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THE NORTH AMERICAN SPECIES OF THE BEE GENUS *LITHURGE* (HYMENOPTERA: MEGACHILIDAE)

Roy R. Snelling

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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THE NORTH AMERICAN SPECIES OF THE BEE GENUS *LITHURGE* (HYMENOPTERA: MEGACHILIDAE)

Roy R. Snelling[1]

ABSTRACT. The North American species of *Lithurge* are reviewed, and a key is given for the separation of both sexes of all species. Supraclypeal structures of the females are illustrated, as are the labral structures of the males. Of the previously described native forms, *L. apicalis* var. *opuntiae* Cockerell and *L. arizonensis* Cockerell are synonyms of *L. apicalis* Cresson (NEW SYNONYMY); *L. apicalis* subsp. *littoralis* Cockerell is a valid species and a senior synonym of *L. bruesi* Mitchell (NEW SYNONYMY). One new species, *L. listrota*, is described from southern California desert regions. All native American species belong to the subgenus *Lithurgopsis*.

Two representatives of the nominate subgenus occur in the New World. The Palaearctic species, *L. chrysurus* (Fonscolombe), is adventive in the eastern United States. A South American species, *L. huberi* Ducke, belongs to the Indo-Australian species group of *L. atratus* F. Smith and may have been introduced into Brazil in historic times.

The South American genera *Trichothurgus* Moure and *Lithurgomma* Moure are merged into a single genus, *Trichothurgus*, and the tribe Trichothurgini is dropped.

INTRODUCTION

The megachilid subfamily Lithurginae includes about 50 species in both Old and New World faunas. Old World species all belong to the nominate subgenus of *Lithurge* Latreille and are present in the southern Palaearctic, Ethiopian and Indo-Australian regions. These species, as far as known, provision their nests with pollen from plants of the families Malvaceae and Compositae.

For the most part, New World species of *Lithurge* belong to the subgenus *Lithurgopsis* Fox and are present in southern North America and South America. One Palaearctic species, *L. chrysurus* (Fonscolombe), is adventive in the eastern United States (Roberts, 1978); a Brazilian species, *L. huberi* Ducke, also belongs to the nominate subgenus and is probably introduced from the Indo-Australian region. Although most *Lithurgopsis* utilize pollen from Cactaceae in their larval cells, a few Argentinian species use malvaceous pollens (J. L. Neff, in litt.). Some Chilean and Argentinian species, formerly placed in *Lithurge*, are now placed in the genera *Trichothurgus* and *Lithurgomma*, both described by Moure (1949); at least one of these is an oligolege on Compositae (J. L. Neff, in litt.).

THE NEW WORLD LITHURGINAE

Most New World Lithurginae have been described in the genus *Lithurgus* Berthold, 1827, an invalid emendation of *Lithurge* Latreille, 1825. Fox (1902) noted that males of the New World species possess tarsal arolia and proposed to remove them to a new genus, *Lithurgopsis*. Subsequent workers have consistently treated *Lithurgopsis* as a subgenus of *Lithurge* (e.g., Michener, 1944; Hurd, 1979).

In addition to the presence of tarsal arolia in *Lithurgopsis* males, there are other features by which members of the subgenus may be separated from the nominotypical subgenus. In females of *Lithurgopsis* the facial prominence, when present, occurs only on the supraclypeal area; in *Lithurge, sensu stricto,* the basal portion of the clypeus is also involved. The first flagellar segment is consistently short in both sexes of *Lithurgopsis*; it is little, if any, longer than the second and often much shorter; the second segment is as long as broad or longer. In *Lithurge, sensu stricto,* the first flagellar segment is as long as broad, or longer, the second segment not more than half as long as the first; the second segment is often conspicuously broader than long.

Lithurge (*L.*) *chrysurus* (Fonscolombe, 1834) is a Palaearctic species that is now introduced and established in the eastern United States. Roberts (1978) reported this Mediterranean species from New Jersey, discussed its nesting biology and behavior, and described the larva and pupa.

Lithurge (*L.*) *huberi* (Ducke, 1907), described from Brazil, is the only South American representative of the nominotypical subgenus. I have seen specimens of both sexes of this species. Morphologically, *L. huberi* is a member of the group of forms related to *L. atratus* (F. Smith). Nominate species of this group range from India to Australia, Melanesia, and Polynesia; according to Michener (1965) there may be but a

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[1] Entomology Section, Natural History Museum of Los Angeles County.

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single species involved. There are no obvious morphological features by which *L. huberi* may be separated from *L. atratus*. It seems likely that *L. huberi* is adventive in Brazil, introduced via infested wood within historic times.

Although most New World Lithurginae belong to the genus *Lithurge*, Moure (1949) described two genera, *Trichothurgus* and *Lithurgomma*, which he placed in the new tribe Trichothurgini. Species of Trichothurgini occur in Peru and Argentina but are primarily Chilean. *Trichothurgus* and *Lithurgomma* differ from *Lithurge* in the elongate labrum and in the shape of the first gastric tergum, which is not flattened as in *Lithurge*. The species of these two genera are large, robust bees with abundant body hairs that conceal most integumentary surfaces.

In *Trichothurgus*, the facial prominence, if present, is on the supraclypeal area and the frons lacks a shiny area in front of the anterior ocellus. Species of *Lithurgomma* have a clypeal prominence, in females only, and there is a large, flattened, shiny area in front of the anterior ocellus. These differences are trivial and do not, in my opinion, justify the status of *Trichothurgus* and *Lithurgomma* as separate genera. My view is that *Lithurgomma* is a junior synonym of *Trichothurgus* (NEW SYNONYMY). The characters of Moure's Trichothurgini will differentiate the expanded genus *Trichothurgus* from *Lithurge*. Concurrently, the tribe Trichothurgini is superfluous; there is no need to place the two genera of Lithurginae in separate tribes.

The known species of *Trichothurgus* are: *T. albiceps* (Friese), *T. alpestris* (Friese), *T. aterrimus* (Cockerell), *T. colloncurensis* Ogloblin, *T. herbsti* (Friese), *T. holomelan* (Moure), *T. laticeps* (Friese), *T. neoqueensis* (Friese), *T. osmioides* (Friese), *T. pseudocellatus* (Moure), *T. shajovskoyi* Ogloblin, and *T. wagenknechti* (Moure).

The few South American species of *Lithurge* have never been critically examined. The North American species were reviewed by Mitchell (1938), who gave a key for the species then known. The biology of no American species has been studied in detail; some notes on *L. apicalis* (Cresson) were published by Parker and Potter (1973), and Brach (1979) reported some observations on *L. gibbosa* (F. Smith). The nesting biology and behavior of the introduced species, *L. chrysurus*, were described by Roberts (1978).

SPECIMENS EXAMINED

During the course of this study, specimens from the following institutional collections were examined: American Museum of Natural History (AMNH), Arizona State University (ARSU), British Museum (Natural History) (BMNH), California Academy of Sciences (CAS), California Department of Food and Agriculture (CDFA), National Museum of Natural History (USNM), Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDM), Texas A and I University (TAI), Texas A and M University (TAMU), University of Arizona (UNAR), University of California, Berkeley (UCB), University of California, Davis (UCD), University of California, Riverside (UCR), University of Colorado (UCOL), University of Kansas (UKAN), University of Nebraska (UNEB), and Utah State University (UTSU). Specimens from the personal collection of T. Griswold are indicated (GRIS).

SYSTEMATICS

In the review by Mitchell (1938), five species were treated in the North American fauna, one with three subspecies. A sixth species was mentioned but not treated as it had been too recently described and was unknown to Mitchell. The present study recognizes eight species, including one adventive species and one that was previously undescribed. The various subspecies attributed to *L. apicalis* by Mitchell (1938) are discussed below. The morphological characteristics of each species are sufficiently distinctive that the previously described species are not redescribed; the keys and figures given here are adequate for their recognition.

Superficially, the various species tend to be quite similar. Females are most notably different from one another in the shape of the elevations or processes of the supraclypeal area. There are differences, also, in the density of the punctures of the clypeus and supraclypeal area, but there is sufficient infraspecific variability to render these unreliable as diagnostic characters.

Males are most readily separated by differences in labral structure. When fresh, individuals of this sex should have the mandibles spread so that the external surface of the labrum is clearly visible. Although the mandibles of a dry specimen can be spread after relaxing the bee, there is a greater chance that the specimen will be damaged.

KEY TO NORTH AMERICAN *LITHURGE*

Males

1a. Tarsal arolia present; first flagellar segment shorter than second (subgenus *Lithurgopsis*) 2
b. Tarsal arolia absent; first flagellar segment distinctly longer than second (subgenus *Lithurge*) .... *chrysurus* (Fonscolombe)
2a. Labrum with a single median tubercle, or none 3
b. Labrum with a pair of erect, slender tubercles (Fig. 4) .... *littoralis* (Cockerell)
3a. Labrum without median tubercle, with a low, transverse basal ridge or swelling (Figs. 6, 10) 4
b. Labrum with an erect, median tubercle, without transverse basal ridge or swelling (Figs. 8, 12) 6
4a. Supraclypeal area gently convex, its upper portion sloping toward antennal sockets, and with a definite median area that is less closely punctate than area near subantennal suture or entire supraclypeal area sparsely and irregularly punctate 5
b. Supraclypeal area uniformly flat between clypeal base and antennal sockets, continguously punctate, punctures coarse and subcontiguous along midline .... *planifrons* (Friese)
5a. First flagellar segment, on shortest side, distinctly broader than long, shorter than pedicel; supraclypeal area about

1.4 times wider than long; legs usually reddish .... *echinocacti* (Cockerell)

b. First flagellar segment, on shortest side, about as long as wide, about as long as pedicel; supraclypeal area about 1.8 times wider than long; legs brown .... *apicalis* (Cresson)

6a. Labrum with a low, often obsolescent, ridge extending obliquely from basal corner to base of median tubercle (Figs. 2, 12) 7

b. Labrum deeply concave on either side of tubercle and with a short, curved ridge from base of tubercle to mid-length of lateral margin (Fig. 8) .... *socorroensis* (Mitchell)

7a. Supraclypeal area slightly protuberant, densely punctate; ocelloccipital distance greater than interocellar distance .... *gibbosa* (F. Smith)

b. Supraclypeal area flat, sparsely punctate, at least in middle; ocelloccipital distance less than interocellar distance .... *listrota* new species

Females

1a. First flagellar segment shorter than second; facial prominence, when present, not as below (subgenus *Lithurgopsis*) 2

b. First flagellar segment distinctly longer than second; facial prominence high, triangular in lateral view, its lower portion sloping toward base of clypeus (subgenus *Lithurge*) .... *chrysurus* (Fonscolombe)

2a. Supraclypeal protuberance nearly as broad as face, extending laterad of subantennal sutures (Figs. 3, 5); malar area distinct and with deep posterior pit (Figs. 3, 5) .. 3

b. Supraclypeal protuberance, when present, much narrower than width of face, not extending laterad of subantennal sutures (Figs. 7, 9, 11); malar area linear, mandible nearly contiguous with eye, posterior pit usually absent (Figs. 1, 7, 9) 4

3a. Labral tubercle with median and sublateral impressions; clypeus without preapical ridge (Fig. 3) .... *littoralis* (Cockerell)

b. Labral tubercle divided in middle only (Fig. 5); clypeus with preapical ridge which is interrupted in middle (Fig. 5) .... *apicalis* (Cresson)

4a. Supraclypeal area distinctly elevated on each side of middle or with a single, transverse, bowed elevation ... 5

b. Supraclypeal area flat, with no protuberance, shiny and very sparsely punctate (Fig. 1) ... *listrota* new species

5a. Supraclypeal area with prominent rounded elevation on either side of middle (Figs. 7, 9); malar area without posterior pit 6

b. Supraclypeal elevation a high, transverse, bowed ridge (Fig. 11); malar area with broad, shallow, posterior pit .... *gibbosa* (F. Smith)

6a. Dorsal margin of pronotum with conspicuous fascia of dense, plumose, white hairs; ocelloccipital distance less than interocellar distance ..... *echinocacti* (Cockerell)

b. Dorsal margin of pronotum without fascia of dense, plumose, white hairs; ocelloccipital distance greater than interocellar distance .... *socorroensis* (Mitchell)

Lithurge (*Lithurgopsis*) *apicalis* (Cresson)

Figures 5, 6

Lithurgus apicalis Cresson, 1875:724. ♀.

Lithurgopsis apicalis var. *opuntiae* Cockerell, 1902:182. ♀. NEW SYNONYMY.

Lithurgus arizonensis Cockerell, 1937:108. ♀. NEW SYNONYMY.

RANGE

South Dakota and Wyoming to western Texas (?), west to Utah, Nevada, and southern California; northern Mexico.

Although this species has been recorded from Texas by previous authors (Cockerell, 1911; Mitchell, 1938), I have seen no material of *L. apicalis* from that State. All specimens from Texas previously identified as *L. apicalis*, that I have examined, proved to be *L. littoralis*.

BIONOMICS

Parker and Potter (1973) published some notes on the nesting habits of *L. apicalis*. The larva has been described by Rozen (1973).

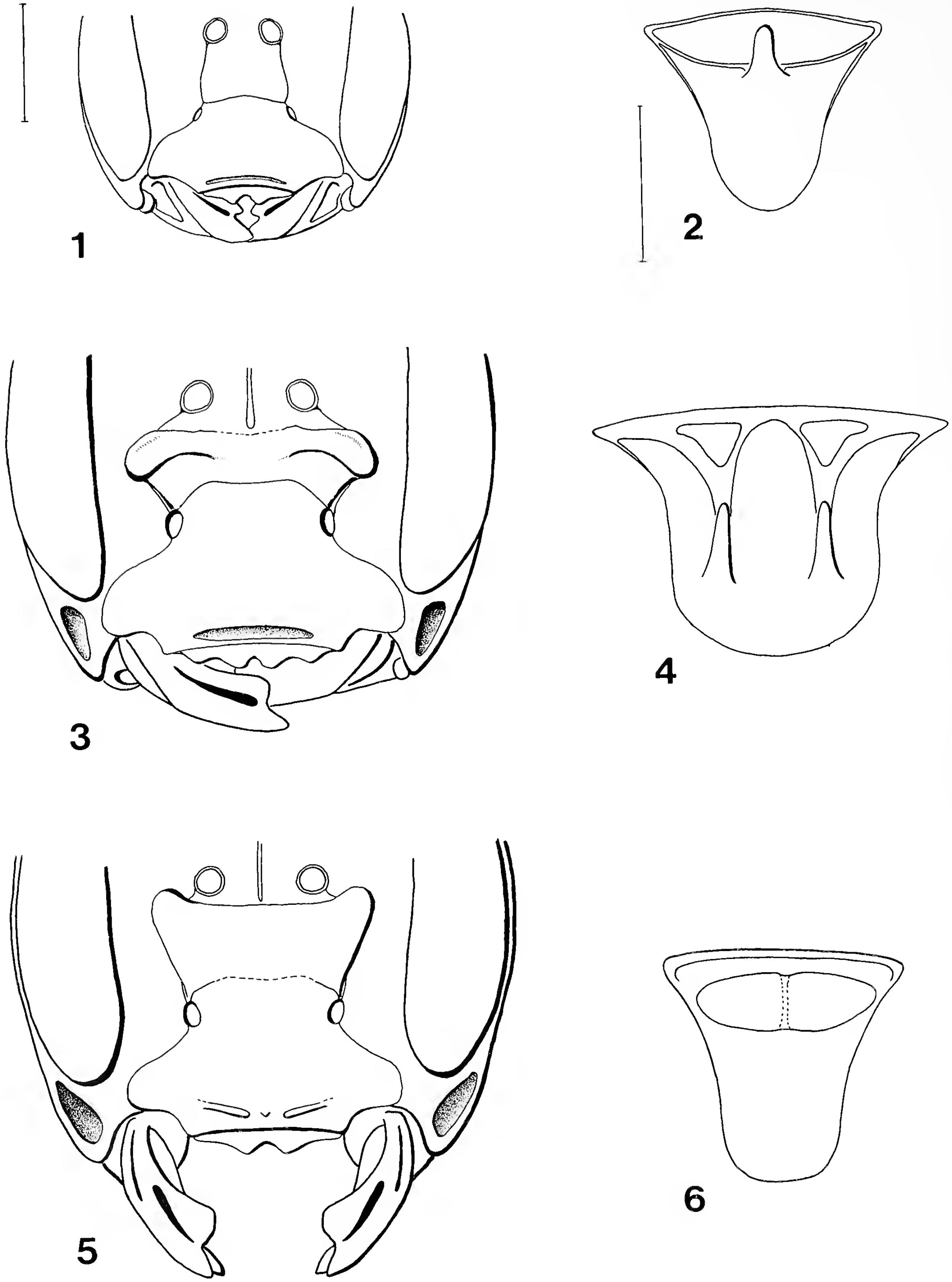
Females provision the cells with pollen from species of *Opuntia*, but both sexes have been taken at flowers of other genera. Hurd (1979) recorded this species on flowers of *Echinocactus*, *Encelia californica*, *Eriogonum*, and *Sphaeralcea*. Previously unpublished floral records include: *Agave nevadensis*, *Argemone platyceros*, *Argemone* sp., *Asclepias erosa*, *Baileya multiradiata*, *Cirsium californicum*, *Cirsium* sp., *Calochortus concolor*, *Chilopsis linearis*, *Cleome serrulata*, *Cnicus* sp., *Grindelia squarrosa*, *Prosopis juliflora*, *Robinia neomexicana*, *Senecio longilobus*, *Verbena stricta*, *Verbesina encelioides*, and "sweet pea."

