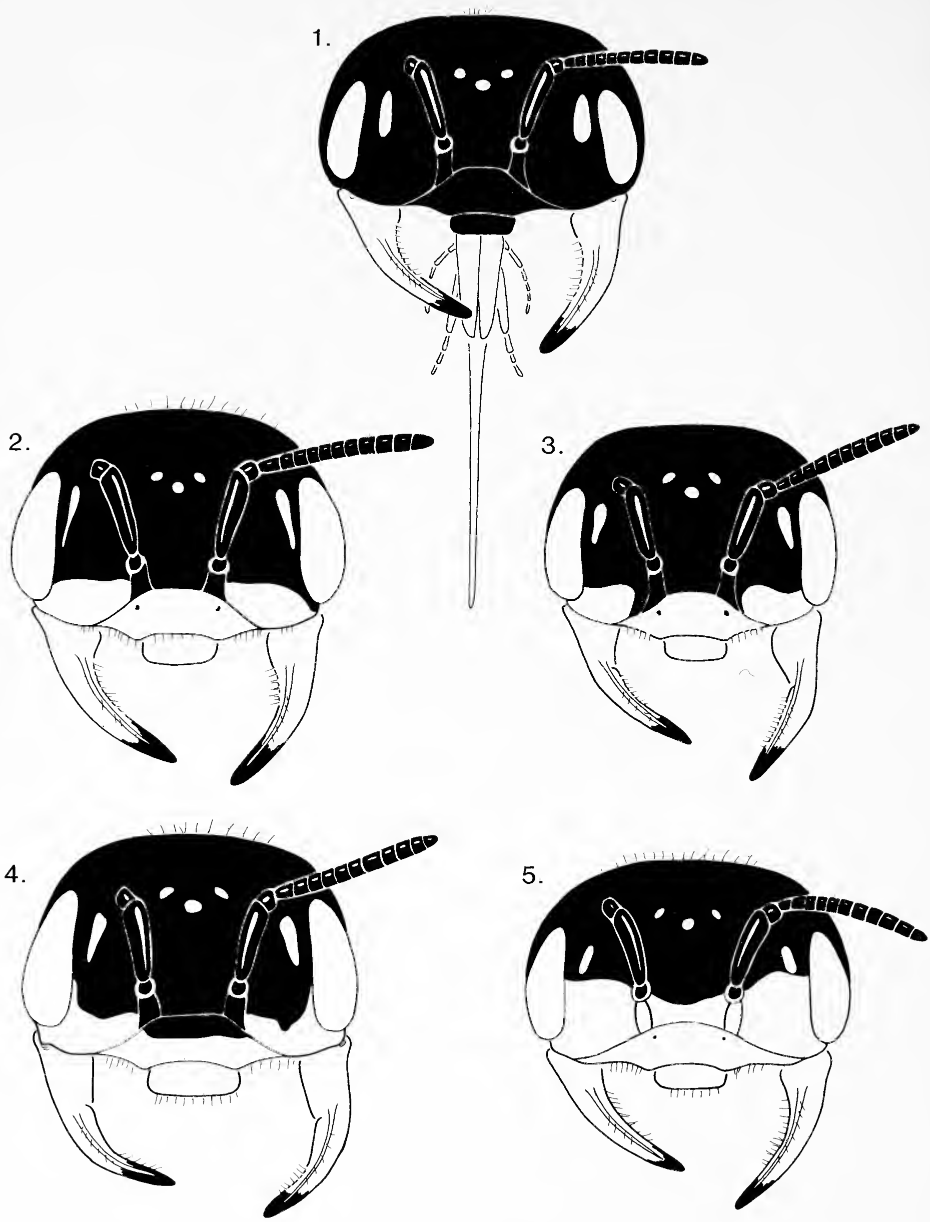


Figures 1–5. Frontal views of male heads; (1) *P. texana,* (2) *P. bicolor,* (3) *P. nahua,* (4) *P. pipiyolin,* (5) *P. sinaloana.*

TL—total length: the sum of HL + length of mesosoma (from anterior margin of mesoscutum to a point directly above metasomal attachment) + length of metasoma (from point of attachment of mesosoma to farthest extremity).

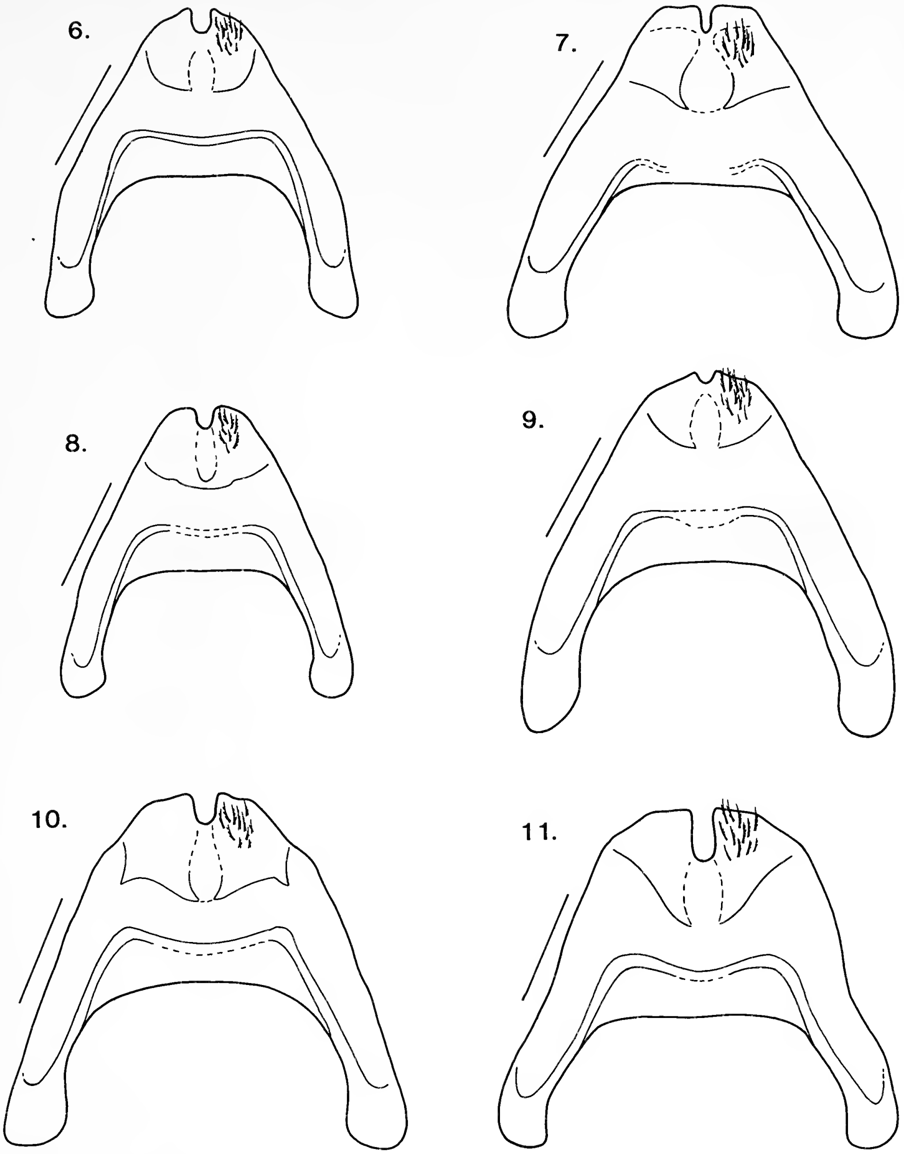
UID—upper interocular distance: with head in frontal view, the minimum distance between the inner eye margins.

WL—wing length: minimum distance from margin of tegula to extremity of wing tip.

The last visible metasomal sternum of the females is characteristically different for each species. In order to be properly examined, it must first be removed and cleared in KOH. For this reason, we have not used these sterna as key characters, although they are illustrated for each species (Figs. 6–11).

KEY TO SPECIES OF *MACROTERA*

1a. Male; antenna with 13 segments 2
b. Female; antenna with 12 segments 7
2a. Lower face with clypeus and lateral face marks yellowish (Figs. 2–5) 3
b. Lower face concolorous with remainder of face, distinctly not yellowish (Fig. 1) 6
3a. Facial fovea long and narrow (but broader above), about parallel with inner eye margin



Figures 6–11. Ventral views of female S6; (6) *P. texana,* (7) *P. bicolor,* (8) *P. nahua,* (9) *P. crassa,* (10) *P. pipiyolin,* (11) *P. sinaloana.* Scale bar = 0.5 mm.

and upper end separated from eye margin by 0.25 times length of fovea or less; mesoscutal interspaces dull and conspicuously tessellate 4

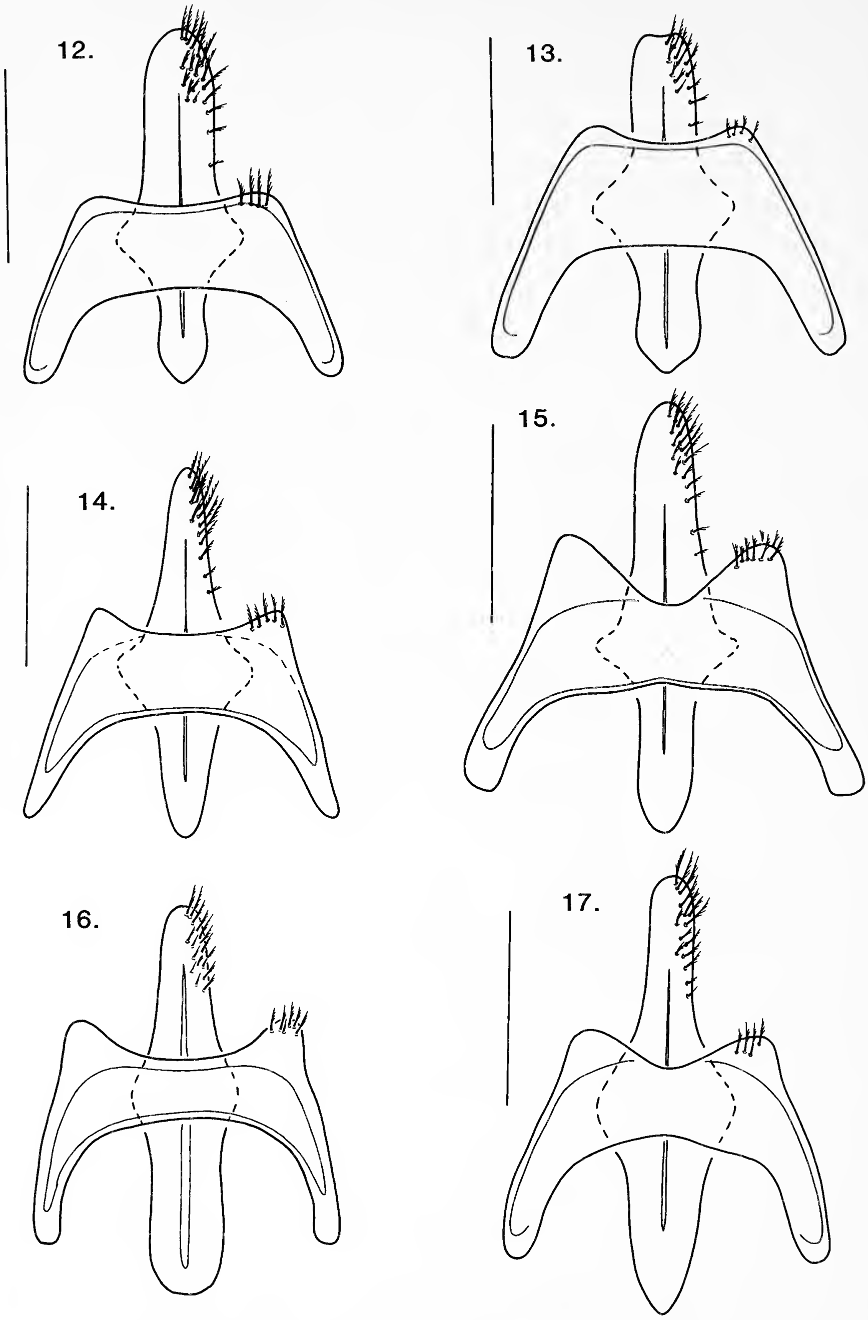
b. Facial fovea short and relatively broad, strongly oblique to inner eye margin, upper end separated from eye margin by about 0.50 times length of fovea (Fig. 5); mesoscutal interspaces distinctly shiny and very weakly tessellate over most of disc .... *sinaloana* Timberlake

4a. Supraclypeal area with distinct impunctate zone along midline; punctures in posteromedian area of mesoscutum and of middle of scutellum mostly separated by a puncture diameter or more .... *bicolor* (F. Smith)

b. Supraclypeal area subcontiguously punctate and without impunctate median zone; punctures of mesoscutum and scutellum uniformly subcontiguous 5

5a. Extreme base of propodeum roughened but without short longitudinal rugulae; aedeagus without ventral hook-like process (Fig. 21) .... *pipiyolin,* new species

b. Extreme base of propodeum roughened and with short longitudinal rugulae; aedeagus with ventral hook-like process (Fig. 22) .... *nahua,* new species



Figures 12–17. Ventral views of male S7 and S8; (12) *P. texana,* (13) *P. crassa,* (14) *P. pipiyolin,* (15) *P. bicolor,* (16) *P. sinaloana,* (17) *P. nahua.* Scale bar = 0.5 mm.

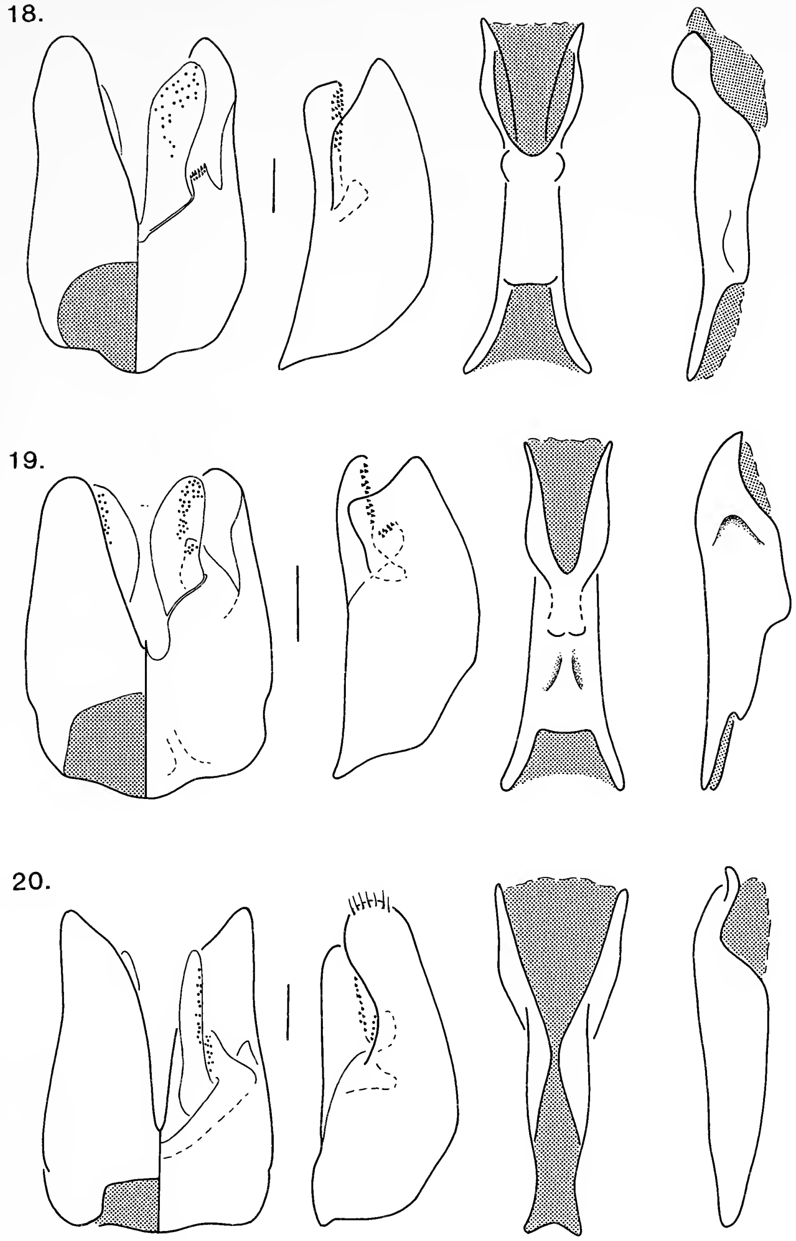
6a. Front of head, including clypeus and paraocular area, with conspicuous hairs, many of them distinctly barbulate; subgenital plate (metasomal sternum 7) broad, apex subtruncate (Fig. 13) .... *crassa* Timberlake

b. Frons with short, simple hairs, clypeus and paraocular area virtually without hairs other than some exceedingly short, simple hairs on clypeus; subgenital plate narrow, apex narrowly rounded (Fig. 12) .. *texana* (Cresson)

7a. Scopal hairs flattened and conspicuously wavy or crinkled 8

b. Scopal hairs simple, i.e., long, somewhat flattened and evenly tapering to acute, often curved apices 9

8a. Extreme base of propodeum roughened but



Figures 18–20. Dorsal, ventral, lateral views of male genital capsule and dorsal and lateral views of the aedeagus; (18) *P. texana,* (19) *P. crassa,* (20) *P. bicolor.* Scale bar = 0.25 mm.

without short longitudinal rugae; side of propodeal disc with some hairs at least 0.07 mm long .... *pipiyolin,* new species

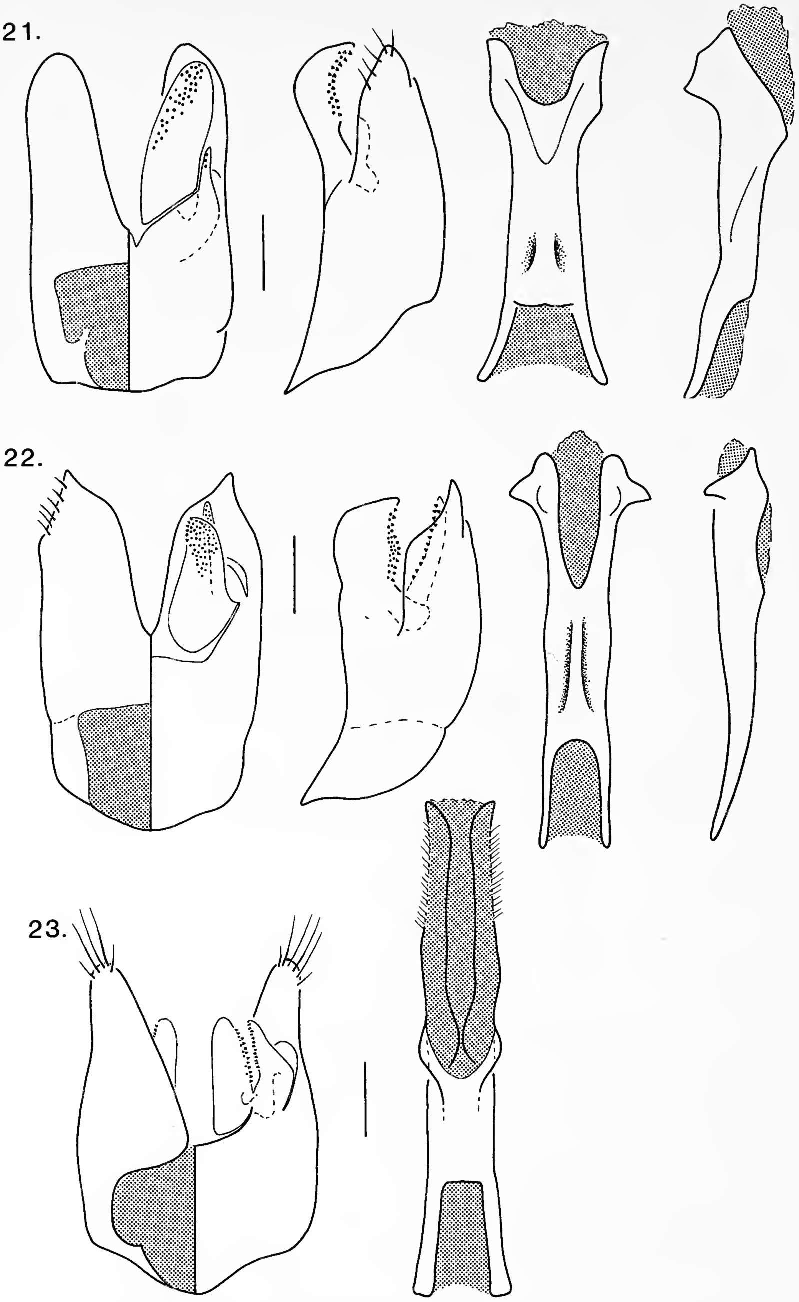
b. Extreme base of propodeum roughened and with several short longitudinal rugae on each side of middle; hairs on side of propodeal disc uniformly very short, none over 0.05 mm long .... *nahua,* new species