DISCUSSION

For many years, *L. apicalis* has been divided into two subspecies: *L. a. apicalis* and *L. a. opuntiae*. The former, with ferruginous hairs on the last tergum of the female, is a northern form, found in South Dakota, Wyoming, Nebraska, Kansas, Colorado, Utah, and Nevada. The southern population, *L. a. opuntiae*, with dark brown hairs on the last tergum of the female, ranges from New Mexico to southern California. Both forms, however, occur in New Mexico, Arizona, and California. In many areas the two occur together, along with many specimens of intermediate character.

In view of the broad zone of intergradation, were mixing of the forms occurs and which actually includes much of the range of *L. a. opuntiae*, it hardly seems desirable to separate the two forms nomenclatorially. Accordingly, *L. a. opuntiae* its here treated as a synonym of *L. apicalis*.

Cockerell (1937) described *L. arizonensis* from two females collected in the Baboquivari Mountains of Arizona. These were said to differ from *L. a. opuntiae* by their more



Figures 1–6. *Lithurge* spp. **Figs. 1, 3, 5,** lower portion of face of female of *L. listrota* (1), *L. littoralis* (3), and *L. apicalis* (5). Scale line = 1.0 mm. **Figs. 2, 4, 6,** labrum of male of *L. listrota* (2), *L. littoralis* (4), and *L. apicalis* (6). Scale line = 0.5 mm.

flattened and coarsely punctate clypeus and by the deeper, sparser facial punctures. I have examined the type of *L. arizonensis* (in the CAS) and find no significant differences between this specimen and other individuals of *L. apicalis.* All the differences cited by Cockerell fall well within the range of character variation that I attribute to this species.

The male from Port Isabel, Texas, described by Cockerell (1917) as *L. apicalis* subsp. *littoralis,* is a distinct species and a senior synonym of *L. bruesi* (see below).

TYPE MATERIAL

Lithurgus apicalis Cresson: female, in Academy of Natural Sciences, Philadelphia. *Lithurgopsis apicalis* var. *opuntiae* Cockerell: no types designated, and none of the original material can be identified with surety. *Lithurgus arizonensis* Cockerell: female, in California Academy of Sciences, San Francisco.

SPECIMENS EXAMINED (566 ♀♀, 423 ♂♂)

UNITED STATES. ARIZONA, *Apache Co.:* White Mts. (CAS); Carrizo (UNAR). *Cochise Co.:* Chiricahua Mts. (Barfoot Park, 8600 ft. elev.; Cave Creek; Pinery Canyon; Portal and vicinity; Southwest Research Station; Sunny Flat; AMNH, ARSU, LACM, UNAR, UCB, UCD, UKAN, UTSU); Huachuca Mts. (Ramsey Canyon; UKAN, UNAR); Mustang Mts. (UKAN); 6 mi. SE of Willcox (AMNH); Douglas (UCB). *Coconino Co.:* 24 mi. W of Cameron (UKAN, UNEB); Fredonia (UTSU); Grand Canyon Natl. Park (LACM, UCD, UNAR); Flagstaff and vicinity (UCB, UNAR, USNM); Oak Creek Canyon (CAS, LACM, UKAN, UNEB, UTSU); Sedona (UKAN, UNAR). *Gila Co.:* Florence (ARSU); 18 mi. SE of Globe (UKAN); 18 mi. S of Payson (UNAR); San Carlos Lake (UNAR). *Greenlee Co.:* 23 mi. N of Clifton (ARSU). *Maricopa Co.:* Granite Reef Dam (ARSU). *Navajo Co.:* Fort Apache (UNAR); Cedar Creek, 15 mi. W of Fort Apache (UNAR); 16 mi. SW of Kayenta (ARSU); Marsh Pass (USNM, UTSU). *Pima Co.:* Baboquivari Mts. (Brown Canyon; Elkhorn Ranch Canyon; AMNH, CAS, LACM, UKAN, UNAR); Redington and Redington Pass (UNAR); Rincon Mts. (Madrona Ranger Station; 1.5 mi. NE of X-9 Ranch; UNAR); Santa Rita Mts. (Gardner Canyon; Madera Canyon; LACM, UKAN, UNAR); Santa Catalina Mts. (Sabino Canyon; UNAR); Silver Bell bajada (LACM); Tucson and vicinity (UCD, UNAR, UNEB, USNM, UTSU). *Pinal Co.:* Oracle (USNM); Superior (B. Thompson Arboretum; UNAR). *Santa Cruz Co.:* Atascosa Mts. (Sycamore Canyon; UNAR); Nogales (USNM); Patagonia (UNAR); Sonoita (LACM). *Yavapai Co.:* Ash Fork (USNM); Hell Canyon (ARSU); Jerome and vicinity (UKAN, UNEB); Mingus Mt. (UTSU); 5 mi. NE of Paulden (ARSU); Prescott and vicinity (LACM, UCB); 24 mi. SE of Wikieup (ARSU). *County unknown:* White River (UNAR; this locality name occurs in three different counties). CALIFORNIA, *Inyo Co.:* Bristlecone Natl. Forest (Schulman Grove; UCD, UTSU); Argus Mts. (LACM); Mountain Spring (UCB); Panamint Mts. (Bennett Peak, 9980 ft. elev.; Frenchman's Canyon, 6800–7200 ft. elev.; GRIS, UCR, UTSU); White Mts. (Wyman Canyon, 8500 ft. elev.; UCB). *Los Angeles Co.:* Eagle Rock (UKAN). *Mono Co.:* Benton (UCD); Cottonwood Creek (9300 ft. elev.; UCB); Mammoth Lake (UCD, UTSU). *Riverside Co.:* Anza and vicinity (CDFA, LACM, UCB, UCD, UTSU); Banning (CAS); Deep Canyon (UCB, UCR); Joshua Tree Natl. Monument (UCR); Mt. San Jacinto (UTSU); 4 mi. S of Palm Desert (UCB); Palm Springs (UCD); Piñon Flat (LACM, UCB, UKAN); Ribbonwood (UCB); Santa Rosa Peak (8000 ft. elev.; CAS). *San Bernardino Co.:* Caruthers Canyon (5650 ft. elev.; GRIS); Cedar Canyon (5100 ft. elev.; GRIS); 9.5 mi. NNE of Cima (4200–4265 ft. elev.; LACM); Cima Dome (5050 ft. elev.; GRIS); Clark Mtn. (6000 ft. elev.; GRIS); Deep Creek Public Camp (LACM); Dove Spring (4600 ft. elev.; GRIS); Falls Public Camp (UCB); Forest Home (CAS, UCR); Granite Mts. (4050 ft. elev., GRIS); Joshua Tree (LACM); Lower Covington Flat (LACM); Mitchell's Caverns (GRIS); s. fork, Santa Ana River (UNEB); Wheaton Springs (UCB). *San Diego Co.:* Anza-Borrego Desert State Park (LACM); 5 mi. W of Borrego Springs (UCD); Jacumba (LACM); 10–11 mi. E of Julian (LACM); Laguna (SDM); Mt. Laguna (UCB); Oak Grove (UCR); San Felipe Wash (LACM, UCR); 2 mi. N of Warner Springs (LACM, UCB, UCD, UTSU). COLORADO, *Alamosa Co.:* Great Sand Dunes Natl. Monument (LACM, UCOL, UKAN). *Archuleta Co.:* Arboles (USNM); Yellow Jacket (UCOL). *Boulder Co.:* Boulder and vicinity (AMNH, UCOL, UKAN); Gregory Canyon (AMNH); Pinecliffe (UKAN). *Chaffee Co.:* Buena Vista (7900–8000 ft. elev.; AMNH). *Costilla Co.:* Fort Garland (UNEB). *Crowley Co.:* Fowler (UCOL). *Delta Co.:* 5 mi. N of Cedaredge (UCOL); Delta (UCOL); Paonia (CAS). *El Paso Co.:* Manitou (UCB, UKAN, USNM); Ute Creek (UNEB). *Fremont Co.:* Cañon City (UKAN); 10 mi. NE of Cotopaxi (5900 ft. elev.; UKAN). *Garfield Co.:* Glenwood Springs (AMNH). *Huerfano Co.:* Cuchara Dam (UCOL); Lathrop State Park (UCOL); 2–3 mi. W of Walsenberg (UCOL, UKAN). *Mesa Co.:* Colorado Natl. Monument (UCOL). *Moffat Co.:* Dinosaur Natl. Monument (Castle Rock; Red Rock Ranch; UCOL). *Montrose Co.:* Naturita (UKAN). *Ouray Co.:* Ridgway (AMNH). KANSAS, *Hamilton Co.:* (UKAN). *Kingman Co.:* Calista (UKAN). *Pratt Co.:* 8 mi. NE of Isabel (UKAN). NEBRASKA, *Arthur Co.:* 4 mi. N of Arthur (UKAN). *Sioux Co.:* Warbonnet Canyon (UNEB). NEVADA, *Clark Co.:* (SDM); Charleston Mts. (Lee Canyon; Willow Creek Camp; AMNH, UCD). *Humboldt Co.:* Winnemucca (UTSU). NEW MEXICO, *Bernalillo Co.:* Cedro Canyon (UKAN); Cienega Canyon (UKAN); Sandia Mts. (UKAN). *Chavez Co.:* Elk (UNAR). *Dona Ana Co.:* Las Cruces (AMNH, BMNH, UCOL, UKAN, UTSU). *Grant Co.:* 13 mi. N of Silver City (6900 ft. elev.; AMNH). *Guadalupe Co.:* Vaughn (UNEB). *Hidalgo Co.:* Post Office Canyon (ARSU). *Lincoln Co.:* Alto (UKAN); Capitan (UNEB); Lincoln (UKAN); Nogal (UKAN, UNEB); Ruidoso and vicinity (AMNH, UKAN). *McKinley Co.:* Pinedale (USNM). *Otero Co.:* High Rolls (AMNH). *Rio Arriba Co.:* Ghost Ranch (UNAR); Echo Canyon (UCR). *Sandoval Co.:* Jemez Spring (AMNH); 10 mi. N of Jemez Spring (7500 ft. elev.; AMNH); San Ysidro (AMNH). *San Juan Co.:* Bloomfield (UTSU). *Santa Fe Co.:* Lamy (USNM); Nambe (UTSU); Santa Fe and vicinity (CAS, UKAN, UNEB). *Torrance Co.:* Durran

(UCB). OKLAHOMA, *Custer Co.:* Weatherford (UKAN). *Cimarron Co.:* Black Mesa (UTSU). SOUTH DAKOTA, *Custer Co.:* Custer (UNEB). UTAH, *Beaver Co.:* Beaver (UTSU); 16 mi. E of Beaver (Keat's Lake, 8800 ft. elev.; AMNH). *Cache Co.:* Logan (UCD). *Duchesne Co.:* Roosevelt (UTSU). *Garfield Co.:* Escalante River (UTSU). *Grand Co.:* Castle Valley (UTSU). *Juab Co.:* Eureka (UTSU). *Kane Co.:* Kanab (UTSU); Navajo Mt. (UTSU). *San Juan Co.:* 5 mi. W of Monticello (Dalton Springs, 850 ft. elev.; AMNH). *Tooele Co.:* (UCD). *Uintah Co.:* Vernal (UTSU). *Utah Co.:* Thistle (UTSU). WYOMING, *Albany Co.:* Laramie and vicinity (UKAN, UTSU). *Sweetwater Co.:* Green River (AMNH). *Weston Co.:* Newcastle (USNM). *MÉXICO.* BAJA CALIFORNIA: Cañon del Tajo (LACM); 3 mi. S of Encinas (UCB) SONORA: San Bernardo (LACM).

Lithurge (*Lithurgopsis*) *echinocacti* (Cockerell)

Figures 9, 10

Lithurgus echinocacti Cockerell, 1898:453. ♀.

RANGE

New Mexico to southern California; northwestern México, south to Nayarit.

BIONOMICS

In Arizona, *L. echinocacti* has been observed nesting in rotted wood (Parker and Potter, 1973). Females collected near Sahuarita, Pima County, Arizona, are noted to have been "boring in post attached to house."

Known pollen sources for females are various species of *Echinocactus*. Other floral records for this bee include *Argemone* sp., *Baccharis* sp., *Baileya pleniradiata, Chilopsis linearis, Ferocactus wislizeni, Heterotheca* sp., *Parkinsonia aculeata,* and *Tamarix pentandra.*

DISCUSSION

This appears to be an uncommon species. Females may be easily recognized by the combination of two conical protuberances on the supraclypeal area, the presence of a pubescent fascia on the dorsal margin of the pronotum, and the usually red legs. Males are similar to those of *L. apicalis* in that both lack labral tubercles, but differ in the narrower supraclypeal area.

TYPE MATERIAL

Lithurgus echinocacti Cockerell: female, present location unknown.

SPECIMENS EXAMINED (38 ♀♀, 97 ♂♂)

UNITED STATES. ARIZONA, *Cochise Co.:* Apache Pass (LACM); 12 mi. E of Benson (Texas Canyon, 4800 ft. elev.; LACM); Portal and vicinity (LACM, UCB, UCR). *Graham Co.:* Dripping Spring, Whitlock Mts. (UNAR). *Pima Co.:* Florida Wash (SDM); Santa Rita Mts. (Box Canyon; Madera Canyon; IBP site; AMNH, LACM, UCD, UNAR, UTSU); Silver Bell bajada (LACM); Mountain View (LACM, UCR); Santa Catalina Mts. (Sabino Canyon; Peppersauce Canyon; AMNH, UCR, UNAR); Continental (UCR, USNM); Baboquivari Mts. (Brown Canyon; Kitts Peak; AMNH, UKAN, UNAR); Sahuarita (UNAR); Tucson and vicinity (AMNH, CAS, UCB, UKAN, UNAR, UTSU). *Pinal Co.:* Oracle and vicinity (CAS, LACM, UCR); Ray (ARSU); Superior (B. Thompson Arboretum; UNAR). *Santa Cruz Co.:* 20 mi. N of Nogales (Tumacacori; UNAR); Peña Blanca (UCD). CALIFORNIA, *Inyo Co.:* 5 mi. E of Valley Wells (UCR). NEW MEXICO, *Hidalgo Co.:* 19 mi. N of Rodeo (UTSU). *MÉXICO.* BAJA CALIFORNIA: 13 mi. SE of Millers Landing (ARSU); 11 mi. E of Rosalillito (UNAR); 13 km. NW of Rosarito (LACM); Valle de Santa Maria (LACM). BAJA CALIFORNIA SUR: 48 km. S of Loreto (LACM); Los Barriles (CDFA). NAYARIT: 43 mi. N of Tepic (UCB). SONORA: Guaymas (UTSU); Río Mayo (UTSU); San Bernardo (LACM).

Lithurge (*Lithurgopsis*) *gibbosa* (F. Smith)

Figures 11, 12, 13

Lithurgus gibbosus F. Smith, 1853:147. ♀.
Lithurgus compressus F. Smith, 1853:147. ♂.

RANGE

North Carolina to Florida, west to Kansas, Oklahoma, and Texas.

BIONOMICS

Notes on the nesting biology of *L. gibbosa* were published by Brach (1979). Females provision cells with pollen from species of *Opuntia.* Mitchell (1962) has recorded this bee from flowers of the genera *Cirsium, Helianthus, Ilex, Pontaderia,* and *Rudbeckia.* I have also seen a few males taken at *Centaurea americana, Ratibida* sp., and *Teucrium* sp. in Texas.

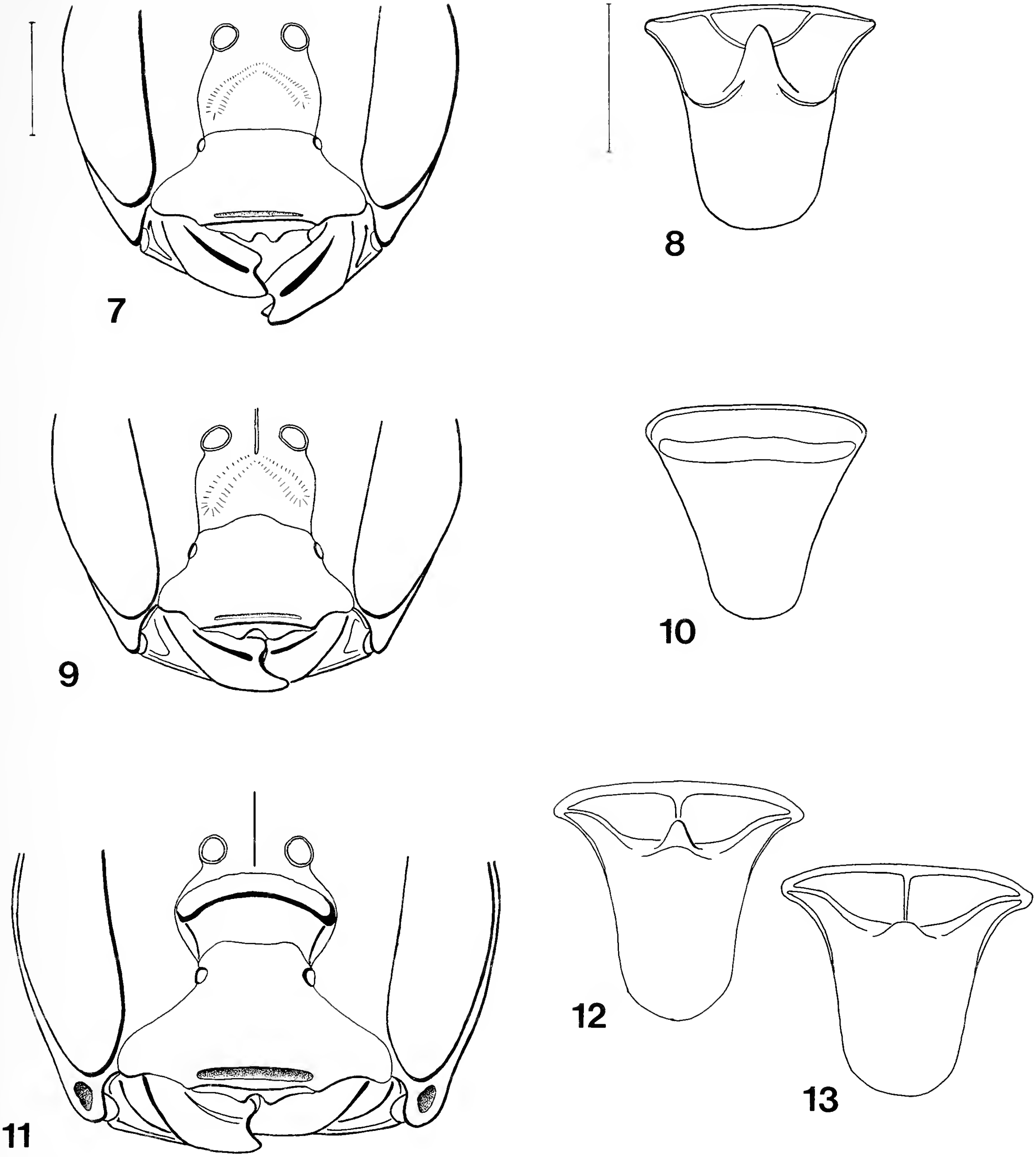
DISCUSSION

The female of *L. gibbosa* is easily recognized by the high, bowed supraclypeal process, similar to that of members of the Palaearctic species allied to *L. cornuta* (Fabricius).

Males are recognizable by the combination of densely punctate supraclypeal area, the presence of a single labral tubercle, and the long ocelloccipital distance. The labral tubercle is a curved, transverse, subapieal ridge; in the center, this ridge is elevated. Males from Florida and Georgia have this median elevation abrupt and quite prominent (Fig. 12). The median elevation in males from Texas is less pronounced (Fig. 13). This difference between specimens from the two areas is consistent but does not correlate with other features.

TYPE MATERIAL

Lithurgus gibbosus F. Smith: females, British Museum (Nat-



Figures 7-13. *Lithurge* spp. **Figs. 7, 9, 11,** lower portion of face of female of *L. socorroensis* (7), *L. echinocacti* (9), and *L. gibbosa* (11). Scale line = 1.0 mm. **Figs. 8, 10, 12, 13,** labrum of male of *L. socorroensis* (8), *L. echinocacti* (10), and *L. gibbosa* from Florida and Texas (12 and 13, respectively). Scale line = 0.5 mm.

ural History). *Lithurgus compressus* F. Smith: male, British Museum (Natural History).

SPECIMENS EXAMINED (123 ♀♀, 98 ♂♂)

UNITED STATES (western records only). KANSAS, *Kingman Co.:* Calista (UKAN). OKLAHOMA, *Caddo Co.:* Red Rock Canyon State Park (UKAN). TEXAS, *Angelina Co.:* 10 mi. N of Lufkin (AMNH). *Bastrop Co.:* Bastrop and vicinity (UKAN, TAMU); McDade (UKAN). *Bexar Co.:* (TAMU, UTSU); San Antonio (USNM). *Brazos Co.:* (TAMU, UCB); College Station (TAMU). *Crockett Co.:* (TAMU). *De Witt Co.:* Cuero (AMNH). *Gillespie Co.:* Fredricksburg (USNM). *Goliad Co.:* (TAMU). *Gonzales Co.:* Palmetto State Park (UCB). *Howard Co.:* Big Spring (USNM). *Jackson Co.:* Edna (UKAN). *Kerr Co.:* Kerrville (USNM). *La Salle Co.:* Cotulla (USNM). *Lee Co.:* Fedor (AMNH, USNM); Giddings (UKAN). *Matagorda Co.:* Matagorda (UKAN). *Maverick Co.:* (AMNH). *Robertson Co.:* (TAMU). *Shackleford Co.:* 3 mi. S of Throckmorton (UKAN). *Torrant Co.:* Fort Worth (TAMU). *Zavalla Co.:* Nueces River (USNM).

Lithurge (*Lithurgopsis*) *listrota*, new species

Figures 1, 2

DIAGNOSIS

Both sexes are separable from all previously described *Lithurgopsis* by the flat supraclypeal area with a shiny impunctate median line that extends onto the clypeus; the male is further distinguished from *L. planifrons,* the only other flat-faced species, by possessing a labral tubercle.

DESCRIPTION

FEMALE. Measurements (mm). Head width 3.2, head length 2.7, wing length 7.5, total length 12.

Head. About 1.2 times broader than long; eyes moderately convergent below, upper interorbital distance about 1.2 times lower; malar space linear, without posterior pit. Transverse basal ridge of labrum low, broadly interrupted in middle. Apical margin of clypeus not thickened. Supraclypeal area flat, about 1.4 times broader than long. Clypeus polished between subcontiguous to dense punctures; supraclypeal area broadly impunctate and polished in middle, elsewhere subcontiguously punctate, interspaces polished. Interocellar distance slightly less than ocelloccipital distance or ocellocular distance. First flagellar segment shorter than pedicel or second flagellar segment; median flagellar segments distinctly broader than long.

Thorax. Anterior half of mesoscutal dorsum sharply scabrous; posterior half of mesoscutum and all of scutellum rugosopunctate.

Color. Blackish brown; legs medium brown; tegula and underside of flagellum ferruginous.

Pilosity. Mostly whitish; reddish hairs along apical margin of clypeus, lower margin of mandible, and inner side of basitarsi; first five gastric terga with distinct fasciae of dense, appressed white hairs; posterior margin of pronotum with fascia of white, plumose hairs; discs of terga two through four with sparse, very short, fuscous hairs; fifth segment with conspicuously longer, denser dark hairs; apical segment densely covered with long, dark brown hairs; scopa whitish; all sterna, except last, with conspicuous apical fascia of dense, appressed, white hairs, last segment with brown hairs.

MALE. Measurements (mm). Head width 2.5 to 3.2, head length 2.0 to 2.6, wing length 5.7 to 7.5, total length 8.3 to 10.5.

Head. Head 1.2 to 1.3 times broader than long; eyes moderately convergent below, upper interorbital distance about 1.2 times lower interorbital distance. Labrum with subbasal, median, erect tubercle and with an obsolete ridge extending from base of tubercle to each basal corner. Supraclypeal area flat, about 1.4 times broader than long. Clypeus weakly shiny between continguous to subcontiguous punctures. Supraclypeal area polished and nearly impunctate in middle, with subcontiguous punctures laterad that are coarser than those of clypeus. Interocellar distance a little greater than either ocelloccipital distance or ocellocular distance. First flagellar segment about as long as pedicel, a little shorter than second flagellar segment.

Thorax. Mesoscutum and scutellum with distinct, contiguous punctures.

Color. As described for female.

Pilosity. Similar to that of female, but hairs at apex of clypeus whitish, dark hairs of discs of gastric terga longer; fasciae of second and third terga interrupted in middle; apical fasciae of sterna longer than in female; apical sternite with pale hairs.

TYPE MATERIAL

All type material is from San Bernardino County, California. Holotype female: Cedar Canyon, 4650 ft. elev. (Sec. 36, T13N, R14E), 18 June 1980 (T. Griswold), on *Eriogonum fasciculatum* ssp. *polifolium.* Allotype: same locality, 13 June 1980 (T. Griswold). Paratypes: 2 ♀♀, 5 ♂♂, same locality, 18 and 30 June 1980 (T. Griswold); 1 ♀, Fenner Valley, 3670 ft. elev. (Sec. 29, T11N, R15E), 17 June 1980 (T. Griswold), on *Chilopsis linearis*; 1 ♂, Colton Hills, 3500 ft. elev. (Sec. 12, T10N, R14E), 17 June 1980 (T. Griswold), on *Ferocactus acanthodes*; 1 ♀, 7 ♂♂, Wild Horse Canyon, 4300 ft. elev. (Sec. 18, T11N, R15E), 6 June 1980 (T. Griswold), on *Opuntia echinocarpa*; 1 ♂, same locality, 27 May 1980 (T. Griswold); 1 ♀, Van Winkle Mts., 10 June 1965 (G. E. Wallace); 11 ♂♂, 9.5 mi. NNE of Cima, 4200–4265 ft. elev. (Morningstar Mine Road), 1–4 June 1977 (R. R. Snelling and C. D. George), on *Encelia californica*; 1 ♂, 10 mi. NE of Earp, 31 March 1959 (A. S. Menke and L. A. Stange). Holotype and allotype in LACM; paratypes in LACM, UCR, and GRIS.

ADDITIONAL SPECIMENS

CALIFORNIA, *Riverside Co.:* 1 ♀, 30 May 1963, on *Opuntia ramosissima*; 2 ♂♂, 3 May 1963, on *Echinocactus* sp.; 1 ♂, 26

April 1963, on *Cereus* sp.; all from Deep Canyon (E. I. Schlinger; UCR).

ETYMOLOGY

From Greek, *listrotos* (leveled), in reference to the flat supraclypeal area of both sexes.

BIONOMICS

Little is known of this species. Floral records within the Cactaceae include the genera *Cereus, Echinocactus, Ferocactus,* and *Opuntia* but are so few that no clear preference can be established. The few females available all bear pollen from Cactaceae. Noncactus floral visits are known for both sexes and are presumed nectar sources.

In the Mojave Desert, from which most specimens were collected, the elevational range is from 3500 to 4650 feet (approximately 1067 to 1417 meters). Many specimens do not bear elevation data, but most, if not all, seem to fall within this range. Most specimens have been collected in June, but the earliest record is 31 March. Within the Mojave Desert, captures range between 27 May and 30 June. Earlier records are all from the margins of the Colorado Desert (Deep Canyon and 10 miles northeast of Earp).

DISCUSSION

Both sexes of *L. listrota* may be readily separated from all known species of *Lithurgopsis* by the flattened supraclypeal area with a shiny, impunctate median line. Since the females of other species all possess some conspicuous modification of the supraclypeal area, the lack of such in the case of the *L. listrota* female is especially obvious.

Males of *L. listrota* differ less conspicuously from those of the other species, since males of none have prominent elevations on the supraclypeal area. But, in these other species, the supraclypeal area is weakly depressed along the midline and weakly elevated toward the subantennal suture on either side. This contour is particularly evident in such species as *L. apicalis.* Only in *L. listrota* and *L. planifrons* is the supraclypeal area completely flat, even though it is slightly elevated above the adjacent areas of the face; males of *L. planifrons* have the median line coarsely and contiguously punctate and lack an erect labral tubercle.

Of the known North American species, only one, *L. apicalis,* is sympatric with *L. listrota.* Males of *L. apicalis* tend to be larger than those of *L. listrota* and possess a relatively strongly elevated supraclypeal area. In addition, the labrum does not bear a median tubercle but has instead a low subbasal ridge.

It is possible that the ranges of *L. listrota* and *L. echinocacti* may overlap in southern California or in Baja California. The male of *L. echinocacti* lacks a median tubercle on the labrum, and the legs are often ferruginous.

Geographically, the nearest species with a labral tubercle is *L. socorroensis* in southern Arizona. In this species, there is a distinct ridge extending laterad from the median tubercle to the margin of the labrum near midlength. In *L. listrota* males, the ridge extends obliquely to the anterolateral corner of the labrum. In addition, the clypeus of *L. socorroensis* males is coarsely punctate, with the punctures discrete, especially in the middle. In contrast, the clypeus of *L. listrota* is finely and contiguously punctate in most areas, with the punctures often distorted.