9a. Propodeal disc with abundant long, conspicuously plumose hairs 10

b. Propodeal disc bare or with sparse, very short and inconspicuous hairs near lateral margin 11

10a. Punctures of clypeal disc subcontiguous, median impunctate line absent or narrow and incomplete; mesoscutum dull and sharply tessellate between punctures .... *bicolor* (F. Smith)

b. Punctures of clypeal disc very irregularly spaced, median impunctate line broad and often poorly defined, disc sometimes with only scattered punctures; mesoscutum shiny and



Figures 21–23. Dorsal, ventral, lateral views of male genital capsule and dorsal and lateral views of the aedeagus; (21) *P. pipiyolin,* (22) *P. nahua,* (23) *P. sinaloana.* Scale bar = 0.25 mm.

weakly tessellate between punctures .... *crassa* Timberlake

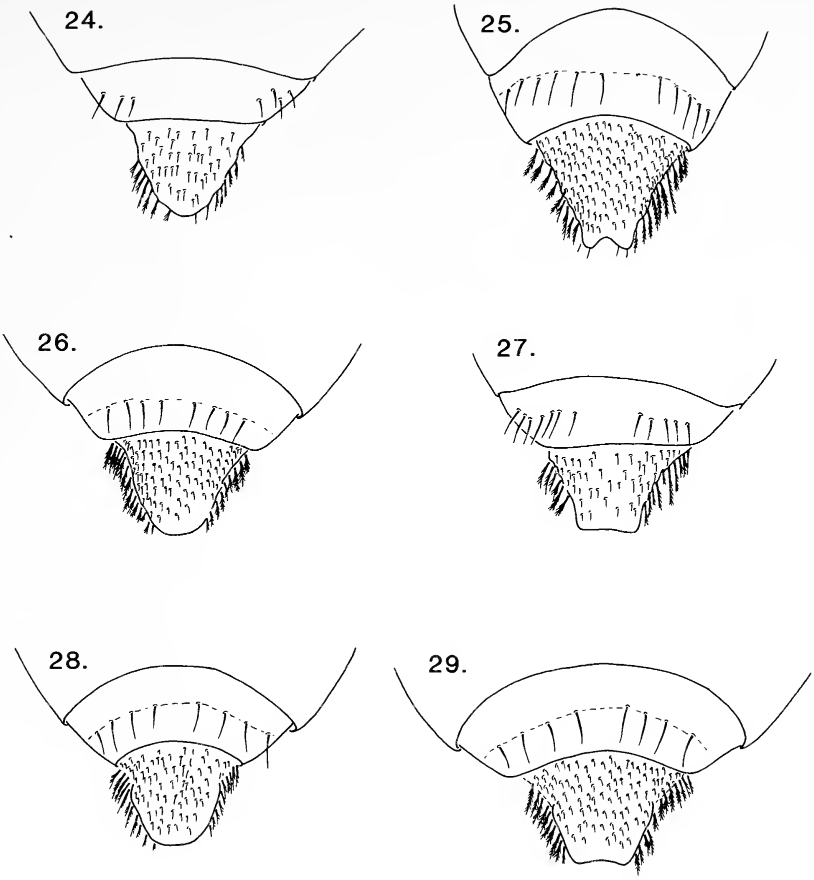
11a. Face between lateral ocelli and upper end of facial foveae slightly shiny, distinctly tessellate between variably spaced, minute punctures, some interspaces several times puncture diameter; middle of scutellum shiny, punctures often separated by several times puncture diameter .... *texana* (Cresson)

b. Face between lateral ocelli and upper end of facial foveae moderately shiny between mixed minute to fine punctures that are mostly separated by about puncture diameter or less; scutellum slightly shiny between mostly subcontiguous punctures .... *sinaloana* Timberlake

Perdita (*Macrotera*) *bicolor* (F. Smith)

Figures 2, 7, 15, 20, 24, 31, 35

Macrotera bicolor F. Smith, 1853:130; ♀.
Perdita bicolor: Cockerell, 1905:321.



Figures 24–29. Dorsal views of male T7; (24) *P. bicolor,* (25) *P. sinaloana,* (26) *P. pipiyolin,* (27) *P. texana,* (28, 29) *P. nahua* (showing extent of intra-specific variation).

Perdita (*Macrotera*) *bicolor:* Timberlake, 1954:352, 353; ♀ ♂. Timberlake, 1958:375, 376; ♂ ♀.

The male of *P. bicolor* is one of four species with yellow face marks. It differs from *P. sinaloana* by the long, narrow facial foveae that are parallel with the inner eye margins (Fig. 2). From *P. pipiyolin* and *P. nahua,* it differs by the distinctly sparser punctation of the supraclypeal area and the center of the mesoscutal disc. Both *P. crassa* and *P. texana* lack yellow face marks.

The presence of numerous long, plumose hairs on the propodeal disc will separate the female from all except *P. crassa.* From that species *P. bicolor* differs in the evenly spaced clypeal punctation, but with a distinct impunctate median line, and the dull, densely tessellate mesoscutal interspaces.

Although most females have metasomal terga 2–5 or 3–5 largely reddish, we have seen a few with the entire metasomal dorsum blackish brown. Females of *P. bicolor* have the inner margins of the forecoxae (in ventral view) straight and the inner apical angle abrupt (Fig. 31).

This species is known only from the eastern highlands of Mexico where it has been collected in the States of Hidalgo and Puebla.

Perdita (*Macrotera*) *crassa* Timberlake

Figures 9, 13, 19, 35

Perdita (*Macrotera*) *crassa* Timberlake, 1958:375, 376–377; ♀ ♂.

Males of *P. crassa* are easily recognized by the lack of yellowish face marks, the densely punctate supraclypeal area, and the broad, apically subtruncate subgenital plate (Fig. 13). The female shares with *P. bicolor* the presence of numerous long plumose hairs on the propodeal disc, but differs from that species in the very irregular spacing of the clypeal punctures and the smooth, shiny interspaces between mesoscutal punctures.

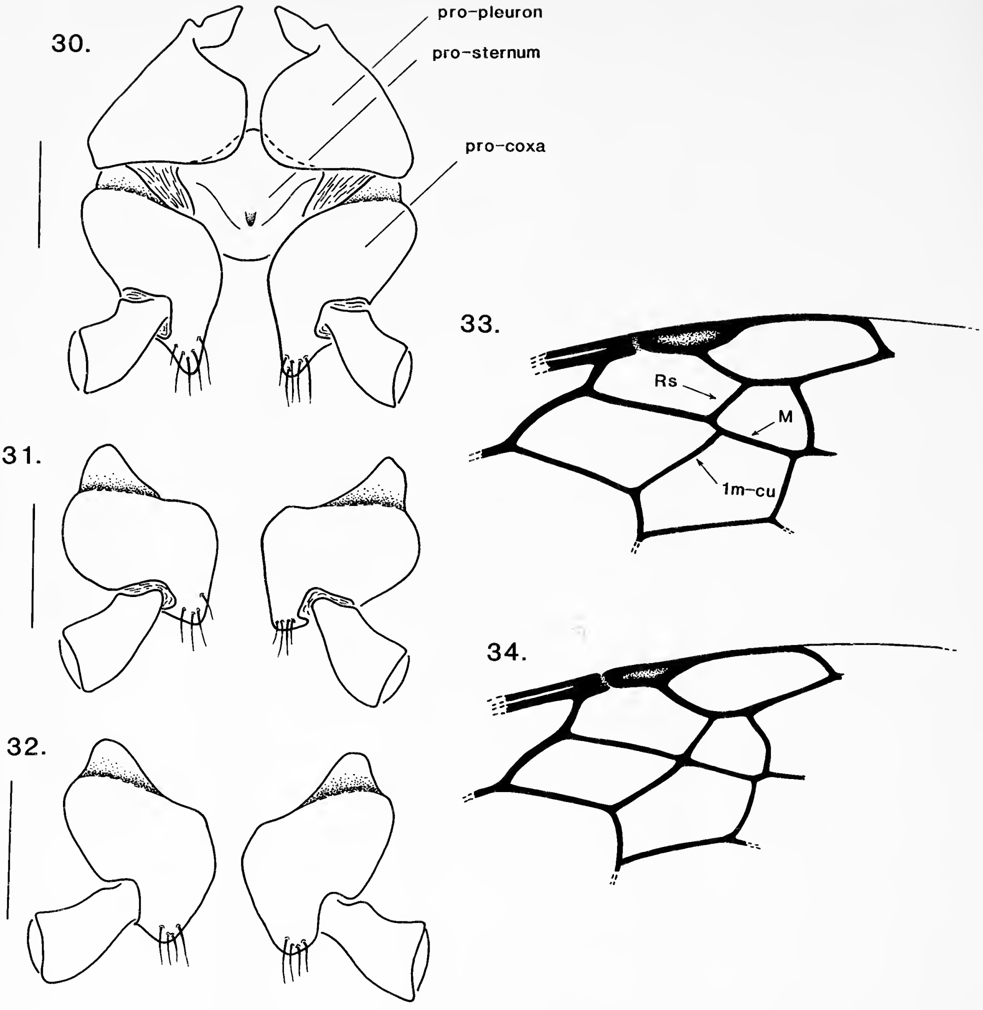
Although presently known only from Texas, *P. crassa* probably will be found to occur in Mexico, at least in the states of Nuevo León and Coahuila.

***Perdita* (*Macrotera*) *nahua,* new species**

Figures 3, 8, 17, 22, 28, 29, 33, 35

DIAGNOSIS

FEMALE. Separable from all *Macrotera* species except *P. pipiyolin* by the distinctly wavy or "crinkled" scopal hairs; differs from *P. pipiyolin* by the



Figures 30–34. **30–32.** Ventral views of female forecoxae; (30) *P. pipiyolin,* (31) *P. bicolor,* (32) *P. texana.* Scale bar = 0.5 mm. **33, 34.** Forewing venation; (33) *P. nahua,* (34) *P. texana.*

distinctly rugulose propodeal base and the very short hairs laterad on the propodeal disc; additionally, the metasoma is reddish to largely brown.

MALE. Separable from *P. crassa* and *P. texana* by the yellow clypeus and lateral face marks; separable from *P. sinaloana* by the long facial fovea that parallels the inner eye margin; separable from *P. bicolor* by the densely punctate supraclypeal area and the shiny, subcontiguously punctate mesoscutal disc; separable from *P. pipiyolin* by the sharply rugulose propodeal base and the prominent ventral process of the penis valve (Fig. 22).

DESCRIPTION

FEMALE. Measurements (mm): Holotype HW 2.42; HL 1.84; WL 5.2; TL 8.8. Paratypes: HW 2.23–2.54; HL 1.77–2.00; WL 4.8–5.5; TL 8.1–9.2.

Head about 1.3 times as broad as long; inner eye margins slightly divergent below, LID about 1.03 times UID; vertexal margin evenly convex in frontal view. Facial fovea linear, parallel to inner eye margin and distinctly broader above. IOD about 1.6 times OD; OOD about 2.9 times OD; OVD about equal to OD. Antennal scape extending almost to level of posterior ocelli; first flagellar segment about as long as broad and no longer than second segment. Clypeus shiny, with or without narrow impunctate median line, but most of disc with subcontiguous moderate punctures. Supraclypeal area duller, punctures fine and contiguous to subcontiguous, sometimes sparse along midline; lower paraocular area shiny between sparse punctures finer than on clypeus, becoming duller above between minute subcontiguous punctures. Frons dull and sharply tessellate between minute subcontiguous punctures. Vertex dull and tessellate, ocellocular area with minute subcontiguous punctures that grade into coarser, more separated punctures on vertexal summit.

Mesoscutum shiny over most of disc, becoming

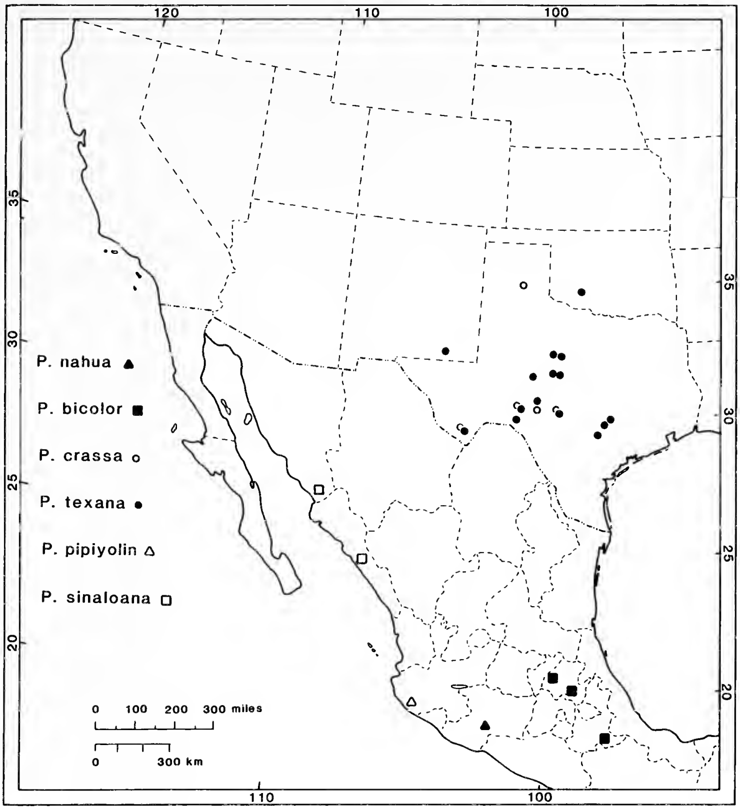


Figure 35. Distribution map of *P.* (*Macrotera*) species.

lightly tessellate toward margins, punctures minute to fine, dense, even along mid-line. Scutellum similar, punctures not noticeably sparser in middle. Metanotum dull, densely tessellate, punctures minute and subcontiguous to contiguous. Mesepisternum slightly shiny and roughened between dense fine punctures. Metepisternum shinier, with scattered fine punctures. Propodeum moderately shiny, basal margin narrowly roughened and with short longitudinal rugulae; lateral portions of disc with fine piligerous punctures. Inner margins of procoxae nearly straight, inner apical angle produced and acute (similar to Fig. 30). Tibial spurs stout, apices abruptly hooked; hairs of metatibial scopa long and distinctly wavy or "crinkled".

Metasoma moderately shiny, terga transversely lineolate, sculpture becoming coarser on succeeding segments, translucent apical margins broad on terga 2–4; punctures ultraminute to minute, denser on successive segments and laterad on each. Pygidial plate broadly rounded or subtruncate at apex, margins slightly reflexed, disc granulopunctate. Sterna similar to terga but discs more densely punctate; S6 as in Figure 8.

Pilosity normal for *Macrotera*; mesoscutal hairs suberect to erect, mostly very short but with scattered longer hairs; hairs across middle one-half of metanotum very short, subappressed, and directed cephalad; lateral margins of propodeal disc with inconspicuous hairs less than 0.05 mm long.

Color head and most of mesosoma dark brownish, mesoscutum darker, antenna and legs paler; metasoma reddish to largely reddish brown, segment margins distinctly reddish. Tegula yellowish. Wings clear light brownish, veins mostly yellowish brown, subcosta and stigma darker.

MALE. Measurements (mm): HW 2.48–2.97; HL 1.44–2.06; WL 5.0–5.6; TL 7.3–8.4.

Head (Fig. 3) broader than mesosoma, about 1.5 times as broad as long; inner eye margins weakly divergent below, LID about 1.05 times UID; vertexal margin nearly flat across middle one-half in anterior view. Facial foveae about as in female but margins less defined. IOD about 2.0 times OD; OOD 4.8–6.0 times OD; OVD 2.5–2.7 times OD. Antennal scape extending to about level of posterior ocelli; first flagellar segment about as long as wide and slightly longer than second segment. Facial sculpture about as in female but clypeal punctures slightly finer, mostly subcontiguous and median impunctate line very narrow or absent; supraclypeal area with median impunctate line narrow or absent.

Mesosoma as described for female, but punctures of disc of mesoscutellum uniformly subcontiguous in center. Femora, especially metafemur, robust; tibial spurs stout, apices abruptly hooked.

Metasoma, except usual sexual differences, as in female; pygidial plate (Fig. 28, 29) broad, with slightly reflexed margins, apex subtruncate, disc distinctly coarsely rugose. Subgenital plate and genitalia as illustrated (Figs. 17, 22).

Pilosity about as in female except scopa lacking, meso- and metatibiae with widely spaced, long, flat, scale-like hairs.

Color as in female except: mandible, except reddish apex; labrum; clypeus, except small to large mediobasal brown spot; lower paraocular area, sometimes including stripe along inner margin of eye nearly to summit, all pale yellowish. Protibia yellowish red, metasoma bright reddish.

TYPE MATERIAL

Holotype female: Ziculcan, Michoacán, MEXICO, 8 July 1988 (G. Rodriguez G.). Paratypes: 5 ♀♀, 4 ♂♂, same data as holotype. Holotype in UNAM; paratypes in LACM, UNAM, USNM.

ETYMOLOGY

This species is named for the Nahua people who inhabited central Mexico prior to the Spanish invasion. The name is a noun in apposition.

DISCUSSION

In most respects both sexes of *P. nahua* are very similar to *P. pipiyolin.* The prominent, acute ventral process of the male aedeagus, however, will permit ready separation of this species from all other *Macrotera* males.

The females of *P. nahua,* together with those of *P. pipiyolin,* have a very characteristic scopa in which the scopal hairs have very attenuated apices that are distinctly wavy or crinkled; in all other species the scopal hairs, although often attenuated, are curled apically. These two species are also characterized by their relatively densely punctate clypeus and mesoscutum. The presence of numerous short, longitudinal to oblique rugules across the base of the propodeum will separate females from *P. nahua* from those of *P. pipiyolin,* as will the reduced and very short pilosity at the side of the propodeal disc.

Females of this species and of *P. pipiyolin* often have vein 1m-cu of the forewing joining M beyond Rs (Fig. 33); in the four remaining species of *Macrotera* 1m-cu and Rs are interstitial (Fig. 34). Little reliance can be placed on this character of venation because some specimens of *P. pipiyolin* have the two veins interstitial.

Of the paratype females of *P. nahua,* one has the entire metasoma bright reddish. In two specimens the terga are largely reddish medially but extensively brownish at the sides. The two remaining females have the metasomal terga mostly dark but with dull reddish margins on segments 1–5.

Although no floral data are provided with these specimens, the pollen in the scopae appears to be that of a cactus species, probably *Opuntia.*

Perdita (*Macrotera*) *pipiyolin*, new species

Figures 4, 10, 14, 21, 26, 30, 35

DIAGNOSIS

FEMALE. Separable from all other species of *Macrotera* except *P. nahua* by the wavy or "crinkled" hairs of the metatibial scopa; separable from *P. nahua* by the weakly roughened propodeal base and the longer hairs laterad on the propodeal disc; *P. pipiyolin* and *P. nahua* are both additionally separable from all other species except *P. texana* by the shiny, densely punctate mesoscutal disc and from *P. texana* by the presence of conspicuous, though short, hairs laterad on the disc of the propodeum.

MALE. Separable from *P. crassa* and *P. texana* by the yellow clypeus and lateral face marks; separable from *P. sinaloana* by the long facial fovea that parallels the inner eye margin; separable from *P. bicolor* by the densely punctate supraclypeal area and the shiny, subcontiguously punctate mesoscutal disc; separable from *P. nahua* by the weakly roughened propodeal base and the lack of a ventral hook-like process on the aedeagus (Fig. 21).