Lithurge (*Lithurgopsis*) *littoralis* (Cockerell)

Figures 3, 4

Lithurgus apicalis littoralis Cockerell, 1917:191. ♂.

Lithurgus bruesi Mitchell, 1927:104. ♂. NEW SYNONYMY.

RANGE

Illinois to New Mexico, south to the State of Oaxaca, México.

BIONOMICS

Parks (1930) observed the behavior of this bee (as *L. bruesi*) in Texas. He noted that females visited *Opuntia lindheimeri, O. ellisiana,* and *Echinocactus setispinosus* for pollen. Nectar sources for both sexes included *Monarda punctata, M. citriodora,* and *Vitex negundo incisa.* Previously unpublished floral records include *Acacia* sp., *Callirhoe involucrata, Colubrina texensis, Opuntia macrorhiza,* and "composite."

DISCUSSION

The type of *L. littoralis,* from Port Isabel, Texas, is in the British Museum (Natural History) and was made available by G. R. Else. This type has been compared with specimens of *L. bruesi*; there is no doubt that the two are conspecific. Mitchell (1938) first suggested that this might be the case but had not seen the type of *L. littoralis.*

TYPE MATERIAL

Lithurgus apicalis littoralis Cockerell: male, in British Museum (Natural History). *Lithurgus bruesi* Mitchell: male, in Museum of Comparative Zoology.

SPECIMENS EXAMINED (86 ♀♀, 87 ♂♂)

UNITED STATES. ILLINOIS, *Jersey Co.:* Principia College, Elsah (UKAN). KANSAS, *Bourbon Co.:* Fort Scott (UKAN). *Johnson Co.:* Olathe (UKAN). NEW MEXICO, *Lincoln Co.:* Nogal (UKAN). OKLAHOMA, *Cimarron Co.:* 14–18 mi. N of Boise City (UTSU). TEXAS, *Aransas Co.:* 10 mi. N of Rockport (UKAN, UNEB). *Bexar Co.:* (AMNH, LACM, TAMU, UKAN, UTSU); San Antonio (TAMU); Ft. Sam Houston (UCB). *Brewster Co.:* Big Bend Natl. Park (The Basin; Window Trail; AMNH, TAMU, UCB, UKAN); 12 mi. NW of Alpine (UKAN). *Cameron Co.:* 18 mi. N of Harlingen (UKAN); McAllen (AMNH); Port Isabel (BMNH). *Duval Co.:* 8 mi. W of Fremont (TAI). *Goliad Co.:* (TAMU). *Hidalgo Co.:* Edinburg (AMNH). *Howard Co.:* Big Spring (USNM). *Jeff Davis Co.:* Davis Mts. (AMNH, UKAN). *Jim Wells Co.:* (TAMU). *Kenedy Co.:* 3 mi. S of Sarita (TAI).

Kerr Co.: Kerrville (UKAN). *Kleberg Co.:* Kingsville and vicinity (TAI, UKAN); Bishop (UKAN). *La Salle Co.:* Cotulla (USNM). *Maverick Co.:* Quemado (UKAN). *Presidio Co.:* 10 mi. SE of Presidio (TAMU). *San Patricio Co.:* (UKAN). *Sutton Co.:* Sonora (UKAN); 45 mi. S of Sonora (UKAN). *Tom Green Co.:* (UKAN). *Travis Co.:* Austin (TAMU). *Uvalde Co.:* Garner State Park (TAMU); Sabinal (USNM); Uvalde (UKAN, UNEB). *Val Verde Co.:* Del Rio (AMNH); 19 mi. S of Langtry (LACM). *Victoria Co.:* Victoria (USNM). *Webb Co.:* 22 mi. S of Laredo (UKAN). *Zavalla Co.:* Nueces River (USNM). *County unknown:* "Lopeno" (UKAN). *MÉXICO.* COAHUILA: 15 mi. N of Saltillo (AMNH). HIDALGO: Pachuca (UTSU). NUEVO LEÓN: 4 mi. W of El Cercado (UCB, UKAN). OAXACA: Matatlán (UCB). PUEBLA: 10.5 mi. E of Azumbilla (TAMU).

Lithurge (*Lithurgopsis*) *planifrons* (Friese)

Lithurgus planifrons Friese, 1908:62. ♂.

RANGE

Central México.

DISCUSSION

No authentic material of *L. planifrons* has been available for study; the species is based on a unique male, and the original description is broad enough that it can be applied to almost any North American *Lithurge* male. Were it not for the descriptive specific epithet chosen by Friese, this would remain a species of questionable identity.

Three males from Chamela, Jalisco, México, collected by S. H. Bullock, are, I believe, representatives of this species. More important than that they agree with the original description is that the face is flat. The supraclypeal area is not at all elevated above the level of the clypeus and does not, in its upper portion, slope toward the antennal sockets. The only other species with a flat supraclypeal area is *L. listrota*; males of *L. listrota* possess a prominent erect tubercle on the labrum, lacking in *L. planifrons.* In addition, males of *L. listrota* have a conspicuous median impunctate line on the supraclypeal area.

Since the male of *L. planifrons* lacks an erect labral tubercle, it resembles males of both *L. apicalis* and *L. echinocacti.* From both of these species, *L. planifrons* is separable by the flat supraclypeal area, which does not have a median impunctate line. Instead, the supraclypeal area is conspicuously more coarsely punctate in the middle than on either side; these coarse punctures are subcontiguous, and a similar central line of coarse punctures is present on the clypeus. The supraclypeal area of *L. apicalis* and *L. echinocacti* is distinctly convex between the clypeal base and the antennal sockets (often depressed in the center in *L. apicalis*), and the middle is distinctly shiny and impunctate (sometimes the entire supraclypeal area sparsely punctate in *L. apicalis*).

The type locality for *L. planifrons* was originally cited as "Jacubaya, Mexico." This is a misprint for Tacabaya, now a suburb of Mexico City.

Lithurge (*Lithurgopsis*) *socorroensis* (Mitchell)

Figures 7, 8

Lithurgus socorroensis Mitchell, 1938:152–154. ♀ ♂.

RANGE

Southern Arizona to Costa Rica; Revillagigedo Archipelago.

BIONOMICS

Little is known of this species, not previously recorded from the mainland. Both sexes have been taken at flowers of *Opuntia* sp. on Socorro Island, the type locality. Males were taken in Arizona on "thistle." In Costa Rica, both sexes have been collected on *Opuntia* sp. and males were on *Cydista heterophylla, Paullinia costaricensis, Pterocarpus rohrii, Securidaca sylvestris,* and "pink bignon vine."

DISCUSSION

Females of this species are similar to those of *L. echinocacti* in the structure of the supraclypeal area. In *L. socorroensis,* the legs are brown, rather than red, and there is no pubescent fascia on the dorsal margin of the pronotum. The male can be recognized by the structure of the labrum, as noted in the key.

TYPE MATERIAL

Lithurgus socorroensis Mitchell: female holotype and allotype in California Academy of Sciences.

SPECIMENS EXAMINED (18 ♀♀, 24 ♂♂)

UNITED STATES. ARIZONA, *Pima Co.:* Santa Catalina Mts. (UNAR); Rincon Mts. (Madrona Ranger Station; UNAR); Baboquivari Mts. (UCR); Continental (UTSU). *MÉXICO.* JALISCO: Guadalajara (UTSU). MORELOS: Cuernavaca (UKAN). PUEBLA: Petlalcingo and vicinity (UCD, UTSU). ISLAS REVILLAGIGEDO: Socorro Island (CAS, LACM, UTSU). SINALOA: 50 mi. NW of Mazatlán (UTSU). VERA CRUZ: 8 mi. SW of Vera Cruz (UTSU). *EL SALVADOR.* LA LIBERTAD: 5 km. NW of Quezaltepec (Hacienda Capolinas; UCR). *COSTA RICA.* GUANACASTE: Hacienda Comelco (LACM, UCB).

Lithurge (*Lithurge*) *chrysurus* (Fonscolombe)

Lithurgus chrysurus Fonscolombe, 1834:220. ♀ ♂.

RANGE

Countries bordering western Mediterranean Sea; adventive in eastern United States.

BIONOMICS

According to Roberts (1978), females construct communal nests in both soft and hard woods, causing serious damage.

Cells are usually separated by wood-dust partitions and are packed with a pollen and nectar mass gathered from *Centaurea maculosa* (Compositae), an introduced weedy plant. When partitions are absent, two or three regularly spaced larvae feed on the single large pollen mass. When larval feeding is completed, the mature larva defecates and spins a pupal cocoon. Immatures overwinter as prepupae, and pupation occurs during the following spring.

DISCUSSION

Friese (1911) gives a complete synonymy for *L. chrysurus*. Roberts (1978) reported this Palaearctic species from New Jersey, where it had been established for at least three years; nesting biology, behavior, and immature morphology were all described by Roberts. In North America, this bee is presently known only in New Jersey, where it is oligolectic on *Centaurea maculosa*, a plant also native to countries bordering the western Mediterranean Sea.

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I am especially grateful to G. R. Else for his assistance in locating, and making available, the type of *L. apicalis littoralis*.

LITERATURE CITED

Berthold, A.A. 1827. Latreille's natürliche Familien des Theirreiche. Weimar, 610 pp.

Brach, V. 1979. Notes on the biology of *Lithurgus gibbosus* Smith in Florida (Hymenoptera: Megachilidae). Bull. So. Calif. Acad. Sci. 77:144–147.

Cockerell, T.D.A. 1898. New and little-known Hymenoptera taken by Prof. C.H.T. Townsend and Mr. C.M. Barber in New Mexico in 1898. Ann. Mag. Nat. Hist. (7) 2:448–457.

———. 1902. The genus *Lithurgopsis*. Entomol. News 13: 182.

———. 1911. Bees in the collection of the United States National Museum. 2. Proc. U.S. Natl. Mus. 40:241–264.

———. 1917. *In* W.P. Cockerell, Collecting bees in southern Texas. Jour. N.Y. Entomol. Soc. 25:187–193.

———. 1937. Bees collected by Mr. and Mrs. J.L. Sperry and Mr. R.H. Andrews in Arizona. Bull. So. Calif. Acad. Sci. 36:107–110.

Cresson, E.T. 1875. Report upon the collections of Hymenoptera, *In* Wheeler, Rept. Geogr. Geol. Explor. Surv. West of 100th Meridian, vol. 5, pp. 707–728.

Ducke, A. 1907. Contribution à la connaissance de la faune hyménoptérologique du nord-est du Brésil. Rev. Entomol. 26:73–96.

Fonscolombe, B. 1834. Notices sur les genres d'Hymenoptères *Lithurgus* et *Philoxera*. Ann. Soc. Entomol. France 3:219–224.

Fox, W.J. 1902. *Lithurgopsis*, a new genus of bees. Entomol. News 13:137–140.

Friese, H. 1908. Die Apidae (Blumenwespen) von Argentina nach den Reisenergebnissen der Herren A.C. Jensen-Haarup und P. Jörgensen in den Jahren 1904–1907. Deutsch. Entomol. Zeits. 1908:1–94.

———. 1911. Apidae I. Megachilinae. Das Tierreich 28: 1–440.

Hurd, P.D., Jr. 1979. *In* K.V. Krombein et al., Catalog of Hymenoptera of America north of Mexico. Washington, D.C. 2:1199–2209.

Latreille, P.A. 1825. Familles naturelles du règne animal. Paris, 570 pp.

Michener, C.D. 1944. Comparative external morphology, phylogeny and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist. 82:151–326.

———. 1965. A classification of the bees of the Australian and South Pacific regions. Bull. Amer. Mus. Nat. Hist. 130:1–362.

Mitchell, T.B. 1927. New megachilid bees. Psyche 34:104–121.

———. 1938. The genus *Lithurgus* (Hymenoptera: Megachilidae). Psyche 45:146–155.

———. 1962. Bees of the eastern United States. N. Car. Agric. Exp. Sta. Tech. Bull. 152:1–557.

Moure, J.S. 1949. Las especies Chilenas de la sub-familia Lithurginae (Hym.-Apoidea). Arq. Mus. Paranaense 7: 265–286.

Parker, F.D., and H.W. Potter. 1973. Biological notes on *Lithurgus apicalis* Cresson (Hymenoptera: Megachilidae). Pan-Pacific Entomol. 49:294–299.

Parks, H.B. 1930. Notes on Texas bees. Bull. Brookl. Entomol. Soc. 25:263–264.

Roberts, R.B. 1978. The nesting biology, behavior and immature stages of *Lithurge chrysurus*, an adventitious wood-boring bee in New Jersey (Hymenoptera: Megagachilidae). Jour. Kans. Entomol. Soc. 51:735–745.

Rozen, J.G., Jr. 1973. Immature stages of lithurgine bees with descriptions of the Megachilidae and Fideliidae based on mature larvae (Hymenoptera, Apoidea). Amer. Mus. Novitates 2527, 14 pp.

Smith, F. 1853. Catalogue of hymenopterous insects in the collection of the British Museum. Part 1, 197 pp. British Museum, London.

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Each manuscript component should begin on a new page, in the following sequence: title page; abstract(s); text; acknowledgments; literature cited; tables, each table—complete with title and footnotes—on a separate page; and figure captions. All pages should be numbered consecutively.

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CONTRIBUTIONS IN SCIENCE

THE TERTIARY SPONGES *APHROCALLISTES* AND *EURETE* FROM WESTERN WASHINGTON AND OREGON

J. Keith Rigby and
David E. Jenkins

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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THE TERTIARY SPONGES *APHROCALLISTES* AND *EURETE* FROM WESTERN WASHINGTON AND OREGON

J. Keith Rigby[1] **and David E. Jenkins**[2]

ABSTRACT. Extensive collections of sponges from the Eocene to Miocene of southwestern Washington and from the Oligocene and Miocene of northwestern Oregon consist mainly of *Aphrocallistes polytretos* n. sp. This new sponge has irregular undulating to tubular walls that look like tiny-celled honeycombs because of their coarse canals. The upper cellular part of the skeleton is made of flattened hexiradiates, but the basal part is irregularly dictyonine.

The less common *Eurete goederti* n. sp., a branching zigzag tubular sponge, occurs in the Oligocene part of the Lincoln Creek Formation in southwestern Washington. Root tufts of large monaxial spicules occur in concretions with both *Eurete* and *Aphrocallistes* but may not be part of either of these sponges.

Distributions of living species of both genera suggest by analogy that the fossils lived at a depth of 300–350 meters. Most occur in coarse clastic units or in calcareous concretions with a mixed diverse fish-echinoid-sponge assemblage. This fauna may have been swept into still deeper water by pulses of high-energy currents, for most sponges and echinoids appear fragmented. Only the root tufts appear to have grown in place.

INTRODUCTION

Numerous fossil sponges have been recovered from concretions eroded out of relatively deep-water marine Eocene to Oligocene sediments near Knappton (Localities 2, 5–7, Figure 1), from Eocene limestone in a quarry near Chinook (Locality 1, Figure 1) in southwestern Washington, from Miocene concretionary beds at Astoria, and from Oligocene deposits near Yaquina (Locality 4, Figure 1) in northwestern Oregon. Near Knappton, the major locality, the sponges are apparently scattered through the formation but are most common in a zone where sponge-bearing concretions are particularly abundant. The major sponge fauna occurs presumably below beds that have produced the mollusks being studied by Ellen James Moore, of the U.S. Geological Survey, and above beds that have produced the silicified micromollusks (bivalves and gastropods) being studied by Carole Hickman, of the University of California Museum of Paleontology. Fossil barnacles have been described by Victor Zullo (1982) from localities both above and below the major sponge zone.

The fossils come, in large part, from concretions weathering out of a Holocene landslide block in the Lincoln Creek Formation and occur as float along the Columbia River terrace. The slump block is in the sea cliff at the head of the bay between Knappton and Grays Point. If, as Moore (personal communication, December, 1981) suggests, "there is a certain amount of stratigraphy preserved in the float from the landslide block," the sponges then are stratigraphically just below the main mollusk-bearing beds. "Because the landslide moved generally parallel with the strike of the beds, a proper stratigraphic sequence seems to have been maintained," according to Moore (personal communication, August, 1982).

The designation Lincoln Formation was initially proposed by Weaver (1912:10–12) for Oligocene beds of western Washington. Weaver (1937) later suggested retaining the name Lincoln Formation for the entire middle Oligocene of Washington. Weaver and others (1944:592) noted the Lincoln beds overlie the Keasey Formation and unconformably underlie the Miocene Astoria Formation. The Lincoln Creek Formation in the Knappton area occurs in an east-dipping homocline, west of outcrops of the Astoria Formation, in the Portuguese Point–Grays Point area west of Frankfurt, Washington (Wells, 1979).

The name Lincoln Creek Formation was proposed by Beikman and others (1967) to replace the Lincoln Formation, which has been preempted several times. In the type area, the formation consists of 700–3000 m (2000–9000 feet) of clastic rocks of predominantly Oligocene age. Lincoln Creek beds unconformably overlap Eocene and older units near Oligocene paleotopographic high areas but rest conformably on Eocene beds within the basins. The Lincoln Creek Formation is overlain by the Astoria (?) Formation in the type region. Molluscan and foraminiferal correlations suggest that the Lincoln Creek Formation ranges from the Late Eocene

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[1] Brigham Young University, Provo, Utah 84602.

[2] Union Oil Company of California, 2323 Knoll Drive, Ventura, California 93003.

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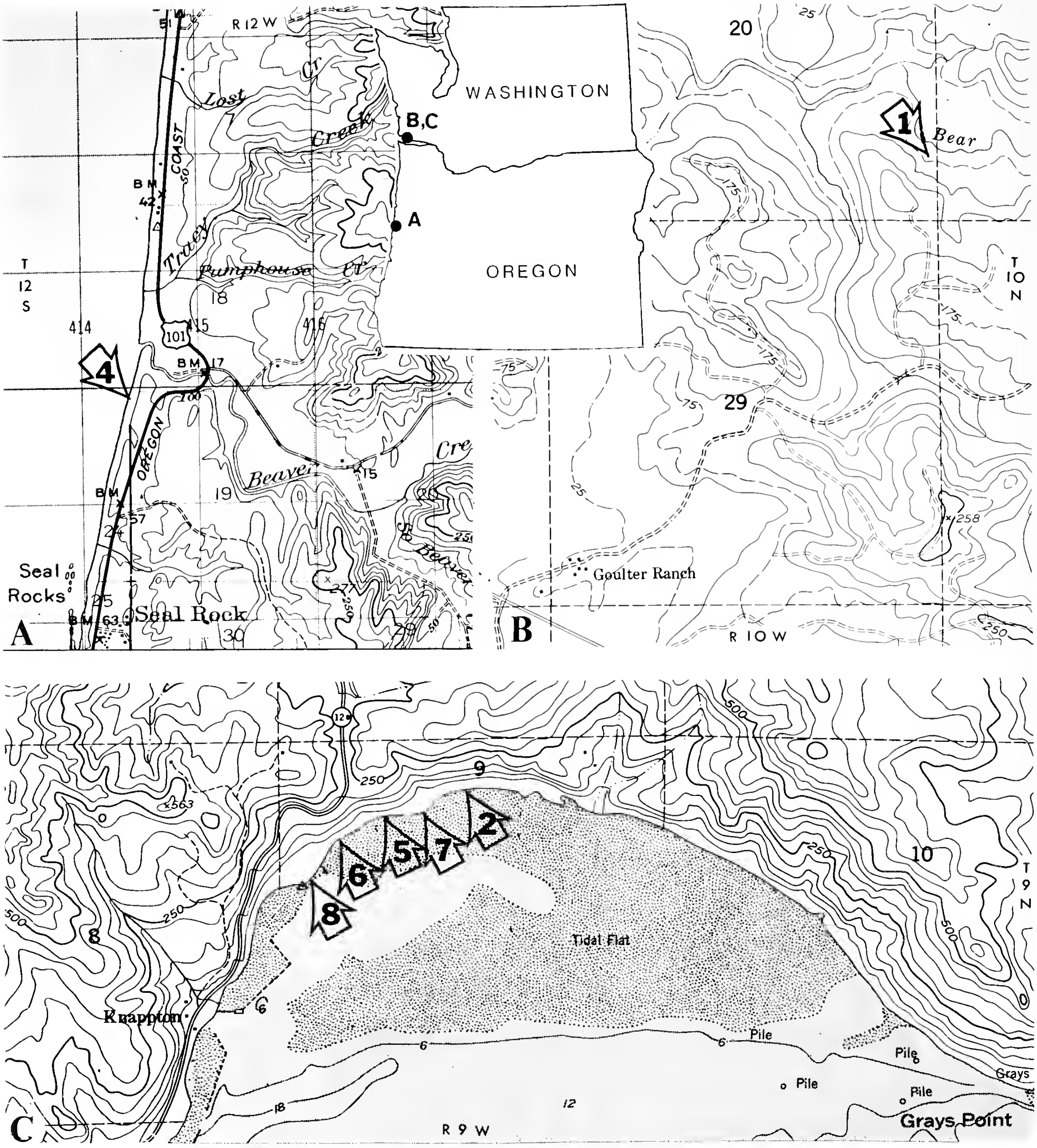

Figure 1. Index maps to sponge localities in southwestern Washington and northwestern Oregon. Arrows indicate collecting localities. A, Ona Beach locality (4, LACMIP 6148) south of Newport and north of Seal Rocks on the coast, Yaquina 15-minute quadrangle, Lincoln County, Oregon. B, Bear River locality where calcified sponges and mollusks occur in "reefoidal" limestone (1, LACMIP 5802), Chinook 7½-minute quadrangle, Pacific County, Washington. C, Knappton localities in the Lincoln Creek Formation where it is exposed in the sea cliff, (8, LACMIP 5787, Oligocene; 2, LACMIP 5842, Upper Oligocene; 5, LACMIP 5843, Lower Oligocene; 6, LACMIP 5844, Eocene; 7, LACMIP 5852, Oligocene) on the north shore of the mouth of the Columbia River, Knappton 7½-minute quadrangle, Pacific County, Washington.

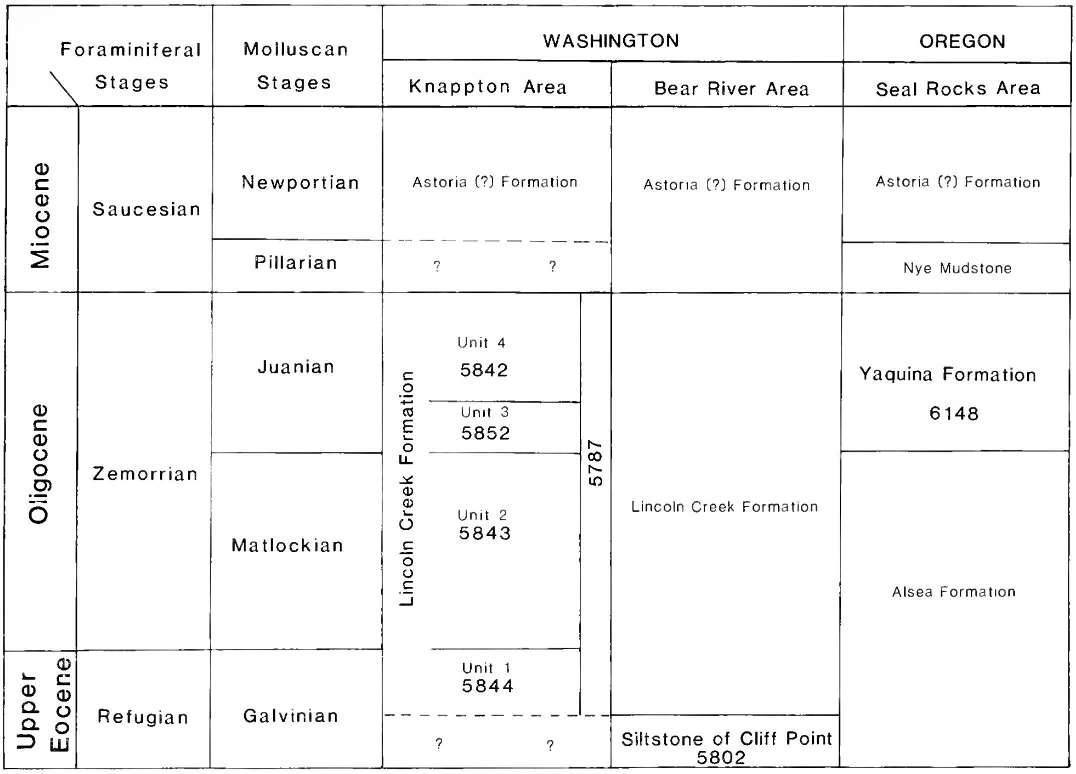

Figure 2. Stratigraphic distribution of localities in the Knappton, Bear River, and Yaquina (Seal Rocks) areas showing relationships of the informal units of James and Gail Goedert, Natural History Museum of Los Angeles County localities, and biostratigraphic zones of the Tertiary section (modified from Zullo, 1982; Wells, 1979; Snavely and others, 1975; Armentrout, 1981; Rau, 1981).

to latest Oligocene (Rau, 1958, 1964, 1981; Armentrout, 1975, 1977, 1981).

James L. Goedert (Zullo, 1982:2–3) has subdivided the Lincoln Creek beds in the Knappton outcrops into four informal units (Figure 2). Unit 1 is a barnacle-bearing concretionary unit associated with the abundant U-shaped trace fossil, *Tisoa*. Unit 2 is characterized by sponges, small aturiid nautiloids, many decapod crustaceans, and marine vertebrate remains associated with tisoid burrows. Unit 3 is characterized by a glass sponge fauna and Unit 4 by an abundance of marine vertebrate and invertebrate fossils, but few sponges. Zullo (1982:2–3, fig. 2) concluded that lower Unit 1 is Upper Eocene, Unit 2 is Lower Oligocene, and Units 3 and 4 are Upper Oligocene (Figure 2).

The sponges noted here from Oregon are reportedly from the Astoria Formation at the type locality in Astoria and from the Yaquina Formation near Seal Rocks. Moore (1963) described outcrops and faunas of Astoria beds in the type area and southward along the Oregon coast for approximately 70 miles. One specimen of *Aphrocallistes* has been figured from the type area of the Astoria Formation by Moore (1963, pl. 32, fig. 16), but the precise locality from which the early collection was made is uncertain. No additional sponges have been reported from other exposures along the sea cliff between Astoria and Newport. However, a few sponges have been recovered from the Yaquina Formation south of Newport, in the Seal Rocks area (Figure 1).

Moore (1963:12) described Astoria beds in the coastal area as mainly marine silty shale and fine-grained sandstone, with interbedded siltstone, coarse-grained sandstone, conglomerate, and tuff. She reported that concretions up to a foot and a half in diameter are common in some places. Such concretions have produced nearly all the sponges from the Astoria, Yaquina, and Lincoln Creek localities. Some concretions contain a varied molluscan fauna, fragments of carbonized wood, many with teredinid borings, marine mammal bones, fish bones and scales, a varied foraminiferal fauna, decapod crustaceans, and barnacle fragments. Many concretions are coarse-grained glauconitic sandstone that shows evidence of vigorous transport. These assemblages may have been mixed, that is may have been derived from a variety of depositional sites, by downslope movement.

The sponges, in general, are delicate and silicified and can be freed from the calcareous matrix. Some concretions were partially etched in dilute acetic acid and screened for recovery of all microorganisms. In general, the concretions are highly argillaceous, often sandy and glauconitic. For complete removal of matrix, the partially etched calcareous muds were gently brushed and washed from the sponge material. Some fine cleaning of specimens was done with a microsandblaster air-abrasive unit. Some delicate etched specimens were hardened in weak acetone-soluble plastic solutions.

LOCALITIES

The fossil sponges described here were all collected by James L. and Gail H. Goedert, except for the sponge reported by Ellen J. Moore (1963:89, pl. 32, fig. 16), and are deposited in the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (abbreviated LACMIP).

LOCALITY 1. Limestone in the siltstone of Cliff Point of Wells (1979) in a quarry in the bluff on the south side of Bear River, 2.2 km (1.4 miles) northeast of Goulter Ranch, on the section line between Sections 20 and 21, T. 10 N., R. 10 W., on the Chinook 7½-minute quadrangle, Pacific County, Washington. LACMIP locality 5802, Upper Eocene.

LOCALITY 2. Lincoln Creek Formation in association with other invertebrate fossils, mammal and fish bones, and plant fragments in calcareous, argillaceous concretions that range from fine-grained to coarsely clastic, from a landslide area at the head of the bay between Knappton and Grays Point in the center N ½ N ½ of Sec. 9, T. 9 N., R. 9 W., on the Knappton 7½-minute quadrangle in Pacific County, Washington. The locality is approximately 1.6 km (1 mile) northeast of Knappton. LACMIP Locality 5842, Upper Oligocene.

LOCALITY 3. Astoria Formation at Astoria, as cited by Moore (1963:90) at her locality 1a, from collections of James D. Dana discussed by Dall (1909:140), Miocene.

LOCALITY 4. Sponges from the Yaquina Formation, in fossiliferous concretions from rocks exposed at Ona Beach, 0.4 km (0.25 mile) south of the mouth of Beaver Creek, west of U.S. Highway 101, 2 km (1.3 miles) north of the community of Seal Rocks, just west of the northwest corner of Sec. 19, T. 12 S., R. 11 W., Lincoln County, Oregon, Yaquina 15-minute quadrangle. LACMIP Locality 6148, Miocene.

LOCALITY 5. Lower Oligocene part of the Lincoln Creek Formation, from concretions weathering out of the sea cliff in the northwestern part of the bay between Grays Point and Knappton, approximately 305 m (1000 feet) south and 430 m (1400 feet) east of the northwest corner of Sec. 9, T. 9 N., R. 9 W., on the Knappton 7½-minute quadrangle, in Pacific County, Washington. The locality is approximately 300 m (1000 feet) west of Locality 2, and 300 m (1000 feet) northeast of Locality 7. LACMIP Locality 5843, Lower Oligocene.

LOCALITY 6. Upper Eocene part of the Lincoln Creek Formation, concretions weathering out of the sea cliff in the western part of the bay between Grays Point and Knappton, approximately 0.8 km (0.5 mile) northeast of Knappton; 122 m (400 feet) east and 520 m (1700 feet) south of the northwest corner of Sec. 9, T. 9 N., R. 9 W., on the Knappton 7½-minute quadrangle, Pacific County, Washington. LACMIP Locality 5844, Upper Eocene.

LOCALITY 7. Oligocene part of the Lincoln Creek Formation, collected from the "sponge zone" in concretions weathering out of the sea cliff, approximately 1.3 km (0.8 mile) northeast of Knappton, 305 m (1000 feet) south and 580 m (1900 feet) east of the northwest corner of Sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, Pacific County, Washington. This is the most productive sponge locality of those cited here. LACMIP Locality 5852, Oligocene.