DESCRIPTION

FEMALE. Measurements (mm): Holotype, HW 2.55; HL 2.10; WL 5.9; TL 10.1. Paratypes: HW 2.39–2.65; HL 1.94–2.13; WL 5.2–6.0; TL 9.3–10.2.

Head about 1.2 times as wide as long; inner eye margins slightly divergent below, LID about 1.04 times UID; vertexal margin evenly convex in frontal view. Facial fovea linear, parallel to inner eye margin, distinctly broader at upper end. IOD about 1.6 times OD; OOD about 2.9 times OD; OVD about equal to OD. Antennal scape extending to level of anterior ocellus; first flagellar segment distinctly longer than broad and about twice as long as second segment. Clypeus shiny, with narrow impunctate median line, but most of disc with subcontiguous moderate punctures. Supraclypeal area duller, punctures fine and contiguous to subcontiguous, sometimes sparse along mid-line; lower paraocular shiny between sparse punctures finer than on clypeus, becoming duller above between minute subcontiguous punctures. Frons dull and sharply tessellate between minute subcontiguous punctures. Vertex dull and tessellate, ocellocular area with minute subcontiguous punctures that grade into coarser, more separated punctures of vertexal summit.

Mesoscutum shiny over most of disc, becoming lightly tessellate toward margins, punctures minute to fine, dense, even along mid-line. Scutellum similar, but punctures noticeably sparser in middle. Metanotum dull, densely tessellate, punctures minute and subcontiguous to contiguous. Mesepisternum slightly shiny and rougher between dense fine punctures. Metepisternum shinier, with scattered fine punctures. Propodeum moderately shiny, basal margin narrowly roughened but without short longitudinal rugulae or punctures; lateral portions of disc with fine piligerous punctures. Inner margin of forecoxa nearly straight, inner apical angle produced and acute (Fig. 30). Tibial spurs stout, with abruptly hooked apices; hairs of metatibial scopa long and distinctly wavy or "crinkled."

Metasoma moderately shiny, terga transversely lineolate, sculpture becoming coarser on succeeding segments, translucent apical margins broad on terga 2–4; punctures ultraminute to minute, denser on successive segments and laterad on each. Pygidial plate broadly rounded or subtruncate at apex, margins slightly reflexed, disc granulopunctate. Sterna similar to terga but discs more densely punctate; S6 as in Figure 10.

Pilosity normal for *Macrotera*; mesoscutal hairs suberect to erect, mostly very short but with scattered longer hairs; hairs across middle one-half of metanotum very short, subappressed and directed cephalad; lateral margins of propodeal disc pilose, some hairs at least 0.07 mm long, hairs becoming very short mediad.

Color of head and most of mesosoma dark brownish, mesoscutum darker, antenna and legs paler; metasoma reddish brown, segment margins paler. Tegula yellowish. Wings clear light brownish, veins mostly yellowish brown, subcosta and stigma darker.

MALE. Measurements (mm): HW 2.32–3.23; HL 1.58–2.13; WL 5.1–5.7; TL 7.9–9.5.

Head (Fig. 4) broader than mesosoma, about 1.5 times as broad as long; inner eye margins weakly divergent below, LID about 1.1 times UID; vertexal margin nearly flat across middle one-half in anterior view. Facial foveae about as in female but margins less defined. IOD 1.5–1.6 times OD; OOD 3.1–4.5 times OD; OVD 2.4–3.0 times OD. Antennal scape extending to about level of posterior ocelli; first flagellar segment about as long as wide and slightly longer than second segment. Facial sculpture about as in female but clypeal punctures slightly finer, mostly subcontiguous, and median impunctate line very narrow or absent; supraclypeal area with median impunctate line narrow or absent.

Mesosoma as described for female, but punctures of disc of mesoscutellum uniformly subcontiguous in center. Femora, especially metafemur, robust; tibial spurs stout, apices abruptly hooked.

Metasoma, except usual sexual differences, as in female; pygidial plate (Fig. 26) broad, with slightly reflexed margins, apex weakly convex to subtruncate, disc with distinct subcontiguous fine punctures. Subgenital plate and genitalia as illustrated (Figs. 14, 21).

Pilosity about as in female except scopa lacking, meso- and metatibiae with widely spaced, long, flat, scale-like hairs.

Color as in female except: mandible, except reddish apex; labrum; clypeus, except small to large mediobasal brown spot; lower paraocular area, sometimes including stripe along inner margin of eye nearly to summit, all pale yellowish. Protibia yellowish red. Metasoma dull reddish.

TYPE MATERIAL

Holotype female: Estación Biologica "Chamela", near San Patricio, Jalisco, Mexico, 7 Sept. 1980 (S.H. Bullock), on *Opuntia* sp. Paratypes (all from Chamela): 5 ♀♀, 15 ♂♂, same data as holotype; 16 ♀♀, 27 ♂♂, 10–14 July 1989 (T. Griswold), on *O. excelsa* (9 ♀♀, 15 ♂♂) and *Lonchocarpus cochleatus* (1 ♀); 2 ♂♂, 20 July 1989 (T. Griswold); 1 ♀, 2 ♂♂, 21 July 1986 (R. Ayala), on *O. excelsa*; 88 ♀♀, 27 ♂♂, 11–14 and 20 July 1989 (C.D. Michener, R.W. Brooks, A. Roig Alsina), on *O. excelsa* (34 ♀♀, 23 ♂♂), *Coccoloba barbadensis* (1 ♀), malaise trap (52 ♀♀). Holotype in collection of UNAM; paratypes in BBSL, LACM, UCR, UKAN, UNAM (Chamela), and USNM.

ETYMOLOGY

The specific name, a noun in apposition, is the singular form of the Nahuatl name for a bee.

DISCUSSION

The similarity of the scopal hairs between this species and *P. nahua* has already been commented on in the discussion of that species. Other similarities have also been noted above. The longer and more abundant pilosity on the propodeal side will separate females of *P. pipiyolin* from those of *P. nahua*, as will the smooth basal area of the propodeum.

Males of the two species are similar and in both species there is a distinct ventral process near the apex of the aedeagus. That of *P. nahua* is small and acute (Fig. 22), whereas in *P. pipiyolin* the process is quite robust and obtuse (Fig. 21). The base of the propodeum in *P. pipiyolin* is, as in females of this species, smooth and without rugulae.

Aside from the variations in size noted above, all specimens are quite consistent in their characters, including color.

All the type locality females appear to be oligoleges on *Opuntia excelsa*; the single female collected on *Lonchocarpus cochleatus* has only *Opuntia* pollen in her scopa.

Perdita (Macrotera) sinaloana Timberlake

Figures 5, 11, 16, 23, 25, 35

Perdita (Macrotera) sinaloana Timberlake, 1958: 375, 376, 377–378; ♀ ♂.

The type pair was collected 50 miles S of Los Mochis, Sinaloa, Mexico. The types are now in the CAS collection. In addition to the types we have seen one female: 25 mi S Navajoa, Sonora, MEXICO, 13 Sept. 1963 (K.H. Janzen; UCB).

The short, oblique facial foveae are especially characteristic of the male. The female most closely resembles that of *P. texana,* another species with few or no hairs at the side of the propodeal disc. In the above key we have chosen not to cite the differences in female mesoscutal punctation noted by Timberlake (1958). The differences do exist but are not as clear-cut as suggested in his key. In *P. texana* the punctures are up to about 0.026 mm in diameter and are mostly separated by about a puncture diameter, but in many specimens there are some interspaces of up to about 2.5 times a puncture diameter in the middle of the disc. In the type female of *P. sinaloana* the punctures of the middle of the disc range between 0.025 and 0.051 mm in diameter, mostly over 0.030 mm. Many interspaces are up to about 3 times a puncture diameter, but some are as little as a puncture diameter. So, although the differences do exist, they are difficult to appreciate if comparative material is not available.

Perdita (Macrotera) texana (Cresson)

Figures 1, 6, 12, 18, 27, 32, 34, 35

Macrotera texana Cresson, 1878:70; ♀.
Macrotera megacephala Cresson, 1878:71; ♂.
Perdita texana: Cockerell, 1896:52.
Perdita secunda Cockerell, 1904:205; ♀. NEW SYNONYMY.
Perdita (Macrotera) texana: Timberlake, 1954:352, 353; ♀ ♂.
Perdita (Macrotera) texana texana: Timberlake, 1958:375, 376; ♀ ♂.
Perdita (Macrotera) texana ablusa Timberlake, 1958:375, 376; ♀ ♂. NEW SYNONYMY.

The type of *P. secunda,* from an unknown locality in Mexico, is in the BMNH. Except for the dark brownish metasoma it appears to be the same as *P. texana,* especially in the punctation of the clypeus, mesoscutum, and scutellum, and the pilosity of the propodeal disc. We do not regard the color difference as significant and so treat *P. secunda* as a synonym of *P. texana.*

We have also synonymized Timberlake's subsp. *ablusa,* described from New Mexico and western Texas. This form was characterized largely on the basis of its more extensive reddish color and paler wings, a trivial distinction at best. And, because such specimens occur sporadically within populations of the "typical" form in central Texas, the distinction appears to be specious as well.

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LATE PLANKTONIC NAUPLIAR DEVELOPMENT OF AN ASCOTHORACIDAN CRUSTACEAN (?PETRARCIDAE) IN THE RED SEA AND A COMPARISON TO THE CIRRIPEDIA

MARK J. GRYGIER

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LATE PLANKTONIC NAUPLIAR DEVELOPMENT OF AN ASCOTHORACIDAN CRUSTACEAN (?PETRARCIDAE) IN THE RED SEA AND A COMPARISON TO THE CIRRIPEDIA

MARK J. GRYGIER[1]

ABSTRACT. Three metanaupliar instars, evidently NIV–VI (or maybe NIII–V), of one or more closely related species of ascothoracidans tentatively identified as Petrarcidae (endoparasites of Scleractinia) are described on the basis of five larvae caught at 0–250 m depth in the central and southern Red Sea. Besides increases in size and in the number of pores and sensilla on the dorsal shield, there are minor increases in the complexity of the appendage armament. Four specimens have abnormalities of at least one appendage. The normal antennae and mandibles are compared with those of NIV–VI in the Cirripedia Thoracica. Unlike cirripeds, the petrarcids have a seta on the antennal coxa and a corolla of claws on the enditic spine of the mandibular basis. The exopods of both limbs have more segments in the petrarcids and, in the mandibles, more setae as well. The antennal basis and first endopodal segment have feathered setae like chthamaloid and some lepadomorph nauplii. There are fewer apical setae on the antennal endopod and more setae on the first segment of the mandibular endopod than in cirriped nauplii. The possibility of homology between cirriped frontolateral horns and a pair of marginal dorsal shield processes in petrarcid nauplii is reconsidered.

INTRODUCTION

Comparative larval development can be of great use in clarifying and corroborating relationships among crustaceans. Recent comparative ontogenetic studies in the Cirripedia include Kado (1982), Moyse (1987), Elfimov (1988), Korn (1988), and Egan and Anderson (1989). In the parasitic group Ascothoracida, which is closely related to the Cirripedia within the maxillopodan subclass Thecostraca, the most accessible nauplius larvae have been brooded ones (reviewed by Grygier, 1987a). Except for the earliest stages, these nauplii are not very useful for comparative study. They do not develop complex appendage armament and, indeed, sometimes have vestigial appendages. Grygier (1987a, 1987b) published some hypotheses about homologous structures and phylogeny in the Maxillopoda based mostly on such larvae, but the dearth of information about free-swimming ascothoracidan nauplii, especially planktotrophs with complex appendage armament, has hindered further progress.

Planktotrophic nauplii seem to occur in three families of Ascothoracida, but no complete planktotrophic naupliar series have been documented. Several Lauridae and Petrarcidae have brooded NI nauplii with large enditic spines on the antennae and mandibles (e.g., Grygier, 1985a, 1985b, 1990c) and so does one species of Synagogidae (Grygier, 1990b), but the corresponding NII is known in detail only in two laurids and one petrarcid (Yosii, 1931; Grygier, 1990a). On the basis of those few cases, Grygier (1990a) listed several differences between the appendages of ascothoracidan NII and cirriped NII nauplii. Three last-instar metanauplii of possible laurids have been described (Grygier, 1987a; Boxshall and Böttger-Schnack, 1988); these should be NVI if the six naupliar instars of the lecithotrophic laurid *Baccalaureus falsiramus* Itô and Grygier (1990) are also typical for planktotrophs. Boxshall and Böttger-Schnack (1988) also described a purported earlier instar (NIII or NIV; discussed by Grygier, 1990a) of one of their forms.

Here I report on a series of three metanaupliar instars of what is probably a petrarcid ascothoracidan collected in plankton in the Red Sea. The Petrarcidae are endoparasites of scleractinian corals. Though this material provides only half the story for this particular species (or set of closely related species), in combination with the known NI and NII of *Zibrowia* sp. (see Grygier, 1990a), five of the supposed six naupliar instars of planktotrophic petrarcids are now known and available for comparison to cirriped nauplii.

METHODS AND MATERIALS

Five specimens were sorted and sent to me by R. Böttger-Schnack, and they are deposited in the Natural History

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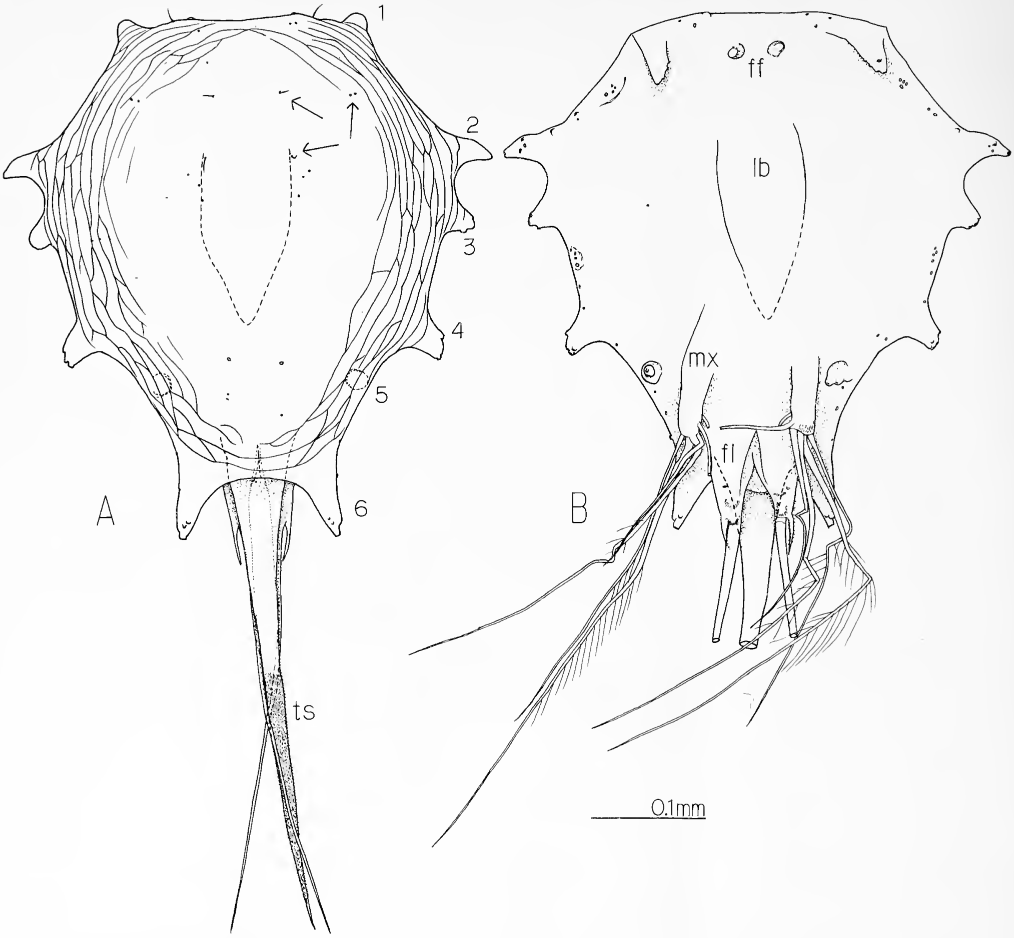

Figure 1. Petrarcid metanauplius NIV (or NIII?) from Red Sea, sta. 703. **A,** dorsal view, appendages omitted, marginal processes numbered, ventral position of labrum indicated by dashed line, two dorsal sensilla and double pore indicated by arrows; **B,** ventral view, first three pairs of appendages and distal parts of caudal armament omitted, broken distal half of labrum marked by dashed line. Abbreviations: ff, frontal filaments; fl, furcal lobe; lb, labrum; mx, maxillule; ts, terminal spine.

Museum of Los Angeles County (LACM). They were taken in vertical hauls of multiple opening–closing nets equipped with 55 μm mesh during "Meteor" Cruise 5, leg 5 in the Red Sea during the summer of 1987 (Weikert, 1988, as cited in Böttger-Schnack, 1991): one NVI (or NV?), sta. 682, central Red Sea, haul 28/4, July 25, 1987, 17:17–17:30, 21°14.1′N, 38°05.3′E, 50–100 m fraction over 1,888 m depth (LACM 87-407.1); one NV (or NIV?), sta. 703, southern Red Sea, haul 39/1, August 3, 1987, 17:29–17:40, 15°34.1′N, 41°54.9′E, 200–250 m fraction over 953 m depth (LACM 87-408.1); one NIV (or NIII?) and two NVI (or NV?), sta. 703, haul 39/5, same data as previous entry but 0–50 m fraction (LACM 87-409.1, 87-409.2, 87-409.3).

Each specimen was drawn in dorsal view in glycerine. Each was also examined in ventral view before dissection, but details of the appendages were difficult to see. Therefore, the three anterior pairs of appendages of all five specimens, and usually also the labrum, were dissected free with a needle and fine forceps and, together with the remaining naupliar body (in ventral view), mounted in glycerine jelly and drawn using standard optics with an open diaphragm, supplemented with phase contrast. The oil immersion lens was used with anisole.

In the following descriptions any seta with two opposing rows of long setules is called plumose except for a few with very closely spaced setules, which are called feathered. Simple setae so-called herein have no long setules but in some cases have rows of very tiny spinules (e.g., on the long furcal setae). The letter designations (a–h) of the antennular setae follow Grygier (1987a) and Itô and Grygier (1990).

DESCRIPTIONS

Description of Nauplius IV (NIII?)

Figures 1, 2

DORSAL SHIELD (Fig. 1A). Kite-shaped, 404 μm long along dorsal midline, 358 μm wide between second and third pairs of marginal processes, shallowly convex. Six pairs of blunt marginal processes: one anterior pair, two lateral pairs, two posterolateral pairs, one posterior pair. Processes directed radially outwards and downwards except fifth pair (straight downwards or even medially; differing from others in its ventral submarginal position) and sixth pair (straight posteriorly). Sixth pair of processes longest, then first and second; third and fifth processes shortest. Number of apical and subapical pores per process: first—4 or 5, second—4, third—3, fourth—4, fifth—2, sixth—5; almost all subapical pores ventral or lateral. Ventral side of shield margin with scattered pores between processes, one anterior pair of pores being slightly raised. Concentric ridge pattern with many oblique connections on outer 40% of shield, possibly some very weak ridges closer to center. Three pairs of short, hairlike sensilla, located on anterior margin, anterodorsally, and mid-dorsally above anterior end of labrum. Dorsal pores not always in precise pairs; on each side two pores behind and medial to first sensillum, two closely set large pores (double pore) lateral to second sensillum, three pores behind third sensillum, and one large and one or two small, posterior pores at about level of fifth pair of marginal processes.

MID-VENTRAL STRUCTURES (Fig. 1B). Pair of papilliform frontal filaments just behind anterior margin, with pore between. Labrum about twice as long as wide, rear half acutely pointed. Setal armament of labrum and ornamentation of ventral body surface unknown due to damage in dissection.