LOCALITY 8. Lincoln Creek Formation on the Columbia River, approximately 122 m (400 feet) east of the boundary between Sections 8 and 9, T. 9 N., R. 9 W., approximately 0.8 km (0.5 mile) northeast of Knappton, Knappton 7½-minute quadrangle, Pacific County, Washington. A general Knappton locality of older collections before units were established. LACMIP Locality 5787, Oligocene.

SYSTEMATICS

Class Hexactinellida Schmidt, 1870

Order Hexactinosa Schrammen, 1903

Suborder Scopularia F. E. Schulze, 1885

Family Aphrocallistidae Gray, 1867

Genus *Aphrocallistes* Gray, 1858

Aphrocallistes polytretos **n. sp.**

Figures 3–10, 13–17, 21

DIAGNOSIS. Branching tubular to cuplike or irregular undulating leaf- or ear-shaped sponges with upper walls perforated by honeycomblike, subprismatic to polygonal primary canals in full diarhysis and open on both sides of the wall. Basal attachment and lower part of walls irregularly dictyonine with fewer canals. Each canal of upper wall outlined by a complex net of siliceous skeletal strands produced by hexiradiate beams whose rays have been distorted to be more or less in the plane of the porous canal walls. No sculp-

Figures 3 through 10. *Aphrocallistes polytretos* n. sp. **(3)** Basal view of two specimens showing dense irregular attachment areas grading up into distal radially canalled area. Paratype, LACMIP 6601, Locality 2, ×1. **(4)** Natural vertical section through an irregularly dictyonine base and associated lower canalled area. Definition of canals increases away from base, along with increase in modification of spicule structure toward hexiradiates. Paratype, LACMIP 6602, Locality 8, ×2. **(5)** Side view of well-preserved paratype with honeycomblike wall and tubular to cuplike form but with broken upper end. Base of this same specimen is shown in upper right of Figure 3. LACMIP 6601, Locality 2, ×2. **(6)** Fragments of sponge showing coarse conglomeratic and glauconitic nature of common matrix. LACMIP 6603, Locality 7, ×1. **(7)** Side view of broad flattened, moderately fine-textured paratype. LACMIP 6604, Locality 7, ×1. **(8)** Side view of holotype showing annular tubular form and honeycombed walls. Reverse side has concave-up, dictyonine-spiculed diaphragmlike interruptions that probably marked pulses in growth. LACMIP 6600, Locality 2, ×1. **(9, 10)** Stereoscopic photomicrographs of skeletal net of the holotype showing canal patterns, shape, and hexiradiate skeleton typical of the middle and distal part of the sponge. LACMIP 6600, Locality 2, ×5.


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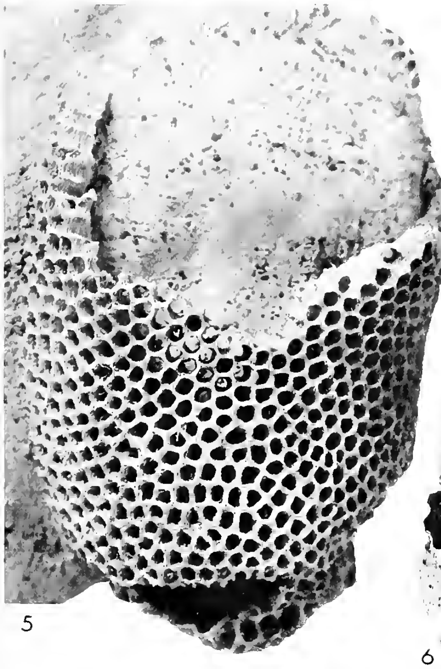
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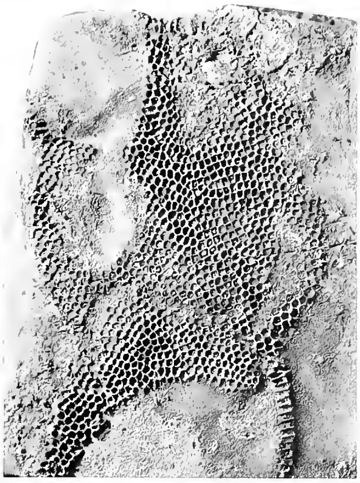
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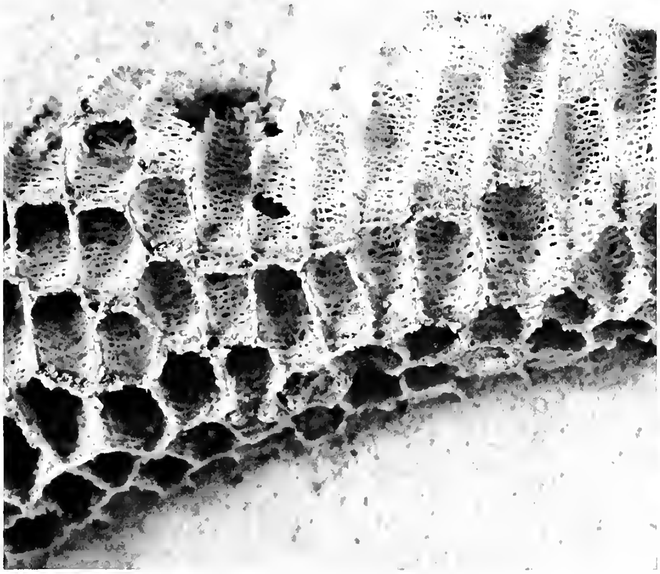
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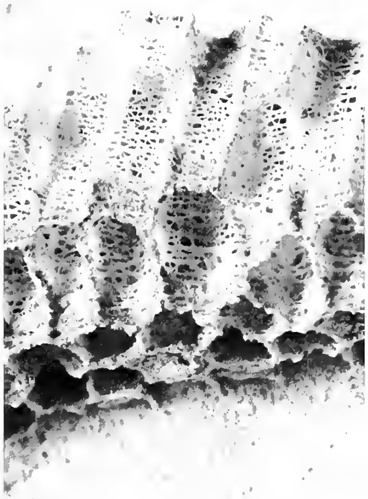
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ture is evident, except for the undulating surfaces. Polygonal canals are generally 1.0–1.5 mm across in a wall 2–5 mm thick. Upper part of skeleton of irregular flattened hexiradiate dictyonal beams with largest, earliest formed beams essentially horizontal but connected with irregularly diagonal and vertical strands in a cross-bracing crudely hexiradiate pattern, like an expanded metal screen, with roughly hexagonal openings often subdivided into triangular sections. All beams fused into a solid network; each is minutely spinose.

Canals much larger and less oblique, and skeleton in mature parts much more hexiradiate-dominated and much less clearly dictyonine, than in *Aphrocallistes vastus whiteavesianus* Lambe and *A. vastus vastus* Schulze. Canals much larger but more closely spaced and more commonly prismatic than in *A. alveolites* Roemer and *A. cylindrodactylus* Schrammen.

DESCRIPTION. Numerous nearly complete siliceous fragments to broken bits of the sponge occur, often as several pieces with different growth forms in single concretions. The holotype is a subtubular undulating sponge with a diameter of 30–35 mm. It is approximately 80 mm tall and is subdivided into three subequal sections with saucer-shaped, noncanalled partitions with a texture like that of bases on other specimens.

The wall expands upward from a thickness of 2.0–2.5 mm in the lower part of the fragment, to 2.5–3.5 mm in the middle segment, and to a maximum of 4.0–4.5 mm at the upper end of the fragment. The arcuate saucer-shaped noncellular partitions are generally 0.5–1.0 mm thick in the center of the tubular opening. The lower segment is approximately 15 mm high, the middle segment is 20 mm high, and the uppermost is 20 mm high, above the uppermost cellular separation. Other fragments show the same range in wall thickness, although most are only undulating irregular platelike bits or tube sections. Some nearly complete cup-shaped sponges show the massive base, a few millimeters across, and a tubular form 8–30 mm in diameter and up to 90 mm long or high.

Individual canals pierce the walls, essentially normally, in full diarhysis. They are 1.0–1.8 mm across on the outside but are only 0.8–1.5 mm across on the inside, showing expansion of the canals related to their radial orientation. They are closely packed, although not in predictable horizontal or vertical series, and are so spaced that 7–8 occur in 10 mm, both horizontally and vertically on the exterior. Many of the canals have rectangular cross sections, but with rounded margins. Hexagonal and pentagonal openings also occur, commonly in the middle unmodified parts of the segments. All canals have porous walls so that there could have been complete interconnection with adjacent ones. Canal walls are perforated at irregular intervals with distinct rounded openings 0.10–0.22 mm across. These are less common than the much smaller and more irregularly sized triangular openings that occur between the diagonal and vertical beams in the hexiradiate-based skeletal net.

The skeleton is composed of fused solid beams that are difficult to separate into single spicular elements. Walls are principally outlined by horizontal fibers that tend to bifurcate horizontally at the wall intersections and vertically in the middle part of the wall. These are the first beams secreted at any level in the skeleton and are the most massive units. They are spaced 5–7 horizontal beams per mm, measured vertically along the canal wall. Most of these strands are 0.06–0.08 mm across, but in some areas where the skeletal net is dense, they have been thickened to 0.10–0.12 mm in diameter. These dominantly horizontal units are crossbraced by diagonal and vertical units in the basic flattened hexiradiate skeleton. Diagonal beams are next to horizontal ones in size and are generally 0.03–0.06 mm across. Vertical beams are apparently the last added and are the smallest, ranging from tiny hairlike spines 0.01 mm across up to rods 0.04–0.05 mm in diameter, fused at both ends. Diagonal beams are less continuous than horizontal ones, and vertical ones are the least continuous. However, vertical beams can be traced completely along the canal wall, in some areas, parallel to the trend of the canals.

Most skeletal elements are shared between two adjacent canals in the thin wall. Elsewhere, particularly in proximal parts of the sponge, double walls occur, with each canal having its own subparallel fused series of elements. These strands bifurcate to produce triangular or polygonal radial openings along the common juncture between three or four adjacent canals.

Beams are apparently solid and appear to have been built by enlargement, with layered secretions over initial small needles or spines. These needles are common in young parts of the skeleton, pointing upward and horizontally from adjacent thicker strands. Some beams are so enlarged that they combine to produce a nearly solid fused wall in the older parts of the net. Exchange between canals is moderately limited in these areas, but in the outer, more open-textured parts,

Figures 11 through 17. Root tufts and *Aphrocallistes polytretos* n. sp. **Figures 11, 12.** Root tufts. **(11)** Large concretion with aligned oxeate root tuft spicules in fine-grained calcareous siltstone, which has undergone some bioturbation (lower right). LACMIP 6611, Locality 7, ×1. **(12)** Large monaxial root tuft spicules in fine-grained siltstone showing packing, shape, and general preservation that indicate they have not been moved after formation of the tuft. LACMIP 6612, Locality 5, ×2. **Figures 13 through 17.** *Aphrocallistes polytretos* n. sp. **(13)** Photomicrograph showing irregular spicules of basal attachment and dense, noncanalled pattern, in left center of Figure 17. LACMIP 6605, Locality 5, ×10. **(14)** Part of a concretion containing *Aphrocallistes* with irregular branching growth form in variously colored fine-grained matrix, which produces blotchy appearance. Paratype, LACMIP 6606, Locality 2, ×1. **(15)** Photomicrograph of lower part of sponge showing thick canal walls and change from dictyonine-based skeleton in lower right to hexiradiate skeleton in upper left. Side of same specimen in Figure 4. Paratype, LACMIP 6602, Locality 8, ×10. **(16)** Photomicrograph of dictyonine part of basal skeleton of paratype illustrated in Figure 4, in left center, but rotated 90 degrees. Somewhat swollen spicule nodes and irregular fabric are characteristic. LACMIP 6602, Locality 2, ×10. **(17)** Irregular basal region and part of honeycomblike tubular wall of paratype. Base shown enlarged in Figure 13. LACMIP 6605, Locality 2, ×2.


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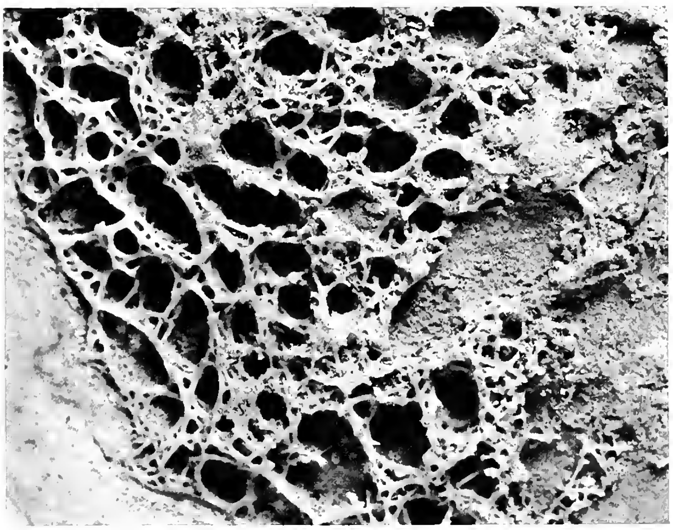
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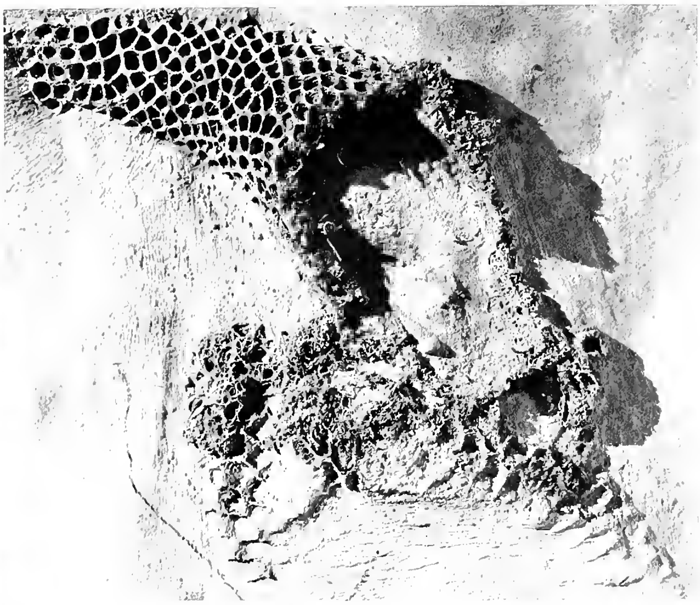
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interchange could have been effected, even through double walls where two skeletal layers separate adjacent canals.

The entire surface of each spicular strand, particularly the thickened ones, is covered by minute conical spines 0.005–0.01 mm high and across. Some tiny elements extend as fine needles from small conical bases. These cones and spines are generally 0.01–0.02 mm apart and appear to be scattered irregularly over the entire surface of the major strands.

DISCUSSION. Generic and family placement of these sponges is based on their peculiar flattened hexactine hexiradiate skeleton. The sponges superficially appear like lithistids, composed of orchoclad dendroclones. The "clads" are fused to "clads" of other spicules to produce a flattened roughly hexagonal series of openings with one spicule axis essentially normal to the long dimensions or axes of the canals, but individual lithistid spicules cannot be identified.

The large canals might be considered as peculiar porous calicles, such as in the sclerosponge *Merlia* or the chaetetids. However, in sclerosponges, the calicles rise from an impervious base rather than forming perforate walls around a subcylindrical or platelike porous sponge.

Schrammen (1912:358), in a summary table of stratigraphic ranges of Cretaceous fossils of northwestern Germany, noted that *Aphrocallistes* ranges from the Late Cretaceous into Recent. He also listed the genus from Tertiary rocks of Russia, Japan, and Oran, but cited no references for those occurrences. Schrammen (1912:219–222) differentiated three species of the genus on general body shape, wall thickness, presence or absence of terminal sieve plates, or whether the forms are many branched or relatively simple structures. In general, the German species have canals considerably more widely separated and distinctly smaller than our specimens.

Schrammen (1912:185) summarized the observed depth ranges of living species of *Aphrocallistes*. In general, their range is from approximately 100–1700 m. Reid (1968:549) cited occurrences of *A. vastus* as shallow as 27.5 m from Puget Sound. He also listed other occurrences off Oregon and Washington in water 97 and 108 m deep. Living species described by Schulze (1887) occur essentially in the North Pacific, from localities in the Philippine Islands, Japan, the Aleutian Islands, and along the coast of Oregon and Washington, California, and Vancouver Island. Thus, it is not surprising to find *Aphrocallistes* in Eocene to Miocene beds in Oregon and Washington.

Aphrocallistes was collected from Astoria beds at Astoria, Oregon, on the south bank of the Columbia River (Dana, 1849). That specimen was noted by Dall (1909:140) and figured by Moore (1963, pl. 32, fig. 16) as an unidentified ophiuroid (?) as an incidental occurrence to her extensive treatment of the Miocene mollusks from the Astoria Formation of Oregon.

Canal patterns in living *Aphrocallistes vastus whiteavesianus* Lambe, illustrated by Reid (1964, text-fig. 47), and *Aphrocallistes vastus vastus* Schulze show markedly oblique canals and clearly defined dietyonine-based skeletons in a moderately rectangular arrangement. Development of hexiradiate patterns is more clearly shown in *Aphrocallistes beatrix* Gray, as figured by Reid (1964, text-fig. 49b). Even in that species, however, there is a moderately oblique orientation to some canals in the gastral region, and wall thicknesses tend to be somewhat greater than in the Tertiary species from Washington and Oregon. Canal dimensions in each of these are considerably smaller than in the fossil *A. polytretos*. There is striking similarity of skeletal arrangements in *A. beatrix* to that of the Tertiary fossils. The walls are somewhat thicker in the Recent species, and the canals tend to be more circular than distinctly prismatic, such as in the fossil forms. Such rounded canals are the general pattern, as well, in the Cretaceous sponges described by Schrammen (1912:219–222). *A. polytretos* is similar to *Aphrocallistes beatrix* in having the dictyonal strands obscure, in contrast to *Aphrocallistes vastus* varieties.

Aphrocallistes beatrix Gray (1858:114–115) was described from the Azores in the Atlantic Ocean. Some of the limited modern distribution is unquestionably related to sampling difficulty and spacing of samples in the 100–1000 m range in the modern oceans.

Associated benthonic foraminifers and mollusks, including the nautiloid *Aturia*, suggest water depths between 300 and 600 m, which is also within the range of modern *Aphrocallistes*. The assemblage may have been transported from moderately shallow waters of 300–400 m and accumulated ultimately in depths as great as 2000–4000 m.

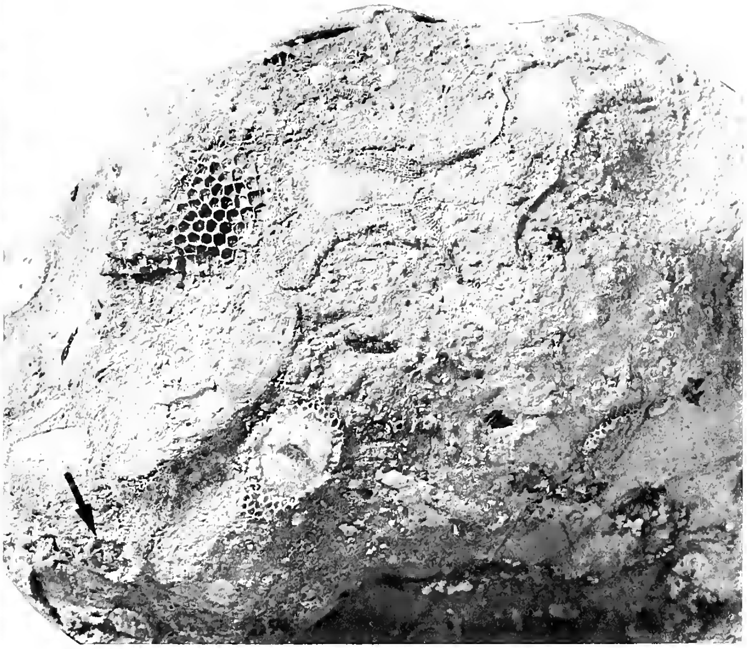
Specific characteristics are the size of individual canals and skeletal elements and the general growth form of the sponges.

Our species is fairly variable and ranges at least from Late Eocene to Miocene. These Tertiary sponges show a general increase in canal size, a decrease in canal wall thickness, and a tendency for a more prismatic canal pattern, when compared to the Cretaceous species from northwestern Germany.

Schrammen (1912:220) noted a terminal or oscular sieve-like diaphragm on branches of *A. alveolites* Roemer and *A.*

Figures 18 through 22. *Eurete goederti* n. sp. and *Aphrocallistes polytretos* n. sp. **Figures 18 through 20 and 22.** Holotype of *Eurete goederti* n. sp. LACMIP 6609, Locality 7. **(18)** Photomicrograph of gastral part of dictyonine skeletal net showing marked regularity of enlarged strands and somewhat smaller cross-connecting beams. Spicule nodes are little swollen. Figure 23 is a drawing of part of the net in the upper left. ×5. **(19)** Holotype of *Eurete goederti* and associated fragments of *Aphrocallistes* in bioclastic matrix of a concretion from Locality 7. The regularly spaced zigzag pattern of the branching sponge is clearly shown. Proximal is to upper right and distal to lower left, where circular cross section shows near shadowed boundary (arrow). ×1. **(20)** Photomicrograph of thin walls of the holotype, with diverging walls that are 3 or 4 spicule complexes thick. Gastral surface is to the right. ×5. **(22)** Well-preserved part of the skeleton showing thickness of the walls in lower part and regular nature of skeleton in middle and upper part. Parts of three dichotomous branches, producing zigzag structure of the sponge, are shown. ×3. **Figure 21.** *Aphrocallistes polytretos* n. sp., paratype illustrated in Figure 17, here enlarged to show smaller hexactine-based spicules partially filling canals. LACMIP 6605, Locality 2, ×15.

18



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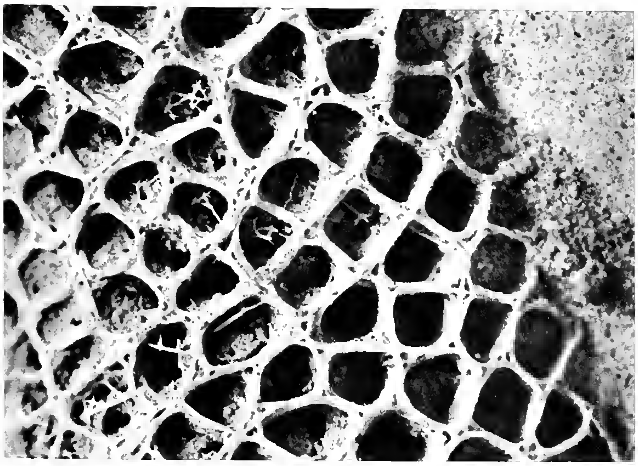

21

22

cylindrodactylus Schrammen. Diaphragms are present in the Washington Oligocene specimens, but in general these are concave-up divisions within tubular parts of the sponge and must mark pulses in growth of the sponge rather than convex-up terminations like those on the German Cretaceous sponges. Orientation in the Tertiary sponges is well defined by development of irregular basal areas, just as the terminations are well defined in Schrammen's *A. cylindrodactylus* by the rounded fingerlike growth.

TYPE SPECIMENS AND AVAILABLE MATERIAL. Holotype LACMIP 6600 from Locality 7, the type locality of the species, and paratypes LACMIP 6601, 6603, 6607, 6608 from Locality 7, LACMIP 6605, 6606 from Locality 5, LACMIP 6604 from Locality 7, LACMIP 6602 from Locality 8. In addition 22 specimens or concretions were obtained from Locality 1, 18 from 2, 1 from 4, 1 from 5, 2 from 6, and 12 from Locality 7. Some concretions contain several specimens or fragments.

ETYMOLOGY. *Poly,* Gr., many; *tretos,* perforated, referring to the many coarse canals through the cellular-appearing wall.

Family Euretidae Zittel, 1877
(*fide* Schulze, 1887)

Subfamily Euretinae Reid, 1958

Genus *Eurete* Semper, 1868

Eurete goederti n. sp.

Figures 18–20, 22, 23

DIAGNOSIS. Dendroid or irregular zigzag heterotomously branching axial tube with short lateral branches, both approximately 8–10 mm in diameter; branches approximately 20 mm apart. Walls 0.5–1.1 mm thick; skeletal net euretoid, lacking prominent ostia and postica; moderately open skeleton lacking well-defined gastral and dermal cortex; strands originate on gastral surface and parallel that surface before arching steeply through the wall. Gastral strands approximately 0.10–0.23 mm apart and 0.10 mm in diameter, with nodes 0.16–0.18 mm in diameter spaced 0.4–0.5 mm apart along strands and cross connected by beams 0.06–0.09 mm across to form rectangular meshes. Nodes slightly to distinctly swollen but not spherical.

Branches more closely and regularly spaced and slightly larger than in *E. lithodendron* Reid, and much better developed than closely spaced, rudimentary branches in *E.* (?) *setosum* Reid. Lacks cortex and ostia that are developed in both *E. lithodendron* and *E.* (?) *setosum*. Growth form and branches more regular than in *E. schmidti treubi* Ijima. Spherical nodes absent at spicule centra, although common in related species.

DESCRIPTION. Several fragments are in the collection. The most complete, the holotype, is a fragment approximately 12 cm high. It is an elongated branched form in which the axial tube has undergone heterotomous division to produce a dichotomous structure in which one of the two branches ceases to grow and the other grows to divide again. This produces a zigzag growth pattern with angles of approximately 120–130 degrees between segments of the axial tube. The axial tubes and branches are 8–10.5 mm in diameter. The short lateral branches are spaced approximately 20 mm apart along the axial tube and are approximately 1 cm long. Oscula occur at the ends of the lateral rudimentary branches and range from openings to somewhat constricted.

Walls of tubes and branches are 0.5–1.1 mm thick and have a generally thin, but well-defined gastral layer of thickened strands and beams. Most of the wall is composed of relatively open-textured endosomal skeleton. A dermal layer is not differentiated in the well-developed dictyonal framework. The thickened gastral layer usually affects only strands and beams at the immediate gastral surface.

Neither ostia nor postica are clearly defined, although some irregular interruptions in the outer part of the skeleton may represent ostia. These are subcircular openings, 0.15–0.3 mm across, and are irregularly developed in the visible exterior. No similar interruptions are evident in the inner part of the skeleton, and water must have passed through the wall via the open skeletal meshes.

Strands of the dictyonal skeleton originate near or at the gastral surface and parallel that surface before swinging abruptly dermally. They terminate as unattached conical to spinelike rays at the outer margin of the wall, where they are often nearly at right angles to the dermal surface. In the gastral layer, strands are parallel and spaced 0.15–0.4 mm apart. They are closest immediately distal to insertion of a new strand, often by "branching," and are farthest apart immediately proximal to the insertion. Spicular nodes are spaced by beams 0.4–0.5 mm long along the gastral strands and are connected laterally by beams 0.10–0.25 mm long, measured horizontally on the gastral surface. Beams of gastral strands are 0.08–0.11 mm in diameter midway between nodes, with most 0.10 mm across. Lateral gastral beams are 0.06–0.09 mm across, with most in the upper end of that range. Nodes are 0.10–0.22 mm in diameter but without much swelling other than slight flaring where rays meet. Nodes throughout the skeleton are not spherical but appear almost rectangular. Most such nodes are 0.16–0.18 mm across in the endosomal part of the wall.

Endosomal and dermal beams are slightly smaller than gastral ones, with common diameters of 0.06–0.10 mm and lengths of 0.2–0.3 mm, thus spacing nodes three-dimensionally that distance within the wall. This part of the wall is less linearly organized than the gastral part and is 2–4 spicules thick. Free beams form only low rounded knobs or cones on the gastral surface but pointed spines on the dermal surface.

Skeletal mesh openings are generally rectangular in the inner part of the skeleton but become much more irregular and commonly triangular in the middle and outer part of the wall.

Adnate small free hexactines occur commonly throughout the skeleton. They are generally attached to a beam by one ray, and the other rays of the tiny spicules are free. They range from small spicules with rays only 0.15 mm long and 0.005 mm in diameter up to larger forms with rays 0.3 mm

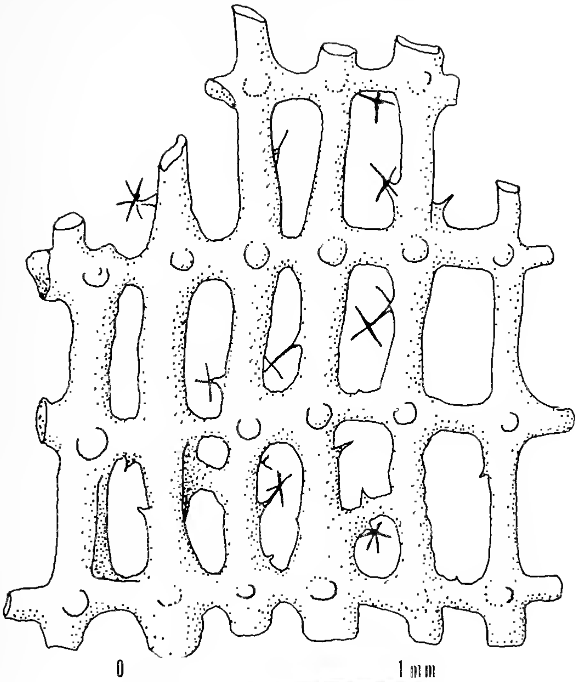

Figure 23. *Eurete goederti* n. sp., drawing of part of the skeleton of the holotype showing smaller attached hexactines and larger beams of gastral dictyonine net. Vertical strands are dominant elements in this part of the net. Distal is toward the top, and proximal is toward the base. LACMIP 6609, Locality 7, approximately ×40.

long and 0.008–0.010 mm across in basal ray diameter. They are frequently oriented with rays parallel to the major dictyonal elements, in the general plane of those elements, or at approximately 45 degrees to those elements where they project out into the "cubic" meshes (Figure 23). Beams in the skeleton all show granular to distinctly spinose surfaces, many of the tiny spines only 0.005 mm across and 0.10 mm or less high.

DISCUSSION. *Eurete goederti* n. sp. is most similar to Cretaceous *E. lithodendron* Reid (1961:34–38, pl. 7, figs. 4a, b) in general growth form but is slightly larger. In addition, branching is more distant in *E. goederti* n. sp., and it lacks a dermal cortex and ostia, which are present in *E. lithodendron.* Modern *E. schmidti treubi* Ijima (1927:170; Reid, 1961:37, fig. 2a) also has a similar growth form but branches considerably more irregularly.

E. (?) *setosum* Reid (1958:38–40), from the Cretaceous of Great Britain, is also a tubular branching form, but its branches are often reduced to rudimentary structures, in contrast to the distinct branches in *E. goederti.* In addition *E.* (?) *setosum* has a dermal cortex and ostia in places, and branches are spaced relatively closely together. Branching in *E. goederti* is considerably more regular than in either *E. lithodendron* Reid, *E.* (?) *setosum* Reid, or in the living *E. schmidti treubi.* The northwestern United States fossil species also lacks spherical spicule nodes that are common in the other species.