ANTENNULE (Fig. 2A). Long, slender, and cylindrical with slight taper; four-segmented, but fourth segment obviously representing three undifferentiated segments. All setae plumose. First segment short and unarmed. Second segment as long as wide, with postaxial (i.e., medial) a-seta and three preaxial (i.e., lateral) rows of spinules. Third segment as long as second, with postaxial b-seta. Proximal third of fourth segment with two preaxial h-setae (h_1, h_2); middle third with very long postaxial d-seta, shorter postaxial e-seta, and long preaxial f-seta; distal third with three long, apical g-setae.

ANTENNA (Fig. 2B). Composed of coxa, basis, 11-segmented exopod (first two segments incompletely separated), and three-segmented endopod. Coxa and basis each partly subdivided along lateral margins. Endopod slightly shorter than exopod, distal three-quarters of each ramus extending beyond margin of dorsal shield (also in mandible). Coxal endite (gnathobase) ending in bifid spine with proximal prong longer and biserially toothed; curved, setiform spine on proximal face of endite, short plumose seta on distal face; row of 10–11 bristles between seta and bifurcation. Basal endite prominent, with long, fine hairs along distal face and with styliform, plumose apical spine and two or three apical setae (one seta apparently lost from each antenna in dissection and all setae broken so armament and length uncertain). First endopodal segment with three feathered setae at midlength; second segment with two long, plumose, distal setae and one shorter, simple seta; third segment with three long, plumose, apical setae. Exopod with posterolateral, longitudinal row of fine hairs on first two segments and 10 long, plumose, natatory setae, one seta each on segments 3–10 and two setae on apical segment; distal four setae progressively shorter than others.

MANDIBLE (Fig. 2C). About two-thirds as long and wide as antenna. Divided into coxa, basis, eight-segmented exopod (first segment an incomplete annulus), and three-segmented endopod as long as exopod and with first segment as long as other two segments combined. Coxa and basis each with partial lateral subdivisions. Coxal endite with conical, bristly spine and somewhat longer plumose seta with stiff setules. Basal endite very complex: simple seta on rear base; plumose seta and array of long, fine hairs on distal face; another plumose seta on posterior side and very short, simple sensillum on anterior side, both just proximal to semicircular corolla of at least seven stout claws; comb of about 15 somewhat flattened, modified setules arising along posteroproximal face of tip of enditic spine and at least two similar setules on anterodistal face near tip. First endopodal segment with two plumose setae and one short, simple seta at midlength of medial margin, another slightly more distal, simple seta on posterior face; second segment with two plumose setae and one simple seta; third segment of right mandible with four long, basally plumose, apical setae and one short, simple seta, but three plumose setae and one simple seta on left mandible. Exopod with posterolateral, longitudinal row of fine hairs along whole length. Seven long, plumose setae distributed one per segment on segments 3–7 and two setae on apical segment; distal setae somewhat shorter than proximal ones.

MAXILLULES (Fig. 1B). Pair of oblong lobes between fifth pair of marginal processes. Proximal region not clearly seen, thus presence of articulation questionable. Distally armed with spinules, four long apical setae (medialmost shortest and, unlike others, simple rather than plumose), and two subapical, probably simple, medial setae of uncertain length (proximal one very short).

CAUDAL REGION (Fig. 1). Furcal lobes each with pore, two arcs of spinules, short, biserially spinulose, lateral apical spine, and long apical seta with rows of minute spinules. Apical seta reaching end of long, thin, medial terminal spine, latter extending 394 μm beyond posterior margin of dorsal shield and bearing "fur" of minute spinules on distal three-quarters.

Description of Nauplius V (NIV?)

Figures 3, 4

DORSAL SHIELD (Fig. 3A). As in NIV but larger, 470 μm long along dorsal midline, 446 μm wide at level between two lateral pairs of marginal processes. Marginal processes arranged as in NIV, sixth pair longest, fifth pair smallest. Number of apical

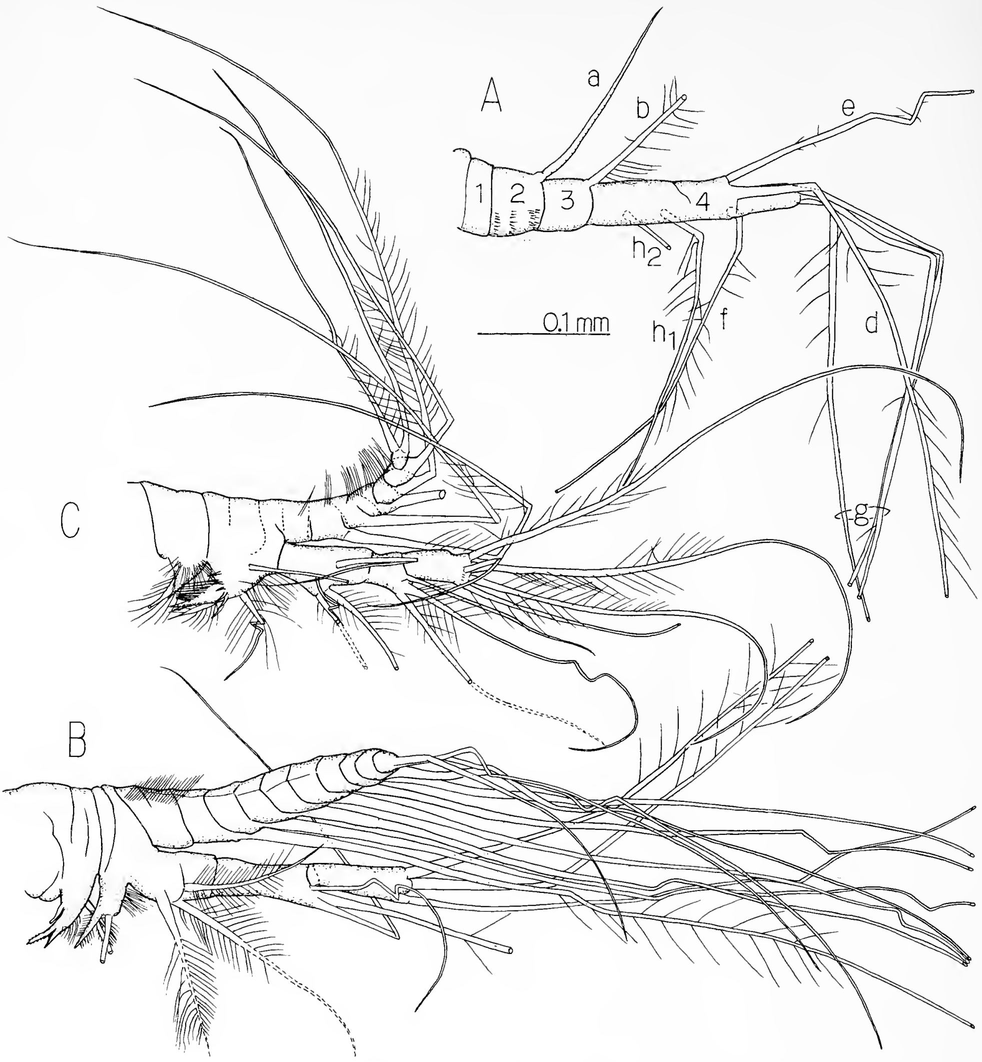

Figure 2. Petrarcid metanauplius NIV (or NIII?) from Red Sea, sta. 703. **A**, right antennule, anterior view, segments numbered and setae designated by letters; **B**, right antenna, posterior view; **C**, right mandible, posterior view. Many setae cut short in A and B, dashed setae in B and C reconstructed based on left member of pair.

and subapical pores per process: first—3 or 4, second—5, third—3?, fourth—4 or 5, fifth—2, sixth—5 or 6. Ventral marginal pores between processes more numerous than in NIV, raised anterior pair present. Dorsal concentric ridges present on outer 25% of shield, with oblique connections usually at levels of marginal processes. Three pairs of short, hairlike sensilla: one pair on anterior margin (left sensillum only seen), one pair anterodorsally, and a posterodorsal pair not present in NIV; no mid-dorsal sensilla observed. Number of dorsal pores increased relative to NIV, 14–15 in discontinuous row on each side of dorsal midline, 7–9 in more lateral position on each side, including double pore retained from NIV.

MID-VENTRAL STRUCTURES. Pair of papilliform frontal filaments just behind anterior margin, with pore between (Fig. 3A). Labrum as in NIV, with sparse, subapical row of long setae on each side (Fig. 3A). Ornamentation of ventral body surface (Fig. 3B, based on NVI but the same as NV): field of tiny cuticular bumps just behind mouth, paired oblique row of spinules extending posteriorly away from mouth, paired longitudinal row of setae (anterior setae stout and in two rows laterally flanked by spinules, middle setae fine, posterior setae again stout), a gap, and paired small field of spinules followed by paired field of fine hairs leading onto bases of maxillules.

ANTENNULE (Fig. 4A). Generally similar to NIV but clearly five-segmented, fifth segment representing two undifferentiated segments. All setae plumose. First segment very short and unarmed. Second and third segments slightly wider than long, with postaxial a-seta and b-seta, respectively; second segment also with single row of spinules. Fourth

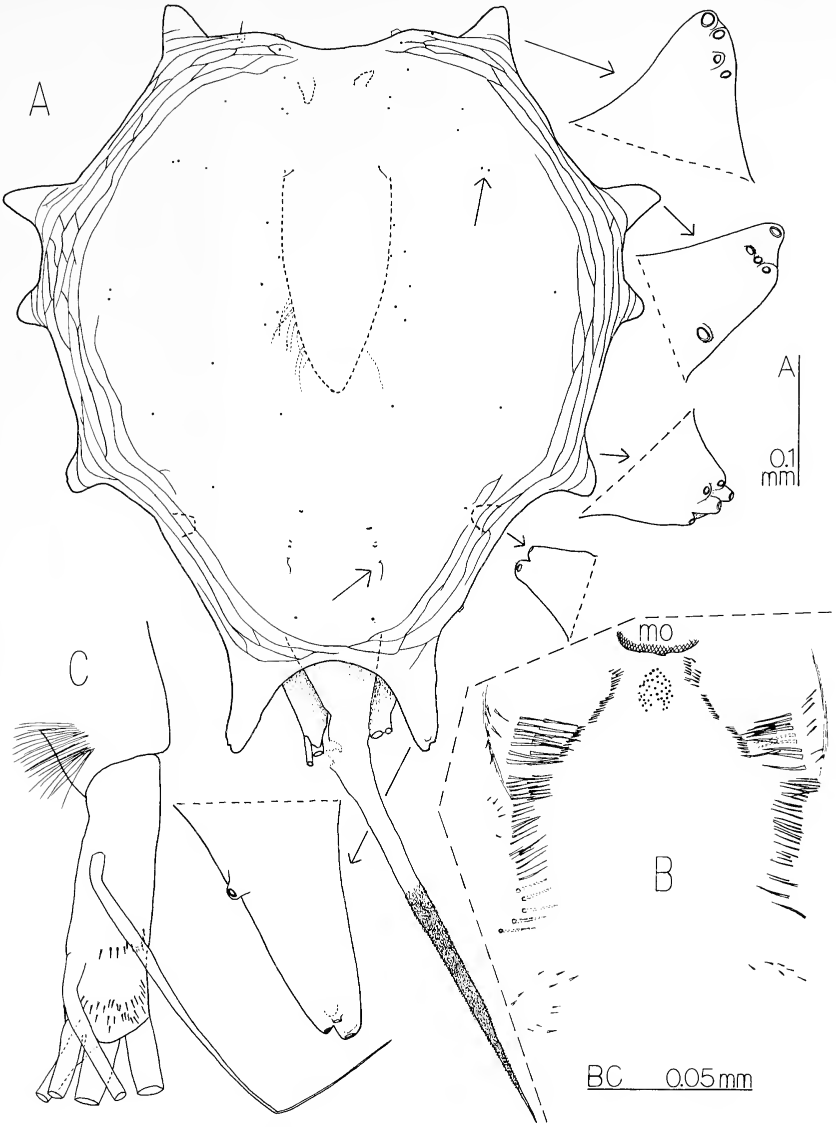

Figure 3. Petrarcid metanauplius NV (or NIV?) from Red Sea, sta. 703. **A,** dorsal view with details of ventral sides of most right marginal processes, appendages omitted, ventral positions of frontal filaments and labrum marked with dashed lines, dorsal double pore and new posterior sensillum marked by arrows. **B,** ventral body ornamentation between mouth (mo) and bases of maxillules, a few missing setae dotted (drawing based on smaller NVI from sta. 703, but condition same in NV); **C,** left maxillule, most setae cut short.

segment with three preaxial h-setae (h_{1-3}), proximal one presumably new in this instar, and new postaxial i-seta. Proximal half of fifth segment with postaxial d-seta and e-seta, and preaxial f-seta; distal half with three long, apical g-setae.

ANTENNA (Fig. 4B–D). Composed of coxa, basis, 12-segmented exopod (first two segments incompletely separated; abnormal right exopod nine-segmented), and three-segmented endopod with all segments equally long. Endopod slightly shorter than exopod. Coxal endite as in NIV. Basal endite apically armed with styliform, plumose spine, two somewhat longer, feathered setae, and one simple seta; distal face with long, fine hairs. Endopod armed as in NIV except for distal patches of spinules on first two segments and new, simple seta on second segment for total of four setae there. Exopod with proximal row of fine hairs as in NIV. Left exopod with 11 plumose, natatory setae, one more than in NIV, with one seta each on segments 3–11 and two on apical segment. Abnormal right exopod also with 11 setae, one seta each on segments 3–5, two setae each on more distal segments, some of latter setae short and of abnormal form.

MANDIBLE (Fig. 4E–H). About two-thirds as long and wide as antenna. Divided into coxa, basis,

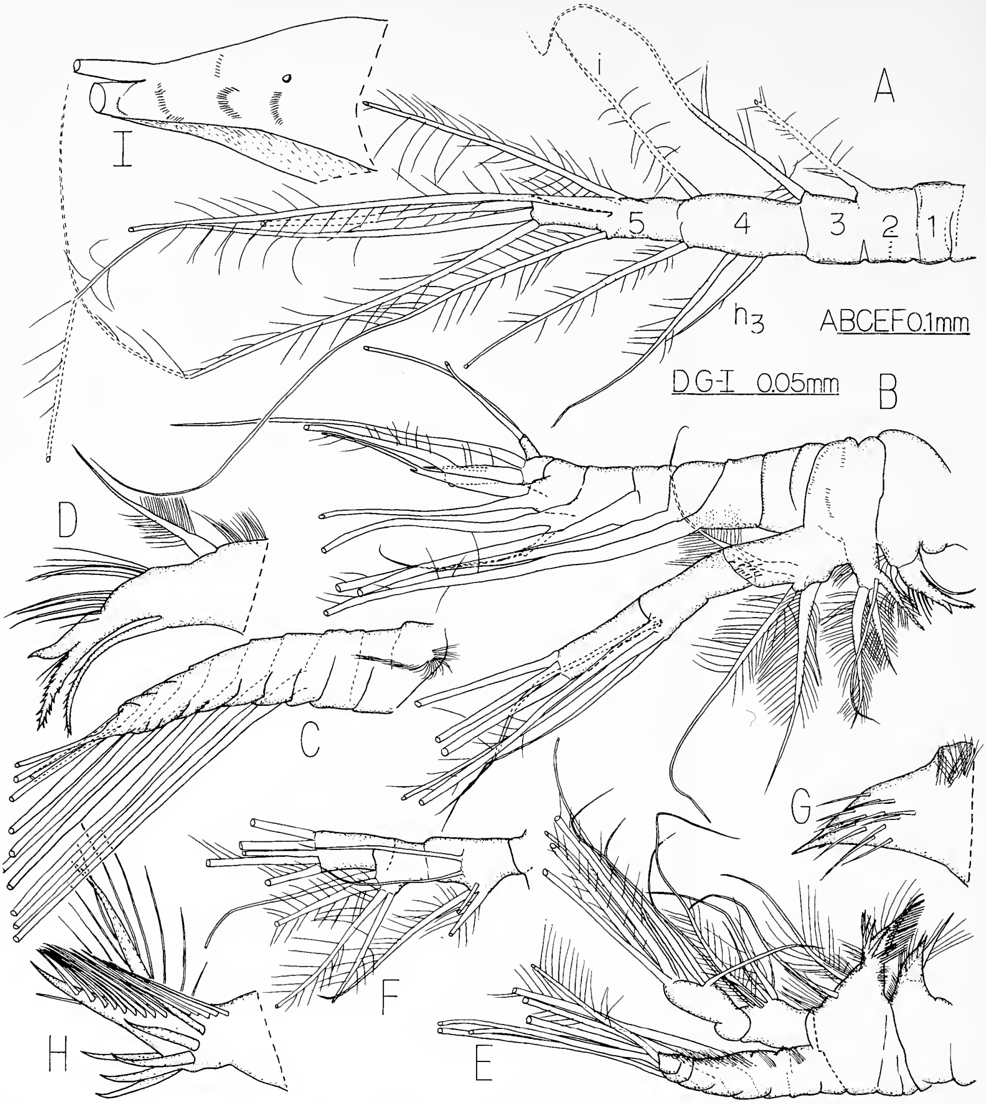

Figure 4. Petrarcid metanauplius NV (or NIV?) from Red Sea, sta. 703. **A,** left antennule, anterior view, segments numbered, letter designations of new setae shown, dashed setae reconstructed from other antennule; **B,** right antenna with abnormal exopod, anterior view; **C,** normal exopod of left antenna, posterior view; **D,** left antennal coxal gnathobase; **E,** right mandible, posterior view, endopod distorted; **F,** better displayed endopod of left mandible, posterior view; **G,** left mandibular coxal enditic spine; **H,** detail of mandibular basal endite from E; **I,** right furcal lobe, setae broken. Many setae cut short in A–C, E, F.

eight-segmented exopod (first segment an incomplete annulus), and three-segmented endopod as long as exopod and with first segment a little shorter than other two combined. Coxal and basal endites as in NIV (Fig. 4G, H). First endopodal segment with three medial setae at midlength, two of them plumose, the other short and simple, and two posterior simple setae, one of latter setae being new in this instar; second segment with three plumose setae, one of them new, and one simple seta (only three setae altogether observed on this segment on right endopod); third segment with five apical setae, number of simple setae among them unclear. Exopod as in NIV.

MAXILLULES (Fig. 3C). Not segmented, oblong, resting flat against ventral body surface and articulated to distinct, hirsute bases. Armed with two arc-shaped patches of spinules, four long, plumose, apical setae, and two probably simple medial setae arising at one-third and two-thirds length, proximal seta shorter than distal one.

CAUDAL REGION. Furcal lobes (Fig. 4I) each with ventral pore and three rows of spinules, one lobe also possibly with distal pore. Furcal setae

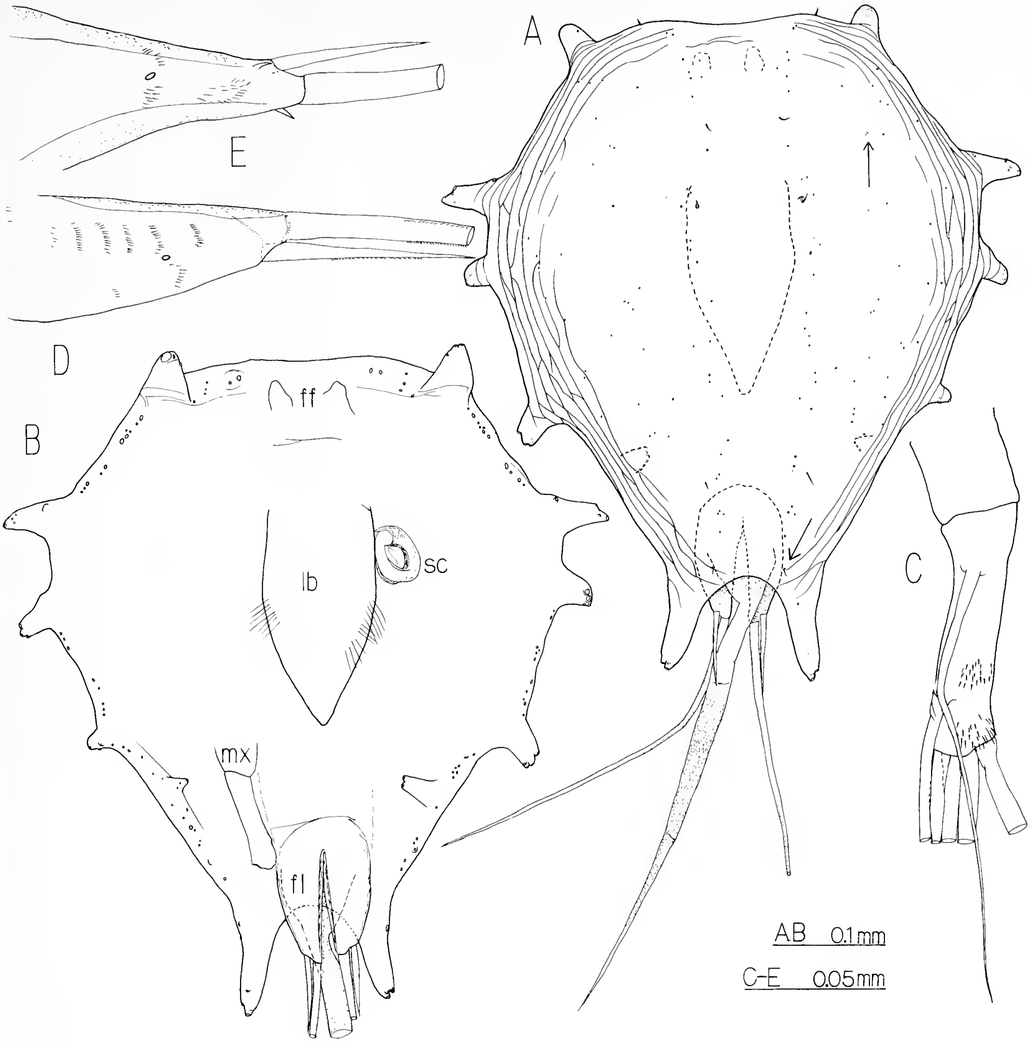

Figure 5. Petrarcid metanauplius NVI (or NV?) from Red Sea, sta. 682 except E, which is large specimen from sta. 703. **A,** dorsal view, appendages omitted, ventral position of labrum shown by dashed line, double pore and new posterior sensillum indicated by arrows; **B,** ventral view, most appendages omitted and caudal armament cut short; **C,** left maxillule, most setae cut short; **D, E,** right and left furcal lobes, respectively, medial apical seta cut short. Abbreviations as in Figure 1 except sc, scarlike vestige of left antenna.

broken off at base, probably two setae of unequal thickness on each lobe. Medial terminal spine (Fig. 3A) as in NIV but relatively shorter, extending 392 μm beyond rear margin of shield (83.4% of shield length versus 97.5% in NIV).

Description of Nauplius VI (NV?)

Figures 5, 6

DORSAL SHIELD (Fig. 5A, B). As in NV but larger, specimens from sta. 703 being 488 μm long by 455 μm wide and 520 μm long by 525 μm wide, specimen from sta. 682 being 490 μm long by 440 μm wide (455 μm wide when flattened); all measurements along same axes utilized above. Marginal processes as in NV. Number of apical and subapical pores per process in specimen from sta. 682: first—4; second—4; third—3 or 4; fourth—4; fifth—2; sixth—4 or 5. Dorsal concentric ridges present on outer 20–25% of shield, with occasional oblique connections. Five pairs of sensilla, including three anterior pairs as in NIV but third pair thicker and not hairlike, and two posterior pairs, rearmost being new in this instar (smaller specimen from sta. 703 seems to lack second and third pairs of anterior sensilla and one rearmost sensillum, other posterior pair accompanied by extra sensillum). Number of dorsal pores increased to 25–37 in discontinuous

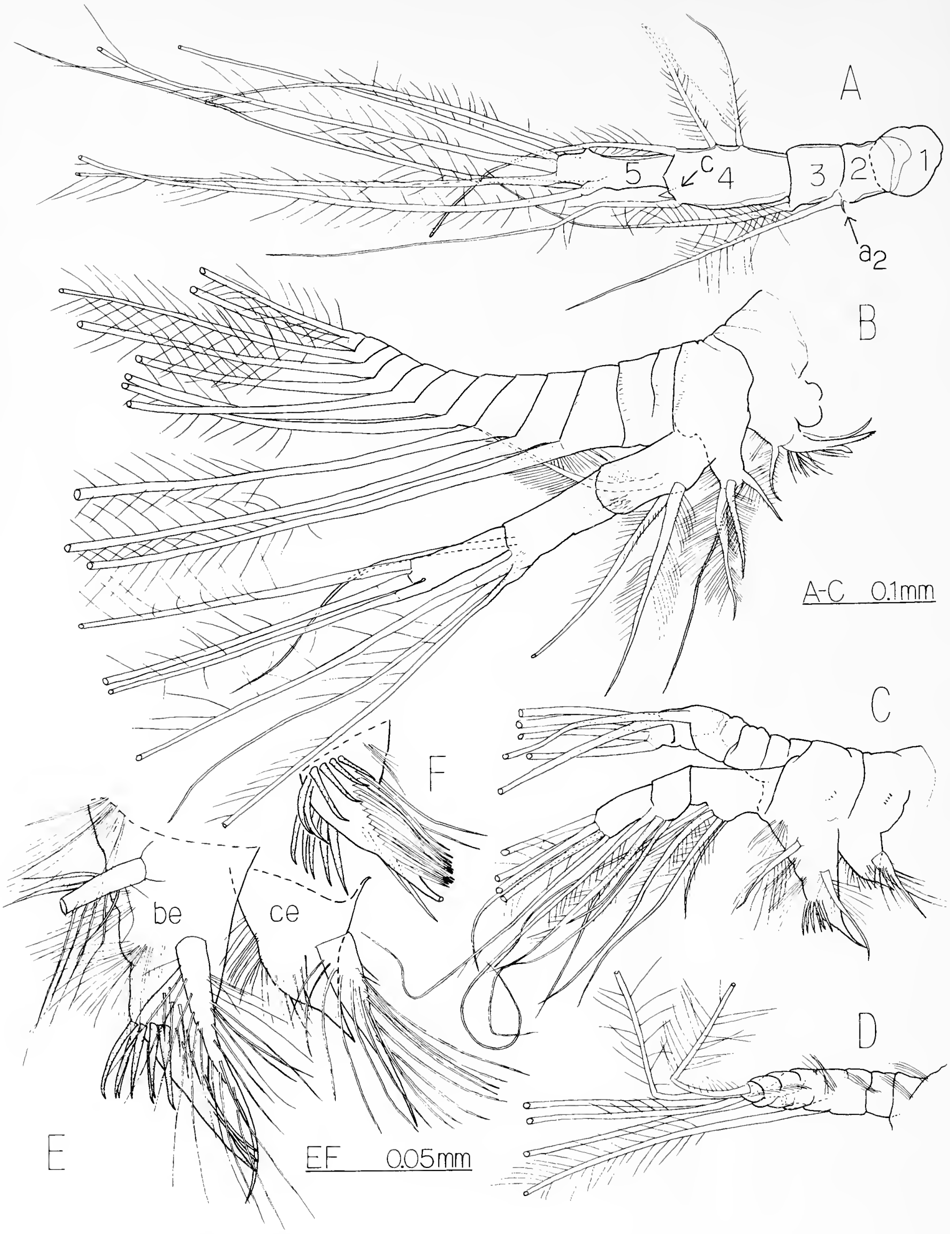

Figure 6. Petrarcid metanauplius NVI (or NV?) from Red Sea, sta. 682 except A, which is small specimen from sta. 703, and B, which is large specimen from sta. 703. **A,** right antennule, anterior view, segments numbered, letter designations of new spines shown, dashed seta reconstructed from other antennule; **B,** right antenna, anterior view; **C,** right mandible with abnormal exopod, anterior view; **D,** normal left mandibular endopod, posterior view; **E,** detail of C, showing endites of coxa (ce) and basis (be); **F,** distal part of left mandibular basal endite, posterior view. Many setae cut short in A–D.

row on each side of midline and 23–33 in more lateral position on each side, including double pore lateral to second sensillum.

MID-VENTRAL STRUCTURES (Fig. 5B). As in NV, except presence of pore between frontal filaments not confirmed in specimen from sta. 682 before dissection.

ANTENNULE (Fig. 6A). Descriptions of paired appendages based on specimen from sta. 682, followed by variability in other specimens; drawings based on all three specimens. Antennules similar to those of NV; setation the same except for new small spine (a_2) next to a-seta on second segment and new claw rudiment (c) next to i-seta on fourth segment (claw rudiment not seen on left antennule).

ANTENNA. Left antenna absent, represented only by bump in middle of circular scar (Fig. 5B). Right antenna (Fig. 6B) composed of coxa, basis, 12-segmented exopod (first two segments incompletely separated, seventh partly subdivided), and three-segmented endopod. Endopod slightly shorter than exopod, with all segments equal in length. Coxal endite as in NIV and NV. Basal endite armed as in NV. First and third endopodal segments as in NV; second segment with one simple and four plumose setae, one more than NV (three of plumose setae seemingly uniserially plumose; one plumose seta replacing NV's newly arisen simple seta). Posterolateral hairs on basal part of exopod not confirmed in this specimen due to unfavorable orientation on slide. Exopod with 12 plumose, natatory setae, one more than NV, one on each segment from third on, except two setae each on apical and fourth from apical segments.

MANDIBLE (Fig. 6C–F). Left mandible with abnormal exopod. Each mandible about two-thirds as large as antenna, with endopod longer than exopod; normal exopod eight-segmented with first segment an incomplete annulus, endopod three-segmented with second segment shorter than other two. Coxal and basal endites as in NIV and NV. Corolla of eight claws on basal endite of right mandible, 11 on left, and several short bristles on distal part of enditic spine opposite comb of modified setae; fine hairs on distal face of this endite clustered in three tufts. First endopodal segment of right mandible with five setae as in NV, two plumose and three simple (latter including one short medial seta and two posterior setae); posterior setae not seen on left mandible. Second endopodal segment with one simple and three plumose setae as in NV. Third endopodal segment with six apical setae, one more than in NV, one of them simple and five plumose. Exopod bearing longitudinal row or tufts of fine hairs posterolaterally. Setation of normal left exopod as in NV. Abnormal right exopod six-segmented (first two segments incompletely separated, fourth rather long and possibly representing two or three segments) with one plumose, natatory seta each on fourth and fifth segments, four on apical segment, total of six setae being one fewer than normal.

VARIABILITY IN APPENDAGES. Small specimen from sta. 703 with distal half of right fifth antennular segment abnormally short. Twelve setae on 13-segmented antennal exopods, first two expodal segments incompletely separated and bearing posterolateral row of fine hairs; apparently one natatory seta each on segments 3–12, two on apical segment. On mandibles, left basal endite with corolla of 10 clawlike setae, right one with eight. Right endopod developed normally, with one simple and three plumose setae on second segment, five setae on third segment, one of them simple; abnormal left endopod with one plumose and one simple seta on second segment and four setae, all plumose, on very short third segment.

In large specimen from sta. 703, a_2-spine unconfirmed on antennule due to orientation on slide. Antennae with 11 setae on 12-segmented exopods, one seta each on segments 3–11 and two on apical segment; proximal two segments with posterolateral row of hairs. On antennal endopod, second segment bearing one simple and three plumose setae (latter perhaps uniserially plumose or nearly so). On mandibular endopod, short medial seta of first segment at least uniserially plumose (simple in other two specimens).

MAXILLULES (Fig. 5C). As in NV except more spinules in already existing patches and first medial seta, a simple one, arising more proximally than in NV.

CAUDAL REGION (Fig. 5A, D, E). Furcal lobes of specimen from sta. 682 with about eight rows of spinules, including some anterior to pore, but no spinules observed anterior to pore in other two specimens. Each lobe bearing short, minutely spinulose, spinelike seta and long, minutely spinulose seta reaching to end of terminal spine. Large specimen from sta. 703 exhibiting two additional spinules apically on left furcal lobe (not seen on other specimens, but generally tips of furcal lobes not fully exposed to view). Medial terminal spine extending 418 μm beyond rear margin of dorsal shield in specimen from sta. 682, 337 μm in smaller specimen from sta. 703, 456 μm in larger specimen (85.3%, 69.1%, and 87.7% of shield length, respectively).

SUMMARY OF NAUPLIAR DEVELOPMENT (Table 1)

From NIV to NV there is an increase in body size and number of dorsal pores. One pair of dorsal sensilla is added to the posterior part of the dorsal shield. Two setae are added to the antennule, and the fourth segment separates from the fifth. The antennal exopod adds one segment and one seta to make 12 segments and 11 setae, while the endopod adds one seta to the second segment, resulting in four setae. On the mandible the endopod adds one seta each to the second and third segments, making five and four setae, respectively, though the latter addition occurs only unilaterally here. The medial setae on the maxillules become longer.

From NV to NVI there is an increase in body size and in the number of dorsal pores. Another pair of posterior dorsal sensilla is added. A small spine and a claw rudiment are added to the antennule. In the antennal exopod there is an inconsistent addition of one segment or one seta to make 12 segments or 13 setae, and one seta may be added to the second endopodal segment; each of these states was observed in only one of three specimens. On the mandibular endopod, a simple seta on the first segment changes to plumose (in one of three specimens) and one apical seta is added to make six (in two out of three specimens). The proximal medial seta on the maxillule moves toward the base.

Spinule rows may be added proximally and small spines apically to the furcal lobes (each seen in one of three specimens).

DISCUSSION

AFFINITIES

Among all known crustacean nauplii, the present specimens are most similar to the NII of *Zibrowia* sp. (Ascothoracida: Petrarcidae) described by Grygier (1990a). Notable features in common include large size; a kite-shaped dorsal shield with pore-bearing marginal processes; three pairs of sensilla on the anterior half of the shield (also true of NII in another ascothoracidan, *Baccalaureus* sp.; Grygier, 1990a); papilliform frontal filaments; elongate, basically six-segmented antennules with imperfect distal segmental divisions; elongate endopods on the antennae and mandibles, and the mandibular endopod longer than the exopod; posterolateral hairs on only the first two segments of the antennal exopods; and a long, pilose, medial terminal spine flanked both by a long pair of furcal setae that arise from sessile furcal lobes and by long maxillular setae. Differences in the present specimens that are not solely attributable to their later ontogenetic stage include a larger dorsal shield relative to the appendages, six rather than four pairs of marginal shield processes, dorsal cuticular ridges, no obvious nauplius eye (preservation artifact?), no band of setae crossing the labrum, and a semicircular corolla of claws on the mandibular basal endite. A tentative assignment of these specimens to the Petrarcidae seems reasonable despite uncertainty about the true significance of these differences.

There is no *a priori* reason to expect that all five specimens belong to the same species. Only about 12 species of Petrarcidae have been named or partly described, none yet from the Red Sea, but this family is known to infest a great number of mostly ahermatypic scleractinian corals in the Indo-West Pacific (Zibrowius and Grygier, 1985; Grygier, 1991). Many undiscovered petrarcids undoubtedly inhabit the Red Sea, and some of them may have nearly identical larvae. Several differences between the two supposed NVI from sta. 703 suggest that they, at least, belong to different species: their great size difference; the somewhat different distribution of dorsal pores on their shields (large specimen with fewer pores parallel to the midline but more pores laterally than small one); the large specimen's extra apical furcal spinules; and the small specimen's lack of some dorsal shield sensilla (possibly an artifact), 13-segmented instead of 12-segmented antennal exopods, and relatively short terminal spine. The more extensive spinulation of the furcal lobes in the supposed NVI from sta. 682 is suggestive of yet a third species. However, the high rate of appendage abnormalities in the present sample (four of five specimens with at least one deformed or missing limb) suggests that a single species might exhibit considerable variability in more subtle features as well. All five specimens are so similar compared to other known nauplii that in the following discussion I will treat them as one species.

DETERMINATION OF INSTARS

Antennular armament provides an easy way to distinguish naupliar instars NII–NVI in ordinary, planktotrophic Cirripedia, since the setae are added in a nearly fixed order. For the time being I am assuming that the same is broadly true for the Ascothoracida. Antennular armament shows that three instars are represented in the present material, the youngest one with two h-setae, the middle one with three h-setae, and the latest one with, in addition to three h-setae, a claw rudiment and a spine accompanying the a-seta. This setal criterion correlates pretty well with the size of the dorsal shield and the abundance of dorsal pores and sensilla in the present material except that one of the supposed NVI is much bigger than the others. Perhaps it is the only true NVI and the other four specimens represent NIII–NV. If so, the only morphological changes besides growth at the molt from NV to NVI are the change of one short seta on the mandibular endopod from simple to (uniserially?) plumose and perhaps the addition of apical spines to the furcal lobes.

The h-setae and the a_2-spine in the present antennular setal patterns match NIV–NVI of *Baccalaureus falsiramus,* which is the only available ascothoracidan species in which all six naupliar instars are known (Itô and Grygier, 1990). However, in that species the very small i-seta first appears at NVI and a small seta joins the b-seta as well as the a-seta at NVI. Therefore, there are incongruities between antennular development in *B. falsiramus* and in the present nauplii.

One might expect to find a cypridiform ascothoracid larva developing within the NVI cuticle of any ascothoracidan. In the present material no well developed ascothoracid larva is yet formed; the NV and NVI specimens have only internal tissue blocks representing the early stages of formation of the ascothoracid larva's thoracomeres and thoracopods and no obvious compound eyes. This, together with the lack of ventral spines representing the thoracopodal setae, suggests that the oldest metanauplii on hand may only be NV, and not NVI. The presence of a claw rudiment does not disprove this, because Grygier (1992) found a small claw rudiment in NV of a lecithotrophic naupliar series similar to that of *Baccalaureus falsiramus.* If the present material does not truly include NVI, then the youngest specimen must represent the next instar after Grygier's (1990a) NII of *Zibrowia* sp. If so, some rather important changes seem to take place at the molt from NII to NIII (Table 1), namely the addition of three segments to the antennal exopods and the change from a single seta representing the maxillule to a large, possibly articulated

Table 1. Setal formulae of naupliar appendages of Petrarcidae in cirriped literature-based format (e.g., Egan & Anderson, 1985), NI–II based on Grygier (1990a) and NIV–VI on present study. Symbols: E, enditic spine and subsidiary armament; F, feathered seta; P, plumose seta (spinulose in NI); S, simple seta; s, small spine; ?, armament element of uncertain nature; italics, preaxial setae. Parentheses recording variation (or . . .) or doubt (?).

Antennule	
NI	*S*:SPS:P:S
NII	*P*:PPP:PP:P:P
NIV	*PP*:*P*:PPP:PP:P:P
NV	*PPP*:*P*:PPP:PP:P:P:P
NVI	*PPP*:*P*:PPP:PP:sP:P:sP

Antenna		
Exopod		Endopod and protopod
NI	P:4P	sPP:SS:EE:Es:Es
NII	PP:5P	PPP:SP:PP:EsP:EP
NIV	PP:8P	PPP:SPP:FFF:E??(?):EsP
NV	PP:9P	PPP:SSPP:FFF:ESFF:EsP
NVI	PP:10P(or 9P) (or PP:P:P:PP:6P)	PPP:SPPPP(or S3P):FFF:ESFF:EsP

Mandible			Maxillule
Exopod		Endopod and protopod	
NI	P:3P	sPP:SP:Es:Es:ss	Absent
NII	PP:4P	sPPP:SP:SPPP:EPP:sP	P
NIV	PP:5P	SPPP(or S4P):SPP:SSPP:ESPP:sP	SPPP:S:S
NV	PP:5P	5?:SPPP(or 3?):SSSPP:ESPP:sP	PPPP:S:S
NVI	PP:5P	S5P:SPPP:SSSPP(or SPP):ESPP:sP	PPPP:S:S

maxillule with six setae. In *B. falsiramus* the molt from NII to NIII is less drastic, involving the addition of at most one segment to the antennal exopod (9- to 10-segmented) and a change from a sessile maxillular seta to two setae on a small, nonarticulated lobe, smaller changes than those postulated here. Nonetheless, *B. falsiramus* has lecithotrophic nauplii, so some simplification in ontogeny relative to planktotrophic forms might be expected.

The following treatment of the present nauplii as NIV–NVI in a comparison with the Cirripedia is conservative. If there is an unknown later instar representing the true NVI, it must have appendages at least as complex as those of the oldest specimen on hand, and perhaps more complex. The same trends documented below would still apply, but merely be amplified.

COMPARISON WITH CIRRIPEDIA (Table 2)

There is a voluminous literature on the naupliar development of Cirripedia. Some recent large-scale works and reviews include Lang (1979), Kado (1982), Moyse (1987), Korn (1988), and Egan and Anderson (1989), which can be consulted for additional literature sources. The present comparison (Table 2) is limited to the review of lepadomorph nauplii by Moyse (1987), a series of papers by Egan and Anderson (1985, 1986, 1987, 1988, 1989) in which larvae representing all the major groups of balanomorph barnacles are described and compared, and an unpublished thesis (Kado, 1982) in which the larvae of 18 diverse thoracicans are described and information on chaetotaxy, including literature data, is concisely and usefully summarized. I have prepared a separate reevaluation of the segmental and setal homologies of the antennules of cirripedes and ascothoracidans (see Grygier, in press) and so will not discuss antennules here.

Antennae (Table 2)

The antennal coxal gnathobases of the present metanauplii and all planktotrophic cirriped nauplii are similar, consisting of a bifid spine, one of whose prongs is biserially dentate (in the Cirripedia this prong may also have basal teeth), a curved setiform spine, and bristles [see Kado (1982) for a detailed survey of the cirriped gnathobase]. The smoothly curved form of the gnathobase in the petrarcids is more similar to that of balanoid nauplii than to the angular gnathobases of lepadomorph and chthamaloid nauplii. The present nauplii have a seta at the base of the coxal endite that cirriped nauplii lack. This seta is also present in NII of *Zibrowia* sp. and of another ascothoracidan in the family Lauridae, *Baccalaureus* sp. (Grygier, 1990a), but in these NII there is no curved, setiform spine. Apparently the latter spine develops in NIII or NIV in the Ascothoracida, while in the Cirripedia it is present from NII.

Table 2. Comparison of antennal and mandibular setal armament of petrarcid (Petr.) nauplii (present study) and cirriped (Cirr.) nauplii (Kado, 1982; Egan and Anderson, 1985, 1986, 1987, 1988, 1989; Moyse, 1987) at NIV–VI. Numerals represent setal counts, alternative states given in parentheses, short sensilla on petrarcid mandibular basis not included. Symbols: E, enditic spine and subsidiary armament; F, feathered seta; s, small spine.

	Exopod		Endopod and protopod				
Instar	Apical	Lateral	Seg. 3	Seg. 2	Seg. 1	Basis	Coxa
Antenna							
NIV							
Petr.	2	8	3	3	3F	E + (2–3?)	Es + 1
Cirr.	2 (3)	7 (6)	4–5	2–3	2 (2F + 1)	E + 3 (E + F + 2)	Es
NV							
Petr.	2	9	3	4	3F	E + 2F + 1	Es + 1
Cirr.	3 (2, 4)	8 (6–7)	4–5	3	2 (3F + 1)	E + 3 (E + F + 2)	Es
NVI							
Petr.	2	10 (9)	3	5	3F	E + 2F + 1	Es + 1
Cirr.	4 (2–3)	8 (6–7)	4–5	2–4	2 (3F + 1(2))	E + 3 (E + F + 2)	Es
Mandible							
NIV							
Petr.	2	5	4–5	3	4	E + 3	s + 1
Cirr.	2	3	4–5	3	E + (2–3)	E (+s) + (2–3)	s + 1
NV							
Petr.	2	5	5	3–4	5	E + 3	s + 1
Cirr.	2	4	5	4	E + (2–3)	E (+s) + (2–3)	s + 1
NVI							
Petr.	2	5	5–6	4	5 (3)	E + 3	s + 1
Cirr.	2	4	4–5	4	E + 3	E (+s) + (2–3)	s + 1

In cirriped NIV–NVI the basis has an enditic spine (referred to in cirriped literature as a cuspidate seta or, in chthamaloids, a hispid seta, both kinds unlike the present spine) and three setae, one of them simple, as in the present petrarcids. While the two non-simple setae are feathered at least in NV–VI in the petrarcids, only one of them is feathered in these instars in chthamaloids, and none in other barnacles.

The antennal exopods of planktotrophic cirriped nauplii have 8–9 setae at NIV, 10–12 at NV, and 9–12 at NVI, 12 being most common. Kado (1982) states that the first of these setae arises from either the second or third segment, often varying within a species, and that there are two setae on the apical segment at NIV, two or usually three setae at NV, and two, three, or usually four apical setae at NVI. Other papers cited above show as many as three apical setae at NIV and four at NV. The current NIV nauplius has 10 setae, the NV has 11, and the NVI larvae have 11 or 12 setae on the antennal exopods, and only two are apical in each instar. Thus the petrarcid NIV has more exopodal setae than the corresponding cirriped instar, but at NV and NVI both groups are usually equal. However, cirriped exopods have fewer segments, generally nine at NIV–VI versus 11–13 in the petrarcid metanauplii, and the greater number of apical setae in the Cirripedia shows that this is due to a suppression of distal segment division compared with the petrarcids. In a few cirripeds like *Lepas* NV–VI (see Moyse, 1987), the first exopodal seta is feathered, but not in the petrarcids. When posterolateral hairs are present on the antennal exopod in cirriped nauplii, they line the whole length, not just the first two segments as in the petrarcids.

It is uncommon in the cirriped literature for the antennal endopodal segments to be referred to by number; rather, setal clusters alone are usually noted and the basal endite may be inaccurately counted as part of the endopod. In planktotrophic cirriped nauplii there are three groups of setae which are clearly homologous to the setae on the three endopodal segments of ascothoracidan nauplii; these show that the first endopodal segment of the cirriped antenna is generally continuous with the basis, and the other segment boundaries, especially between the second and third segments, are often poorly expressed. According to the surveyed cirriped literature, NIV may have an endopodal setal count (from proximal to distal) of from 2-3-4 or 3-2-4 to 3-3-5, NV may have 2-3-4 to 4-3-5, and NVI may have 2-3-4 to 5-5-5. The present petrarcid nauplii have counts of 3-3-3 at NIV, 3-4-3 at NV, and 3-(4–5)-3 at NVI. Cirripeds never have three setae on the first segment in NV and NVI, only two or four to five; when there are four or five setae (in lepadomorphs, verrucomorphs, and chthamaloids), three of them are feathered as in the petrarcids, and the remaining simple ones are absent from the petrarcids. Coronuloids and balanoids lack feathered setae. Cirriped nauplii have more setae on the third segment in all three instars compared to the petrarcids (four or five versus three).

Mandible (Table 2)

The coxal endites of cirripeds and petrarcids are alike. The basal endite has three prominent setae, or four in some lepadomorphs like *Lepas* (see Moyse, 1987). This number includes the enditic spine, which is usually referred to as a cuspidate seta. The spine has some stiff bristles but completely lacks the corolla of claws that is present in the petrarcids. Thus the number of prominent true setae in cirripeds, as opposed to this spine, is either two or three, and three matches the condition in the present petrarcid nauplii. Many cirripeds, but not lepadids, have an additional small spine distally on the basis that petrarcids lack.

In cirriped mandibular exopods, five setae on four segments at NIV and six setae on five segments at NV and NVI seem to be nearly universal. In contrast, there are seven setae on eight segments at all three instars in the petrarcid metanauplii. A complete row of posterolateral hairs is common to both.

The cirriped naupliar mandibular endopod is rather like the antennal one except the two distal segments are often fully fused. Nonetheless, the setal clusters remain distinct. The terminology in the literature parallels that for the antennal endopods, and the setal counts (from proximal to distal) recorded there range from 3-3-4 to 4-3-5 at NIV, 3-4-5 to 4-4-5 at NV, and 4-4-4 to 4-4-5 at NIV. On the first segment one of the setae, usually called a cuspidate seta, is actually a spine that is more complexly armed than the enditic spine of the basis. In contrast, the petrarcid metanauplii have only true setae on this segment, and the total number of armament elements there in NV–VI is five in the petrarcids versus three or four in cirripeds. Six setae on the distal segment at NVI, occurring inconsistently in the present specimens, also surpasses cirripeds.

Maxillules

Maxillular rudiments gradually develop first as setal arcs and then as setose lobes on the sides of the body in cirriped nauplii. They generally do not become articulated until NVI at the earliest, while this occurs at NV or possibly NIV in the present petrarcids.

Caudal Armament

Unlike the present specimens, cirriped nauplii never have furcal setae but usually have a pair of furcal spines on a short or long stalk or, in a few lepadomorphs, sessile furcal spines.

Other Remarks

When there are differences in the numbers of segments or setae in the antennae and mandibles in the present petrarcid metanauplii and their counterpart instars in the Cirripedia, the former usually have more segments or more setae, as in the exopods of both limbs and the first endopodal segment of the mandible (Table 2). In such cases the petrarcid condition can be considered plesiomorphic by the criterion of oligomerization [see Huys and Boxshall (1991) for a detailed application of this criterion]. The only consistent exception, where the cirripeds always have more setae and perhaps the more plesiomorphic condition, is on the third endopodal segment of the antenna. Large subsets of cirriped nauplii exhibit two other features that might be plesiomorphies: one or two simple setae on the first endopodal segment of the antenna in addition to three feathered setae shared with the petrarcids and a small distal spine on the mandibular basis that petrarcids lack.

A separate topic is the question of a homologue of cirriped frontolateral horns in the Ascothoracida. A pair of frontolateral horns arising from the dorsal shield of the nauplius has been considered the single most diagnostic feature of the Cirripedia plus Rhizocephala. However, Grygier (1990a) has suggested that the anterior pair of marginal shield processes of the ascothoracidan *Zibrowia* sp. at NII might be homologous to frontolateral horns and represent their ancestral state. Besides having a corresponding form and position, both structures have two apical pores. Therefore it is significant that the marginal processes in the present metanauplii, except the fifth pair, have more than two and up to five pores (up to four pores in the first pair). Two pores at NII is just the first step in an ontogenetic series. For the previously recorded coincidence in the number of pores to retain any phylogenetic significance, it is necessary to regard the cirriped frontolateral horns as paedomorphic, maintained through all the naupliar stages in a condition equivalent to the ascothoracidan NII. In *Zibrowia* sp. NII, the pores on the processes were highlighted by the absence of pores between the processes. Now it is clear that pores are gradually added all around the margin of the shield, on and off the processes, as larval molts take place, and that all the pores are homologous to the equatorial pores of other ascothoracidan nauplii. Homology of the marginal processes with the marginal gland papillae of lepadomorph nauplii, as discussed by Grygier (1991a), remains a likely possibility.

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NOVAFABRICIA BRUNNEA (HARTMAN, 1969), NEW COMBINATION, WITH AN UPDATE ON RELATIONSHIPS AMONG FABRICIINAE TAXA (POLYCHAETA: SABELLIDAE)

KIRK FITZHUGH

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NOVAFABRICIA BRUNNEA (HARTMAN, 1969), NEW COMBINATION, WITH AN UPDATE ON RELATIONSHIPS AMONG FABRICIINAE TAXA (POLYCHAETA: SABELLIDAE)

KIRK FITZHUGH[1]

ABSTRACT. The fabriciin sabellid species, *Fabricia brunnea* Hartman, 1969, from central California, is assigned to the genus *Novafabricia* Fitzhugh, 1990, based on information provided by recently collected specimens. In particular, thoracic notosetal pseudospatulate setae were found to be limited to setigers 3–5, a feature not ascertainable from the type series. Support for this change comes from a cladistic analysis involving *N. brunnea* and other Fabriciinae genera and species. The number of *Novafabricia* species is raised to at least seven. As part of this analysis, the status and relationships of the monotypic genus, *Pseudofabricia* Cantone, 1972 (type species *P. aberrans*), *Novafabricia bilobata* Martin and Giangrande, 1991, and *Augeneriella alata* Hartmann-Schröder, 1991, are evaluated. Based on the original description, *A. alata* is a member of the undescribed taxon "Genus A" (*sensu* Fitzhugh, 1989). Results of the analysis support the recognition of *Pseudofabricia* and the generic placement of *N. bilobata.* Cladistic relationships among the seven species of *Novafabricia,* including *N. brunnea,* are analyzed and discussed. A key to *Novafabricia* species is provided.

INTRODUCTION

As part of my recent revision (Fitzhugh, 1990a) of the genus *Fabricia* Blainville, 1828, I included a partial redescription of *Fabricia brunnea* Hartman, 1969, based on syntype material from Moss Beach, central California. At that time, I regarded this species as *incertae sedis* as the distribution of thoracic notopodial pseudospatulate setae were neither indicated by Hartman (1969) nor could it subsequently be determined from the syntypes, most notosetae having been broken off. The purpose of the present paper is, in part, to redescribe this species based on recent material.

My revision (Fitzhugh, 1990a) of *Fabricia* limited the taxon to a single species, *Fabricia stellaris* (Müller, 1774), including several subspecies of questionable status. Given the evidence at hand, I suggested that such *incertae sedis* species as *F. brunnea* and *F. oregonica* Banse, 1956, would likely be shown to be members of other genera. As such, I noted that *Fabricia* might very well be monotypic, not allowing definition of the genus in terms of synapomorphy. Taking this situation into account and in conjunction with results from recent cladistic analyses (i.e., Fitzhugh, 1991a, 1992b) of Fabriciinae genera (*sensu* Fitzhugh, 1991a), the generic placement of *F. brunnea* must be judged relative to other fabriciin taxa. This is accomplished here by extending the cladistic analyses of fabriciin genera and species by Fitzhugh (1991a, 1992b) to include *F. brunnea.*

As part of this analysis, validity of the monotypic genus, *Pseudofabricia* Cantone, 1972, can now be assessed as a result of the redescription of *P. aberrans* by Giangrande and Cantone (1990). The original description of this species was based on specimens lacking a branchial crown, and the description of setal forms was too incomplete to have allowed inclusion of the species in earlier cladistic analyses. Attention is also given here to the species *Novafabricia bilobata* Martin and Giangrande, 1991, again for the purpose of confirming the generic placement of this species. Also of relevance to this analysis is a preliminary examination of the generic status of *Augeneriella alata* Hartmann-Schröder, 1991.

Material examined for this study was either obtained from or has been deposited in the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History (LACM-AHF).

Novafabricia brunnea (Hartman, 1969), new combination

Fabricia brunnea Hartman, 1969:695–696, figs. 1–5; Fitzhugh, 1990a:9–12, figs. 2–4.

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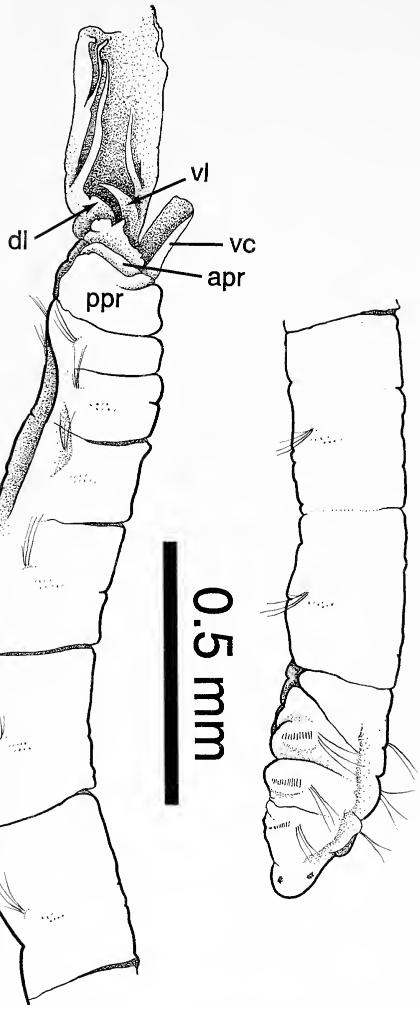


Figure 1. *Novafabricia brunnea* (LACM-AHF 1651). Entire animal in lateral view (right side; right half of branchial crown removed); figure is split between setigers 6 and 7. Abbreviations: apr, anterior peristomial ring; vc, ventral lobe-like extension of anterior peristomial ring; dl, dorsal lip; ppr, posterior peristomial ring; vl, ventral lip-like process.

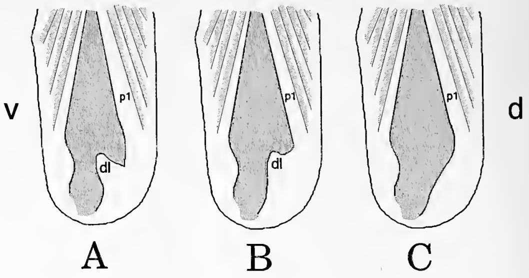


Figure 2. Slightly schematic view of the inner margin of the branchial crown, indicating possible states of dorsal-lip development in fabriciin taxa (cf. character 2, Table 2): **A**, dorsal lip as a triangular lobe, with dorsal margin well separated from proximalmost pinnule of dorsal radiole; **B**, dorsal lip with dorsal margin fused with proximalmost pinnule; C, dorsal lip absent. Abbreviations: d, dorsal body margin; dl, dorsal lip; pl, proximalmost pinnule of dorsal radiole; v, ventral body margin.

MATERIAL EXAMINED. California, San Luis Obispo County; 5 complete and 1 incomplete (branchial crown missing) specimens (LACM-AHF 1651). Syntypes of *Fabricia brunnea* (LACM-AHF 3380), 12 specimens.

DESCRIPTION. All specimens in good condition with 8 thoracic and 3 abdominal setigers. Total length ranges from about 2.0 to 3.0 mm, branchial crown comprises about 0.5 mm of this length. Three pairs of radioles with filamentous distal ends of same width as pinnules. Each radiole with 5–6 pairs of pinnules, all terminating at about same height as radioles. Dorsal lips low, distally rounded; inner margin distinctly fused to most proximal pinnule of dorsal radiole. Ventral lip-like process present at base of most proximal pinnule of ventral radiole. Body cylindrical, anterior and posterior ends slightly tapered. Peristomial eyes dark gray, rounded to crescentic, obscured by body-wall pigment; pygidial eyes black, rounded. Anterior margin of anterior peristomial ring a low ridge dorsally and laterally; ventrally a broad, tongue-like lobe, lateral margins only slightly tapered, distally rounded, about 3.5–4 times length of remainder of anterior ring. Anterior peristomial ring (excluding ventral lobe) distinctly narrower than posterior ring. Posterior ring about 2–2.5 times longer than anterior ring. Annulation between rings distinct except along middorsum. Setiger 1 about same width as posterior peristomial ring, wider than long; setigers 2–6 or 7 successively longer, setiger 5 about as wide as long; setiger 8 about same length as setiger 6. Setiger 9 about one-half length of setiger 8; setigers 10–11 successively shorter. Pygidium roughly triangular, rounded, about same length as setiger 11. Superior thoracic notosetae elongate, narrowly hooded; 5–6 per fascicle. Inferior thoracic notosetae with pseudospatulate setae in setigers 3–5; 1 per fascicle; other setigers with elongate, narrowly hooded setae. Abdominal neurosetae modified, elongate, narrowly hooded; 2–4 per fascicle. Thoracic acicular uncini in single or irregular double rows; 6–9 per fascicle; large tooth above main fang; hood present. Abdominal uncini with 5–6 teeth in profile, 4–5 teeth per row; manubrium twice as long as dentate region; manubrium constricted below dentate region, slight proximal expansion to rounded or quadrangular base; 10–13 per fascicle. Entire or proximal half of branchial crown light brown; peristomial rings and setigers 1–2 dark brown, pigmentation diminishing in posterior thoracic setigers; remaining setigers cream colored. Tube material absent; no brooding observed. Methyl green staining produces no distinct patterns.

DISTRIBUTION AND HABITAT. Central California, San Mateo County, Moss Beach, tide pool

Table 1. Current generic distributions of species described in *Augeneriella*.

Species currently recognized as members of *Augeneriella* (*sensu* Fitzhugh 1989, 1990e)	*Augeneriella* species assignable to "Genus A" (*sensu* Fitzhugh, 1989)
A. hummelinki hummelinki Banse, 1957	*A. dubia* Hartmann-Schröder, 1965
A. hummelinki indica Banse, 1959	*A.* cf. *dubia* (*sensu* Rouse, 1990)
A. lagunari Gitay, 1970	*A. alata* Hartmann-Schröder, 1991
A. bansei Hartmann-Schröder, 1986	
A. pectinata Fitzhugh, 1990e	
A. basifurcata Fitzhugh, 1990e	
A. mossambica (Day, 1957)	

among other sabellids (type locality); San Luis Obispo County, Montana de Oro State Park (35°16′16″N, 120°53′15″W), small cove adjacent to recreational area, exposed rock bench at low tide, in crevices among clumps of dense, low-growing green algae.

In addition to the type specimens, Hartman (1969: 693) also includes in *Fabricia brunnea* some of the specimens identified as *F. sabella* (*non* Ehrenberg, 1836) by Berkeley (1930) from Nanaimo, British Columbia, Canada. While I have not pursued this matter, it appears likely that Hartman did not base this conclusion on an actual examination of these specimens but, instead, relied on illustrations in Berkeley's paper, leaving open the question of such a northern distribution.

REMARKS. With the placement of *Fabricia brunnea* in *Novafabricia* Fitzhugh, 1990, the latter genus now contains at least seven species (e.g., Table 3, Fig. 3). The status of *N. gerdi* (Hartmann-Schröder, 1974) as a possible junior synonym of *Fabricia bansei* Day, 1961, has yet to be resolved (Fitzhugh, 1990d:12–13). Support for this new combination comes from the cladistic analyses presented below. In short, the features determining the generic placement of *Novafabricia brunnea* include the presence of pseudospatulate setae in setigers 3–5, also seen in *N. gerdi, N. infratorquata* (Fitzhugh, 1983), and *N. triangularis* Fitzhugh, 1990, and the reduced condition of dorsal lips, which is the synapomorphy defining the genus (see below).

The specimens of *Novafabricia brunnea* described here are virtually identical to the syntypes except that the former have a darker pigmented anterior end. While the ventral lobe of the anterior peristomial ring shows the same pronounced elongation (Fig. 1) seen in *N. chilensis* (Hartmann-Schröder, 1962), the distribution of pseudospatulates is different (setigers 3–6 in *N. chilensis*), as is the dentition pattern in abdominal uncini (cf. Fitzhugh, 1990d). Both species do, however, show the same ventral lip-like outgrowths at the bases of the ventralmost radioles (Fitzhugh, 1990a:fig. 3B, 1990d: fig. 6B; Fig. 1).

Development of the dorsal lips also appears to be slightly greater in *Novafabricia brunnea* (Fig. 1; Fitzhugh, 1990a:fig. 3B) than is seen in *N. chilensis* (Fitzhugh, 1990d:fig. 6B). For example, I originally noted (Fitzhugh, 1990a:12) that in *N. brunnea* the "dorsal lips are not as well developed as those of *Fabricia stellaris*, but are more distinct than what is seen in [other species of *Novafabricia*]." Unfortunately, this generalization is not sufficient to describe any particular dissimilarities or structural relationships between dorsal-lip forms in Fabriciinae taxa.

At this time, three states can be recognized among Fabriciinae taxa for dorsal lips (Fig. 2): (1) well-developed, triangular lobes that are distinctly separated from the dorsalmost radioles by a deep, V-shaped notch (Fig. 2A; e.g., *Fabricia, Fabriciola* Friedrich, 1939, *Augeneriella* Banse, 1957); (2) poorly to relatively well-developed ridges that are distinctly fused to the most proximal pinnule of the dorsal radioles, leaving only a shallow, U-shaped groove between the lip and pinnule (Fig. 2B; e.g., *Novafabricia,* some species of *Pseudofabriciola* Fitzhugh, 1990); or (3) dorsal lips are completely absent (Fig. 2C; e.g., *Fabricinuda* Fitzhugh, 1990). Distinguishing dorsal lips on the basis of separation from the dorsal radioles provides a more definite means of identifying different states.

A REAPPRAISAL OF CLADISTIC RELATIONSHIPS AMONG FABRICIINAE TAXA

Cladistic relationships among fabriciin taxa have recently been analyzed at several hierarchical levels (Fitzhugh, 1991a, 1991b, 1992a, 1992b) subsequent to results of a cladistic analysis of Sabellidae (*sensu lato*) genera by Fitzhugh (1989). As a result of a series of revisions of fabriciin genera (i.e., Fitzhugh, 1990a, 1990b, 1990c, 1990d, 1990e), I examined (Fitzhugh, 1991a) relationships among most fabriciin taxa, the results of which support the monophyly of all included genera. A similar analysis was later performed (Fitzhugh, 1992b) with the inclusion of *Monroika africana* (Monro, 1939) and a new genus and species from Australia, *Parafabricia ventricingulata* Fitzhugh, 1992. With the addition of several new species as well as redescriptions of some older species, further work on cladistic relationships at the specific level has been carried out for *Pseudofabriciola* (Fitzhugh, 1991b; Fitzhugh et

Table 2. Characters and states used to determine cladistic relationships of Fabriciinae taxa. State "0" is plesiomorphic based on out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

1. Ventral filamentous appendages: (0) absent; (1) nonvascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
2. Dorsal lips: (0) well-developed, triangular lobes, with dorsal margins well separated from proximalmost pinnules of dorsal radioles; (1) with dorsal margins fused with proximalmost radioles, forming low to moderately narrow ridges; (2) absent.
3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally somewhat; (2) extensively shifted dorsally.
4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate and/or with a peduncle-like process.
5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a narrow lobe; (1) low membranous collar; (2) membranous collar low dorsally and laterally, higher ventrally; (3) very high membranous collar of even width; (4) very high membranous collar that flares anteriorly; (5) low ridge dorsally and laterally, ventrally as a broad lobe; (6) low ridge dorsally and laterally, ventrally as a tongue-like lobe; (7) low ridge all around; (8) low ridge all around except for dorsolateral lobes.
6. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and surface smooth.
7. Middorsal collar margin: (0) separate; (1) entire; (2) notched.
8. Dorsolateral incisions on anterior margin of anterior peristomial ring collar: (0) absent; (1) present.
9. Anterior peristomial ring dimensions: (0) wider than long; (1) at least as long as wide.
10. Peristomial eyes in lateral view: (0) well developed and round; (1) poorly developed and crescentic; (2) absent.
11. Distribution of inferior thoracic pseudospatulate notosetae, in setigers 2–8: (0) absent; (1) 2–5; (2) 3–5; (3) 3–6; (4) 3–7; (5) 3–8; (6) broadly hooded, flagellate in 3–7.
12. Thoracic uncini: (0) without large tooth above main fang; (1) large tooth above main fang.
13. Thoracic uncini main fang: (0) slender; (1) swollen.
14. Abdominal uncini teeth: (0) >1 row of teeth; (1) 1 row of teeth.
15. Abdominal uncini breast: (0) oriopsis-like; (1) manubrium about 2.0 times longer than dentate region; (2) manubrium about 1.5 times longer than dentate region; (3) manubrium same length as dentate region.
16. Pygidial eyes: (0) absent; (1) present.
17. Radioles: (0) 3 or more pairs; (1) 2 pairs.
18. Body-wall spicules: (0) absent; (1) present.
19. Branchial hearts: (0) absent; (1) present.
20. Displaced pinnules (e.g., *Manayunkia, Monroika*): (0) absent; (1) present.
21. Thoracic uncini shape: (0) typical fabriciin shape; (1) *Manayunkia*/Genus A-type.
22. Pinnule arrangement: (0) distinctly pectinate; reduced to two (1) to four (2) pinnules at bases of branchial lobes.
23. Abdominal neuropodial pin-head setae: (0) absent; (1) present.

al., 1993) and *Fabriciola* (Fitzhugh, 1992a). The present cladistic analysis is a compilation of these studies and provides the empirical basis for revising the generic status of *Fabricia brunnea.*

A taxon that has not been considered in past cladistic analyses is the monotypic genus *Pseudofabricia* Cantone. The original description of the type species, *P. aberrans,* was based on specimens lacking a branchial crown, and details of thoracic notosetal types and distributions were vague. With the discovery of complete specimens, Giangrande and Cantone (1990) have thoroughly redescribed the species. Giangrande and Cantone did, however, assume the validity of *Pseudofabricia* relative to other fabriciin genera without any rigorous analysis of the relationship of *P. aberrans* to other fabriciin species. Inclusion of *P. aberrans* in the present analysis will determine the support for recognizing this genus.

Similarly, in their description of *Novafabricia bilobata,* Martin and Giangrande (1991) placed this species in *Novafabricia* in accordance with Fitzhugh's (1990d; see also Fitzhugh, 1991a, 1992b) suggestion that monophyly of the genus rests on the reduction of dorsal lips to low, narrow ridges. This dorsal-lip condition is, however, not unique to *Novafabricia* but is commonly seen in *Pseudofabriciola* species (e.g., Fitzhugh, 1990d, 1991b; Fitzhugh et al., 1993). Thus, *Novafabricia bilobata* is included in this analysis to assess its placement in this genus.

Augeneriella alata, from the Great Barrier Reef, was recently described by Hartmann-Schröder (1991) on the basis of a single specimen characterized by the absence of peristomial and pygidial eyes, eight thoracic and four abdominal setigers, a pair of unbranched, vascularized, ventral filamentous appendages, and the anterior peristomial ring collar being ventrally developed into a broad, lip-like extension. These features, along with Hartmann-Schröder's (1991:fig. 91) illustration of thoracic uncini, clearly indicate this is a species belonging to "Genus A" (*sensu* Fitzhugh, 1989), which is in the process of being formally described (Fitzhugh and Rouse, in prep.). When originally described by Fitzhugh (1989), "Genus A" was known to comprise *A. dubia* Hartmann-Schröder, 1965, and an undescribed species from the Indian Ocean.

Hartmann-Schröder (1991) noted similarities between *A. alata* and *A. dubia,* including the presence of four (as opposed to three) abdominal setigers and the absence of peristomial and pygidial eyes, but allied these species with *A. bansei* Hartmann-

Table 3. Character-state matrix for the 43 fabriciin species based on character states presented in Table 1. Species included in the analysis for the first time are indicated in bold. *Augeneriella bansei* Hartmann-Schröder is not included since it is based on a single, incomplete specimen.

	Characters and states																						
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Manayunkia speciosa	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0
M. baicalensis	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0
M. aestuarina	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0
M. brasiliensis	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	2	0
M. polaris	2	0	0	0	2	0	0	0	0	0	3	0	0	0	1	0	1	0	1	0	1	1	0
Monroika africana	2	0	0	0	2	0	0	0	0	2	2	1	0	0	3	0	1	0	1	1	0	0	0
Augeneriella dubia	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0
Genus A sp.	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0
Fabriciola baltica	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
F. berkeleyi	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
F. ghardaqa	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
F. tonerella	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	?
F. mediaseta	1	0	0	0	1	0	0	0	0	0	6	0	0	0	1	1	0	0	1	0	0	0	1
F. brevibranchiata	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
F. cf. *berkeleyi*	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1
Pseudofabriciola australiensis	2	0	0	1	4	2	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0	0
P. longa	0	1	0	1	3	2	1	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0
P. incisura	2	0	0	1	4	2	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0	0
P. capensis	0	0	0	1	3	1	1	1	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0
P. filamentosa	0	?	0	1	3	2	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
P. californica	0	0	0	1	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0
P. analis	0	1	0	1	4	2	1	1	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0
P. longipyga	?	?	?	?	4	2	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Fabricia stellaris	0	0	0	0	5	0	0	0	0	0	4	1	0	0	1	1	0	0	1	0	0	0	0
Pseudofabricia aberrans	0	0	0	0	5	0	0	0	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0
Augeneriella hummelincki	3	0	0	0	5	0	0	0	0	0	3	1	0	0	1	1	0	0	1	0	0	0	0
A. lagunari	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0
A. pectinata	3	0	0	0	5	0	0	0	0	0	3	1	0	0	3	1	0	0	1	0	0	0	0
A. basifurcata	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0
A. mossambica	3	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
Novafabricia chilensis	0	1	0	0	6	0	0	0	0	0	3	1	0	1	3	1	0	0	1	0	0	0	0
N. gerdi	0	1	0	0	5	0	0	0	0	0	2	1	0	1	3	1	0	0	1	0	0	0	0
N. infratorquata	0	1	0	0	5	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0
N. triangularis	0	1	0	0	5	0	0	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0
N. tenuiseta	0	1	0	0	5	0	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0
N. bilobata	0	1	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
N. brunnea	0	1	0	0	6	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0
Parafabricia ventricingulata	0	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
Fabricinuda limnicola	2	2	0	0	7	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
F. bikinii	2	2	2	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
F. trilobata	2	2	1	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
F. pseudocollaris	2	2	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
F. pseudopalpa	0	0	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0

Schröder, 1986, as all these species have unbranched ventral filamentous appendages. Unfortunately, Hartmann-Schröder (1991) neither commented on nor cited my (Fitzhugh, 1989; see also Fitzhugh, 1991a, 1992b) finding that *A. dubia* is clearly a member of "Genus A" and cladistically is quite far removed from *Augeneriella.* Furthermore, no mention was made of my (Fitzhugh 1990e) revision of *Augeneriella,* where I predicted that the presence of unbranched ventral filamentous appendages in the holotype of *A. bansei,* the only known specimen of the species, is likely an anomalous feature. Hartmann-Schröder (1991) also failed to mention or compare *A. alata* to Rouse's (1990)

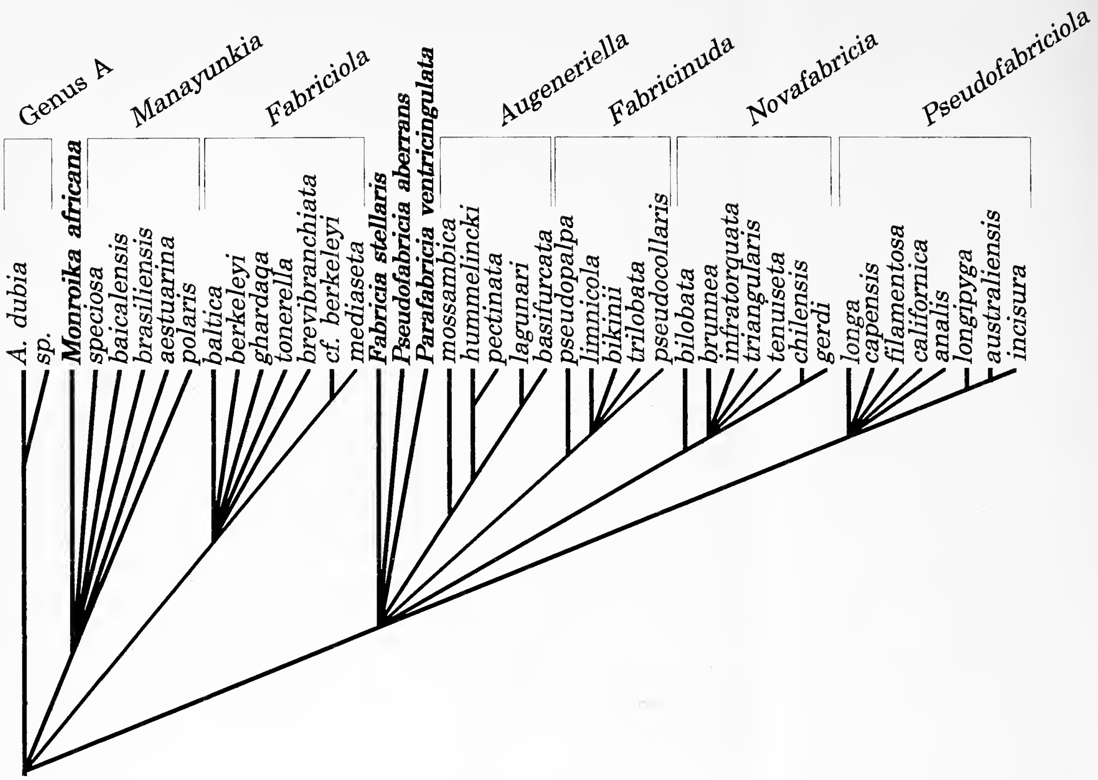


Figure 3. Strict consensus cladogram for fabriciin taxa based on 1,418 minimum-length cladograms. Monotypic genera are indicated in bold.

numerous specimens of *A.* cf. *dubia,* also from the Great Barrier Reef, though she does cite this paper in relation to *Oriopsis* Caullery and Mesnil, 1896. Thus, for the purposes of the present analysis, *A. alata,* although recognized as a member of "Genus A" (Table 1), is not included in the analysis since distinctions between species of that group are still being determined (Fitzhugh and Rouse, in prep.).

METHODS AND MATERIALS

The analysis includes 43 fabriciin species distributed among 11 genera. Most genera are represented by all described species except in the cases of *Manayunkia* Leidy, 1858, *Fabriciola,* and *Augeneriella* (see Fitzhugh, 1992b, for details). *Fabricia* is only represented by the nominate subspecies, *F. stellaris stellaris* (Müller, 1774; see Fitzhugh, 1990a). *Pseudofabricia aberrans* is included on the basis of preserved specimens and the description by Giangrande and Cantone (1990). Data used for the inclusion of *Novafabricia bilobata* are from the original description (Martin and Giangrande, 1991).

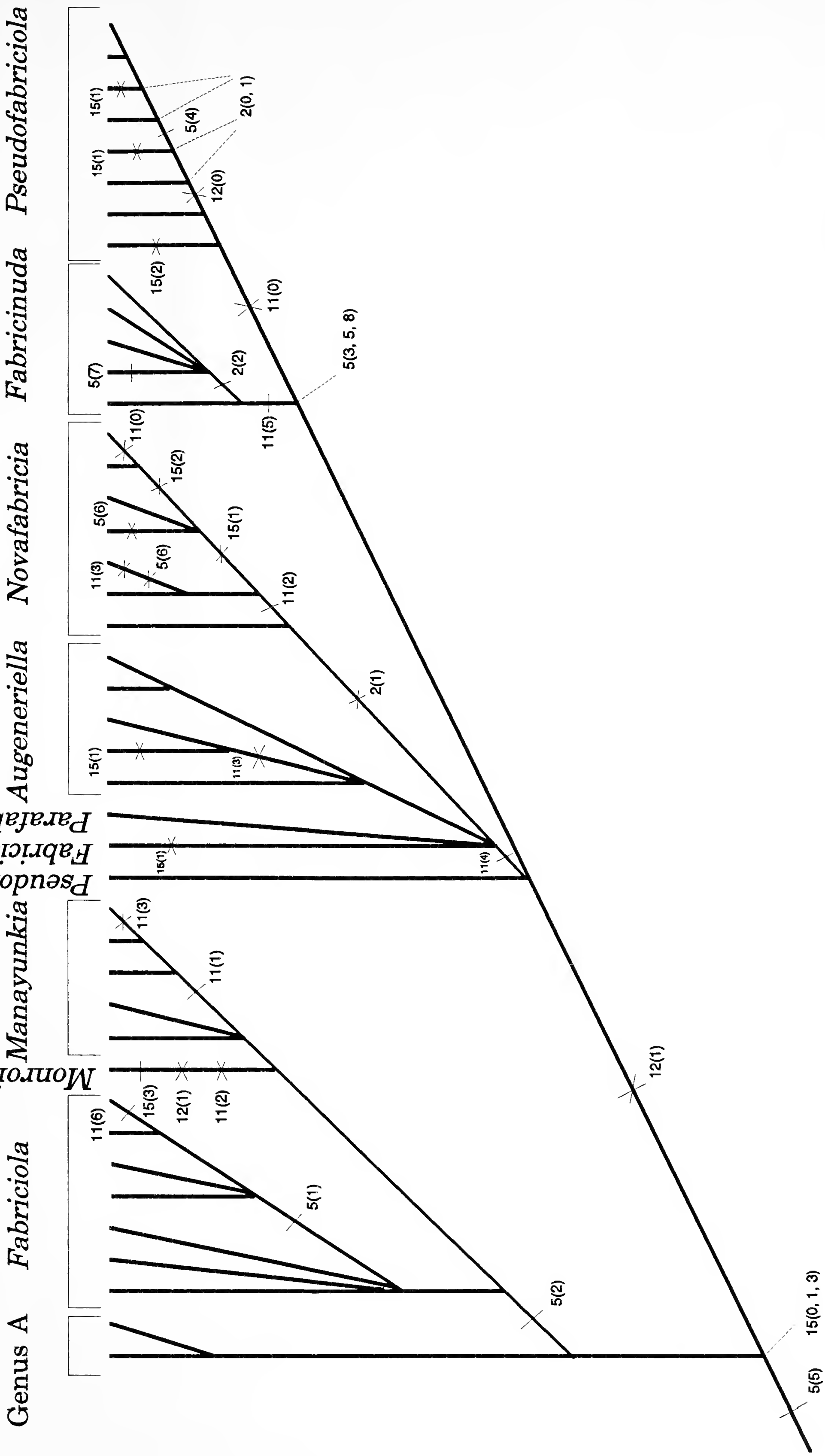
A total of 45 apomorphic states were used, distributed among 23 characters. Characters and states are presented in Table 2. Most characters are the same as those used by Fitzhugh (1992b), though some modifications have been incorporated as a result of studies by Fitzhugh (1991b, 1992a) and Fitzhugh et al. (1993).

States for character 2 have been modified. In previous studies, state 2(1) was described as "dorsal lips low, narrow ridges" and the plesiomorphic state as "well-developed, triangular lobes." As noted above, the dorsal lips of *N. brunnea* are slightly more developed than in other members of this genus. The separation between character states 2(0) and 2(1) is here shifted to indicate the degree of fusion with the first radioles (i.e., showing a conspicuous demarcation as opposed to being distinctly fused to the first radioles; Table 2).

The distribution of states among taxa is pre-

⟶

Figure 4. One of 1,418 minimum-length cladograms for fabriciin taxa (species indicated but not named), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella, Novafabricia, Fabricinuda,* and *Pseudofabriciola* relative to the monotypic genera *Fabricia, Pseudofabricia,* and *Parafabricia.* Slashes = synapomorphies, ×'s = homoplasies. Ambiguous character-state assignments are shown at nodes. See Table 2 for explanations of character states.


Genus A
Fabriciola
Monroika
Manayunkia
Pseudofabricia
Fabricia
Parafabricia
Augeneriella
Novafabricia
Fabricinuda
Pseudofabriciola
5(5)
15(0, 1, 3)
12(1)
5(2)
5(1)
11(6)
15(3)
12(1)
11(2)
11(1)
11(3)
15(1)
11(4)
15(1)
11(3)
2(1)
11(2)
11(3)
5(6)
5(6)
15(1)
15(2)
11(0)
5(3, 5, 8)
11(5)
5(7)
2(2)
15(2)
11(0)
12(0)
15(1)
5(4)
15(1)
2(0, 1)

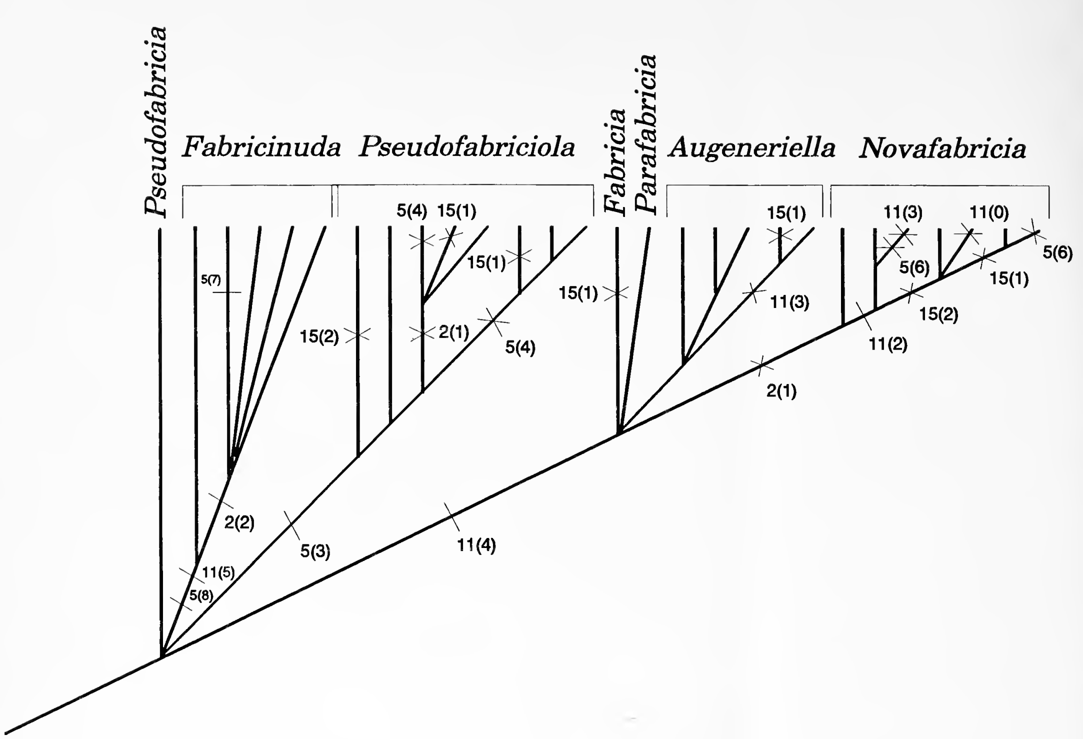


Figure 5. A portion of a cladogram of fabriciin taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella, Novafabricia, Fabricinuda,* and *Pseudofabriciola* relative to the monotypic genera *Fabricia, Pseudofabricia,* and *Parafabricia.* See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

sented in Table 3. Character-state polarities are based on out-group comparisons as performed by Fitzhugh (1991a, 1991b, 1992a, 1992b), and multistate characters were treated as nonadditive.

Cladograms were constructed using the combination of commands **mhennig*; bb*** in the computer program Hennig86, developed by Farris (1988). Lengths, consistency, and retention indices (ci and ri, respectively) and character-state transformation series were determined with the **xsteps** command using the **h** and **c** options.

RESULTS

A total of 1,418 minimum-length cladograms was produced, which is only a subset of the total number of cladograms possible using the **mhennig*; bb*** tree-building commands; the limiting factor in this case was the amount of available computer memory. Each cladogram has a length of 68 steps, with a ci of 0.66 and ri of 0.86.

The inclusion of *Pseudofabricia* allows for a greater degree of instability at the generic level, which contributes to the larger number of cladograms (Fig. 3) than previously reported (Fitzhugh, 1991a, 1992b). Specific-level topologies appear to be roughly similar to what have been described by Fitzhugh (1991a, 1991b, 1992a, 1992b) and Fitzhugh et al. (1993) except in the case of *Novafabricia,* which is examined in greater detail in the analysis below. Six of the seven non-monotypic genera clearly remain monophyletic (Fig. 3). The one exception, involving the relationship of the monotypic genus *Monroika* Hartman, 1951, to *Manayunkia,* has been analyzed and discussed in detail by Fitzhugh (1992b). The validity of the three remaining monotypic genera—*Fabricia, Pseudofabricia,* and *Parafabricia*—is upheld. (Fig. 3).

In all topologies, *Pseudofabricia* is a member of the clade containing *Fabricia, Parafabricia, Augeneriella, Novafabricia, Fabricinuda,* and *Pseudofabriciola* (Figs. 3–6); this clade is defined by the presence of a large tooth above the main fang in thoracic uncini [state 12(1); Fig. 4]. The placement of *Pseudofabricia* within this clade is quite variable. For example, the genus can form a basal trichotomy with several genera (Figs. 4–5) or can have a more exclusive relationship to some other genera within this clade (Fig. 6).

With *Novafabricia* still defined by the reduction of the dorsal lips to low ridges [state 2(1)], the new combination *N. brunnea* is upheld, as is Martin and Giangrande's (1991) placement of *N. bilobata* in this genus (Figs. 3–6). The results of additional analyses on the relationships of *Novafabricia* species are presented below.

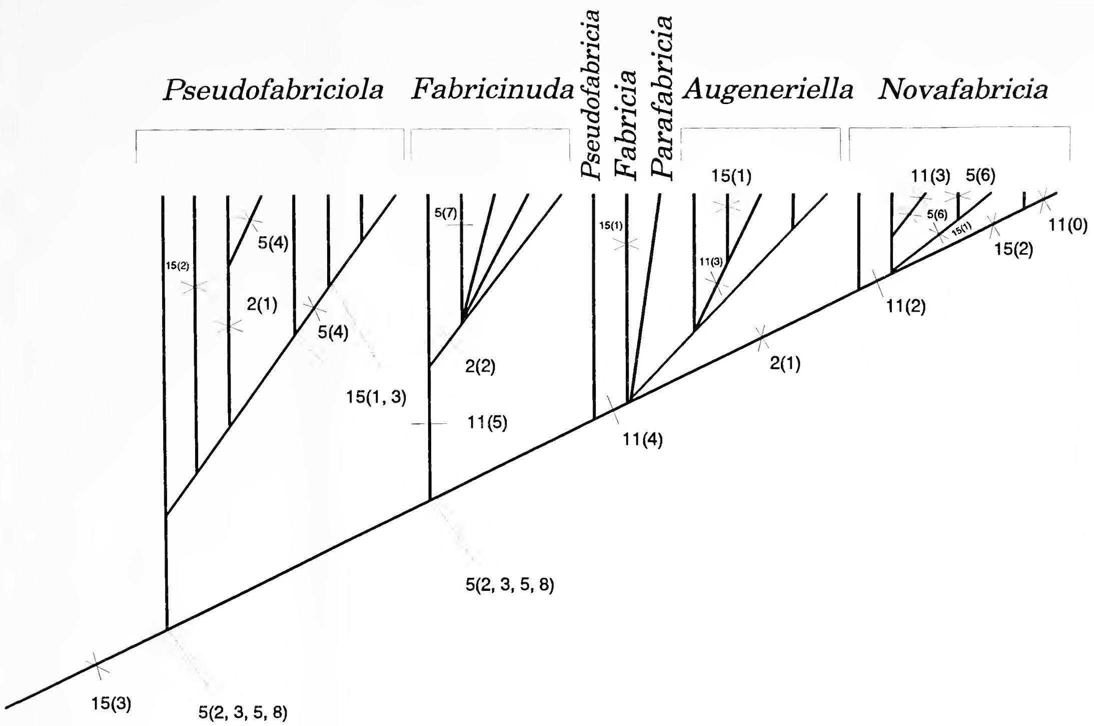


Figure 6. A portion of a cladogram of fabriciin taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella, Novafabricia, Fabricinuda,* and *Pseudofabriciola* relative to the monotypic genera *Fabricia, Pseudofabricia,* and *Parafabricia.* See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

CLADISTIC RELATIONSHIPS AMONG *NOVAFABRICIA* SPECIES

A more detailed analysis of relationships among the seven *Novafabricia* species is presented here to examine more accurately the variability of these relationships, especially relative to results of previous analyses (e.g., Fitzhugh, 1991a, 1992b).

METHODS AND MATERIALS

The present analysis involved the seven *Novafabricia* species in the previous analysis. From the results of that latter analysis, five characters (Table 4) are instrumental in discerning relationships among *Novafabricia* species. Note, however, that the plesiomorphic state for character 11 (distribution of thoracic pseudospatulate setae) in Table 4 has been altered from what is shown in Table 2. This modification is in accord with the plesiomorphic state as determined in the previous analysis. All multistate characters were, however, treated as nonadditive. The distribution of character states among species is presented in Table 5. Cladograms were constructed using the **ie*** command in Hennig86.

RESULTS

Four minimum-length cladograms (Fig. 7) were produced using the data matrix in Table 5, each

Table 4. Characters and states used in the determination of cladistic relationships among *Novafabricia* species. Characters are numbered as in Table 1, though the general character-state polarity for character 11 is based on the cladistic results obtained from the matrix in Table 2. State "0" is plesiomorphic based on these out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

2. Dorsal lips: (0) triangular lobes with dorsal margins well separated from first radiole; (1) dorsal margins fused with proximalmost radiole of first radiole forming low to moderate narrow ridge.
5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a broad lobe; (1) low ridge dorsally and laterally, ventrally as a tongue-like lobe.
11. Distribution of inferior thoracic pseudospatulate notosetae in setigers 2–8: (0) 3–7; (1) 3–5; (2) 3–6; (3) absent.
14. Abdominal uncini teeth: (0) >1 row of teeth; (1) 1 row of teeth.
15. Abdominal uncini breast: (0) manubrium same length as dentate region; (1) manubrium about 1.5 times longer than dentate region; (2) manubrium about 2.0 times longer than dentate region.

Table 5. Character-state matrix for all species of *Novafabricia* based on character states presented in Table 3.

Species	Characters and states				
	2	5	11	14	15
Outgroup	0	0	0	0	0
N. bilobata	1	0	0	0	0
N. brunnea	1	1	1	0	2
N. chilensis	1	1	2	1	0
N. gerdi	1	0	1	1	0
N. infratorquata	1	0	1	0	2
N. tenuiseta	1	0	3	0	1
N. triangularis	1	0	1	0	1

with a length of 9 steps and a ci and ri of 0.88 and 0.80, respectively. Among these cladograms, only the placements of *Novafabricia bilobata* and a clade containing *N. chilensis* and *N. gerdi* are stable. *Novafabricia bilobata* is the sister group to all other species by way of having thoracic pseudospatulate setae in setigers 3–7 [state 11(0)]. The *N. chilensis–N. gerdi* clade is defined by the presence of a single row of teeth in abdominal uncini [state 14(1)]. In three topologies (Fig. 7A–C) this clade is the sister group to the clade containing *N. infratorquata, N. brunnea, N. tenuiseta* Fitzhugh, 1990, and *N. triangularis.* In the fourth topology (Fig. 7D), the *N. chilensis–N. gerdi* clade forms a trichotomy with a clade containing *N. infratorquata* and *N. brunnea* and another clade with *N. tenuiseta* and *N. triangularis.*

DISCUSSION

The increased lack of resolution at the generic level as well as the larger number of cladograms produced in the first analysis as compared to what are reported in earlier studies (e.g., Fitzhugh, 1991a, 1992b) is directly related to the inclusion of *Pseudofabricia aberrans* and *Novafabricia bilobata.* Being primarily characterized by plesiomorphic features, especially the absence of thoracic pseudospatulate setae [state 11(0); Table 2], the placement of *Pseudofabricia* is quite unstable and allows for a larger number of topologies involving this genus and *Augeneriella, Novafabricia, Fabricinuda,* and *Pseudofabriciola* (cf. Fitzhugh, 1991a, 1992b).

As noted by Martin and Giangrande (1991), *Novafabricia bilobata* is very distinct from other *Novafabricia* species by the presence of pseudospatulate setae in setigers 3–7 [state 11(4); Table 2]. In relating *Novafabricia* species to other fabriciin taxa, the presence of character state 11(4) within *Novafabricia* has resulted in substantial changes in patterns of relationship among these species as well as resultant hypotheses of transformation series.

For example, in the analyses conducted by Fitzhugh (1991a, 1992b; Fig. 8B, C) for the then known five species, the presence of pseudospatulate setae

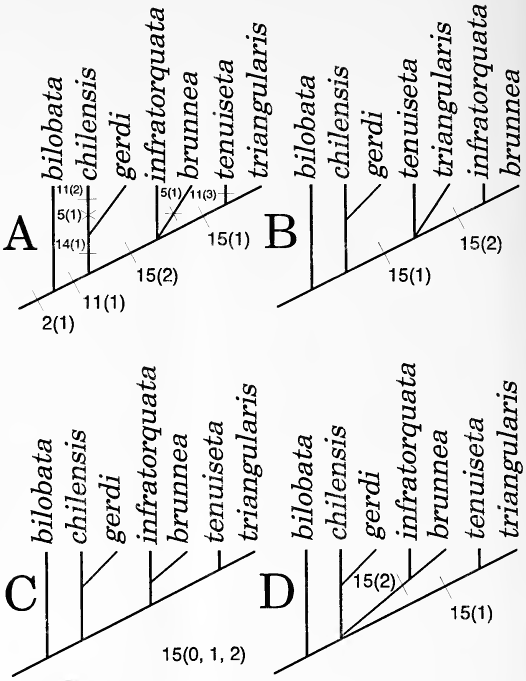


Figure 7. Possible minimum-length cladograms for *Novafabricia* species. All character-state changes are shown in A. Character-state changes in B–D are as in A except where indicated. See Fig. 4 for explanations of character-state changes and Table 4 for descriptions of character states.

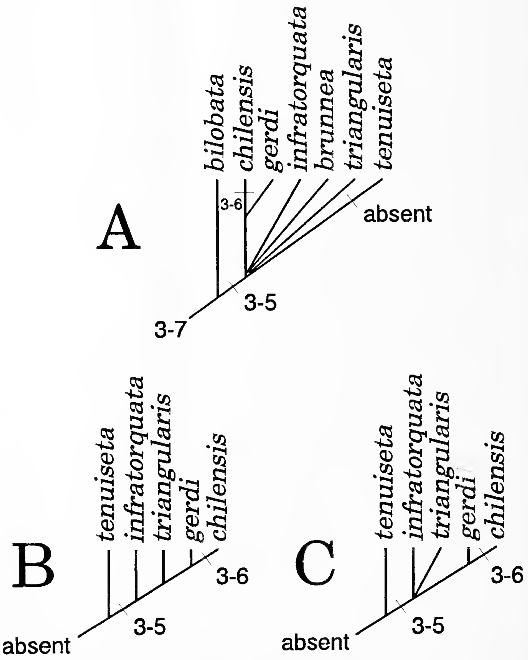


Figure 8. Past and present patterns of relationships among *Novafabricia* species, indicating the presence, distribution, and polarity of thoracic pseudospatulate setae: **A**, strict consensus cladogram of the four topologies in Fig. 7; **B**, topology from Fitzhugh (1991a:fig. 9); **C**, topology from Fitzhugh (1992b:fig. 5).

is a derived condition within *Novafabricia* as well as being homoplasious relative to other fabriciin genera. The nature of this transformation series resulted from the absence of pseudospatulates in *N. tenuiseta*, which was the sister group to all other *Novafabricia* species. Thus, *N. tenuiseta* displays the more general fabriciin condition of lacking pseudospatulates.

With the inclusion of *Novafabricia bilobata*, however, the transformation series for pseudospatulates is altered, as is shown in the present analysis of relationships among *Novafabricia* species (Figs. 7–8), such that the presence of pseudospatulates in setigers 3–7 [state 11(0); Table 4] is now the plesiomorphic condition for the genus. An additional result is the placement of *N. tenuiseta* at a more exclusive sister-group position by the presence of only elongate, narrowly hooded setae in setigers 2–8 [state 11(3); Table 4]. Relative to other fabriciin taxa, this setal distribution is hypothesized to be a reversal.

KEY TO SPECIES OF *NOVAFABRICIA*

1a. Inferior thoracic notosetae of setigers 2–8 short, elongate, narrowly hooded .... *N. tenuiseta* Fitzhugh
b. At least some inferior thoracic notosetae are pseudospatulate 2
2a. Inferior thoracic pseudospatulate notosetae limited to setigers 3–5 4
b. Pseudospatulates in setigers 3–6 or 3–7 ... 3
3a. Pseudospatulates in setigers 3–6 .... *N. chilensis* (Hartmann-Schröder)
b. Pseudospatulates in setigers 3–7 .... *N. bilobata* Martin and Giangrande
4a. Ventral lobe-like extension of anterior peristomial ring triangular in shape 5
b. Ventral extension as a broad, tongue-shaped lobe .... *N. brunnea* (Hartman), new combination
5a. Abdominal uncini viewed *in situ* with prominent, single proximal row of teeth distally surmounted by 1–2 multidentate rows .... *N. gerdi* (Hartmann-Schröder)
b. Abdominal uncini with at least several rows of teeth throughout 6
6a. Manubrium of abdominal uncini about same length as dentate region .... *N. triangularis* Fitzhugh
b. Manubrium of abdominal uncini two times longer than dentate region .... *N. infratorquata* (Fitzhugh)

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