Depth ranges of living species of *Eurete* were summarized by Schrammen (1912:184–185), based upon work by Schulze and Carter. Shallowest occurrence cited by Schrammen is 220 m for *Eurete carteri* Schulze, and deepest is 717 m for *E. erectum* Schulze. Most species are listed from depths of 300 or 360 meters. Reid (1968:549) listed *Aphrocallistes vastus* Schulze as having been collected in depths of 27.5 m (Puget Sound), 97 m (Oregon), and 108 m (Vancouver, British Columbia) but noted that the Puget Sound site is the shallowest authenticated record of modern dictyonine hexactinellids. By analogy it seems likely that the Washington Oligocene species had a depth range of 100–350 m. The fragmental nature of our material, however, suggests that the assemblage may have been transported. Downslope transport is suggested by occurrence of these and associated fossils in thin, coarse, sandy to glauconitic beds, intercalated as high-energy pulses in the dominantly fine-grained sequence.

TYPE SPECIMENS AND AVAILABLE MATERIAL. The holotype, LACMIP 6609, is the largest fragment and occurs with *Aphrocallistes* fragments, pieces of wood, fish fragments, and foraminifers in a coarse sandy siltstone from Locality 7, the type locality of the sponge species. The paratype (LACMIP 6610) and an additional, more fragmental piece of *Eurete* are also from the same locality. One concretion from Locality 8 also contains tiny scraps of dictyonal skeleton that are probably from *E. goederti*; these are too small to determine growth habit and other relationships but have the same proportions in the gastral net as the holotype of *E. goederti.*

ETYMOLOGY. *Goederti,* named for James Goedert, on whose collections this and parallel studies of other groups are largely based.

Order, Family, Genus Uncertain

Hexactinellid Root Tufts

Figures 11, 12

Several concretions contain moderately well organized root tufts of hexactinellid sponges. These are composed of concentrically layered, aligned, large, doubly tapering oxeas (?), with maximum diameters of 1.1–1.4 mm at approximately midlength. Neither entire length nor preserved tips were observed on any single spicule, but spicule fragments at least 3 or 4 cm long occur in fine-grained calcareous siltstone where sharp tips and double taper are well shown. They form clusters 3 or 4 cm across and are commonly isolated from other sponges. In one small concretion from Locality 2, isolated large root tuft spicules occur embedded in irregular basal spicular masses of *Aphrocallistes.* Bases of other specimens of the species do not have such spicules and apparently were cemented to bivalve or gastropod fragments or pebbles. This implies that the tuft spicules are not an integral part of *Aphrocallistes* but that the sponge from Locality 2 overgrew exposed root tuft spicules, which formed a solid substrate "island" on the muddy bottom. Concretions, without *Aphrocallistes,* from the same locality contain both root tuft clusters and fragments of *Eurete,* but the sponge fragments and root spicules are not intergrown and may be unrelated biologically. The root tufts may represent sponges not otherwise preserved in the collections. Taxonomic relationships of root tufts are unknown.

FIGURED SPECIMENS AND AVAILABLE MATERIAL. Figured specimen LACMIP 6612 is from Locality 5, and 6611 is from Locality 7. Five other concretions containing tuft fragments were collected from Locality 2, and one was collected from Locality 5.

Similar root tufts of large bundled oxeas, which show concentric layering, occur at two other localities (Armentrout, personal communication, 1982). One such tuft was collected by Susan Bee, from Portland State University, from Late Eocene siltstone of the upper member of the Keasey Formation. The fossil was float in a 5-m high railroad cut south of and upslope from the abandoned railroad trestle across Highway 47, between Buxton and Vernonia, approximately 20 m (80 feet) west and 210 m (700 feet) north of the southeast corner of Sec. 8, T. 3 N., R. 4 W., on the Vernonia 7½-minute quadrangle, Washington County, Oregon (Locality Tok-M112 of Warren and others, 1945).

The other tuft was collected from Late Eocene siltstone of the Lincoln Creek Formation by J.M. Armentrout. It came from the upper 3-m (10-foot) interval at the top of a cliff on the south side of Canyon River, just upstream from a logging road bridge, approximately 240 m (800 feet) west and 67 m (220 feet) north of the southeast corner of Sec. 13, T. 21 N., R. 6 W., on the Grisdale 15-minute quadrangle, Grays Harbor County, Washington (Locality CR9 and 10 of Armentrout, 1973).

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LITERATURE CITED

Armentrout, J.M. 1973. Molluscan paleontology and biostratigraphy of the Lincoln Creek Formation, late Eocene-Oligocene, southwestern Washington. (Ph.D. dissertation) University of Washington, Seattle, 478 pp.

———. 1975. Molluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. *In* Weaver, D. (ed.), Future Energy Horizons of the Pacific Coast; Paleogene Symposium and selected technical papers. Annual Meeting of the Pacific Sections, American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, Society of Economic Geologists, Long Beach, California, pp. 14–48.

———. 1977. Cenozoic molluscan stages of Oregon and Washington. Abstracts with Programs. Geological Society of America 9(7):882–883.

———. 1981. Correlation and ages of Cenozoic biostratigraphic units in Oregon and Washington. *In* Armentrout, J.M. (ed.), Pacific Northwest Cenozoic Biostratigraphy, Geological Society of America Special Paper 184, pp. 137–148.

Beikman, H.N., W.W. Rau, and H.C. Wagner. 1967. The Lincoln Creek Formation, Grays Harbor Basin, southwestern Washington. U.S. Geological Survey Bulletin 1244-I:I1–I114.

Dall, W.H. 1909. Contributions to the Tertiary paleontology of the Pacific coast, I. The Miocene of Astoria and Coos Bay, Oregon. U.S. Geological Survey Professional Paper 59, 278 pp.

Dana, J.D. 1849. Geological observations of Oregon and northern California, U.S. Exploration Expedition 1838–1842 under the command of Charles Wilkes, Geology, v. 10, pp. 611–678; Appendix, pp. 722–723, 729–730; Atlas.

Gray, J.E. 1858. On *Aphrocallistes*, a new genus of Spongiadae from Malacca. Proceedings of the Zoological Society of London 26:114–115.

———. 1867. Notes on the arrangement of sponges, with a description of some new genera. Proceedings of the Zoological Society of London, 1867, pp. 492–558.

Ijima, I. 1927. The Hexactinellida of the Siboga Expedition. Siboga-Expeditie, Leiden, v. 6, 383 pp.

Moore, E. J. 1963. Miocene marine mollusks from the Astoria Formation of Oregon. U.S. Geological Survey Professional Paper 419, 109 pp.

Rau, W.W. 1958. Stratigraphy and foraminiferal zonation in some of the Tertiary rocks of southwestern Washington. U.S. Geological Survey Oil and Gas Investigations Chart OC-57, 2 sheets.

———. 1964. Foraminifera from the northern Olympic Peninsula, Washington. U.S. Geological Survey Professional Paper 375-G:G1–G33.

———. 1981. Pacific Northwest Tertiary benthic foraminiferal biostratigraphic framework—An overview. *In* Armentrout, J.M. (ed.), Pacific Northwest Cenozoic Biostratigraphy, Geological Society of America Special Paper 184, pp. 76–84.

Reid, R.E.H. 1958–64. A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Palaeontographical Society, London. 1958, Part I, pp. i–xlvi; 1958, Part II, pp. xlvii–xlviii, 1–26; 1961, Part III, pp. 27–48; 1964, Part IV, pp. xlix–cliv.

———. 1968. Bathymetric distributions of Calcarea and Hexactinellida in the present and the past. Geological Magazine 105(6):546–559.

Schrammen, A. 1912. Die Kieselspongien der oberen Kreide von Nordwestdeutschland; II Teil, Triaxonia (Hexactinellida). Palaeontographica, Supplement 5, pp. 177–385.

Schulze, F.E. 1887. Report on the Hexactinellida collected by H.M.S. *Challenger* during the years 1873–76. Report of Scientific Results of the Voyage of the H.M.S. *Challenger*, Zoology 21:1–513.

Semper, C. 1869. Einige neue Kieselschwamme der Philippen: *Hyalonema Schultzei* n. sp. und *Eurete* n. g. Verhandlungen der Physikalisch-Medicinischen Gesellschaft in Wurzburg, new series, 1868, 1:29–30 (also published in 1868, Annals and Magazine of Natural History 2:372–373).

Snavely, P.D., Jr., N.S. MacLeod, W.W. Rau, W.O. Addicott, and J.E. Pearl. 1975. Alsea Formation—An Oligocene marine sedimentary sequence in the Oregon Coast Range. U.S. Geological Survey Bulletin 1395-F:F1–F20.

Warren, W.C., R.M. Grivetti, and H. Norbisrath. 1945. Geology of northwestern Oregon. U.S. Geological Survey Oil and Gas Investigations, Preliminary Map 42.

Weaver, C.E. 1912. A preliminary report on the Tertiary paleontology of western Washington. Washington Geological Survey Bulletin 15:1–80.

———. 1937. Tertiary stratigraphy of western Washington and northwestern Oregon. Washington University (Seattle) Publications Geology 4:1–266.

Weaver, C.E., and others. 1944. Correlation of the marine Cenozoic formations of western North America (Chart no. 11). Geological Society of Ameriea Bulletin 55:569–598.

Wells, R.E. 1979. Geologic map of the Cape Disappointment-Naselle River area, Pacific County, Washington. U.S. Geological Survey Open-File Report 79-389.

Zullo, V.A. 1982. *Arcoscalpellum* Hoek and *Solidobalanus* Hoek (Cirripedia, Thoracia) from the Paleogene of Pacific County, Washington, with a description of a new species of *Arcoscalpellum*. Natural History Museum of Los Angeles County, Contributions in Science 336:1–9.

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CONTRIBUTIONS IN SCIENCE

NEW GENERA AND A NEW SPECIES OF CENTRAL AMERICAN SALAMANDERS, WITH A REVIEW OF THE TROPICAL GENERA (AMPHIBIA, CAUDATA, PLETHODONTIDAE)

David B. Wake and
Paul Elias

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NEW GENERA AND A NEW SPECIES OF CENTRAL AMERICAN SALAMANDERS, WITH A REVIEW OF THE TROPICAL GENERA (AMPHIBIA, CAUDATA, PLETHODONTIDAE)

David B. Wake[1,2] **and**
Paul Elias[1]

ABSTRACT. A new genus and species of plethodontid bolitoglossine salamander is described from material collected in northwestern Guatemala. *Bradytriton silus* new genus, new species, is unique in a combination of structural characteristics that includes a laterally compressed tail, stocky body with no clearly defined neck, and short, slender limbs bearing syndactylous hands and feet. To diagnose the new genus, an analysis of the entire neotropical assemblage of plethodontid salamanders was undertaken. Approximately 138 species belong to the supergenus *Bolitoglossa* and 11 genera are recognized. The genus *Chiropterotriton* is shown to be polyphyletic; thus, two new genera are described. *Nototriton* new genus, includes the *picadoi* group of *Chiropterotriton* beta. *Dendrotriton* new genus, includes the *bromeliacia* group of *Chiropterotriton* beta. Those species formerly called *Chiropterotriton* alpha remain as the sole representatives of the genus. Eight of the eleven neotropical genera are shown to be monophyletic. Of the three exceptional genera, both *Dendrotriton* and *Nototriton* are nonparaphyletic relative to all genera except *Oedipina,* but *Dendrotriton* is easily distinguished from *Oedipina. Nototriton* may be paraphyletic relative to *Oedipina,* but the two genera can be readily distinguished on the basis of major differences in ecology and shape. *Pseudoeurycea* comprises morphologically generalized species that may not be far removed from the morphology of the ancestral stock of the entire neotropical group. Only *Nyctanolis* and *Chiropterotriton* are more plesiomorphic than *Pseudoeurycea.* Lists of species assigned to the genera are provided. Potential relationships within the supergenus *Bolitoglossa* are discussed, but parallelism and convergence have been so extensive that no definitive statement concerning generic affinities is possible.

RESUMEN. Un nuevo género y especie de salamandra plethodóntida bolitoglossina se describe en base a material recolectado en el noroeste de Guatemala. *Bradytriton silus,* nuevo género, nueva especie, es peculiar por su combinación de caracteres que incluye una cola comprimida lateralmente, un cuerpo macizo con cuello escasamente definido, y patas delgadas y cortas provistas de manos y pies syndáctilos. Para diagnosticar este nuevo género se realizó un análisis del grupo completo de salamandras plethodóntidas neotropicales. Las aproximadamente 138 especies pertenecen al supergénero *Bolitoglossa,* en el cual se reconocen 11 géneros. El género *Chiropterotriton* se señala como polifilético y por lo tanto dos nuevos géneros se describen. *Nototriton,* nuevo género, incluye el grupo *picadoi* de *Chiropterotriton* beta. *Dendrotriton,* nuevo género, incluye el grupo *bromeliacia* de *Chiropterotriton* beta. Las especies previamente incluídas en *Chiropterotriton* alfa permanecen como las únicas representantes de este género. Ocho de los once géneros neotropicales se señalan como monofiléticos. De los tres géneros restantes, tanto *Dendrotriton* como *Nototriton* son monofiléticos en relación a todos los géneros excepto *Oedipina,* aunque *Dendrotriton* es fácilmente distinguible de *Oedipina. Nototriton* podría ser parafilético en relación a *Oedipina,* pero estos dos géneros pueden ser rápidamente reconocidos en base a sus marcadas diferencias en ecología y forma corporal. *Pseudoeurycea* comprende especies morfológicamente generalizadas que podrían estar no muy alejadas de la morfología del grupo ancestral del ensamble neotropical analizado. Sólo *Nyctanolis* y *Chiropterotriton* son más plesiomórficos que *Pseudoeurycea.* Listas de las especies asignadas a cada género se presentan. También se discuten las potenciales relaciones dentro del supergénero *Bolitoglossa,* pero paralelismos y convergencias han sido tan prevalentes que ninguna opinión definitiva puede plantearse en cuanto a afinidades genéricas.

INTRODUCTION

In the summer of 1974, the junior author collected several species of salamanders in a remote area in northwestern Guatemala. Included in this collection were three species that obviously were undescribed. Subsequent morphological analysis showed that two of the new species have combinations of traits that require them to be placed into two new genera. One of these (*Nyctanolis*) has been described elsewhere (Elias and Wake, 1983). In this paper we describe the second new genus. We also report the results of a detailed

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1. Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720.

2. Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

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analysis of all of the currently recognized genera of tropical salamanders. As a result of this analysis, which was a necessary background for the description of the new genera and species, two additional new genera are erected. These are described herein, and diagnostic characters are given for all existing genera of tropical salamanders. In addition, all recognized species of tropical salamanders are referred to a genus, and relationships among the genera are examined. This analysis reinforces previous views (Wake, 1966; Wake and Lynch, 1976) that there has been very extensive parallelism and convergence during the adaptive radiation of plethodontid salamanders in the New World tropics.

BACKGROUND

Although several genera of New World tropical salamander species were described in the nineteenth century, and some knowledge of the diversity of the group was available at that time, the most authoritative taxonomic work on these salamanders during the early part of the twentieth century (Dunn, 1926) placed all tropical species in a single plethodontid genus, *Oedipus*. Dunn considered *Oedipus* to be "a large, modern genus of some 30 species. The extremes are quite different but there are many connecting links." There was little increase in knowledge of tropical salamanders until the mid-1930's, when Schmidt, Taylor, and other workers began publishing their results (for historical summary, see Wake, 1972, and Smith and Smith, 1976). Taylor (1940) showed that *Oedipus* was a preoccupied name, and substituted the old name *Bolitoglossa* for the entire assemblage, except for a group of diminutive species, which he placed in Cope's (1869) old genus *Thorius*. Shortly thereafter, Taylor (1944) undertook a radical revision of all the neotropical salamanders, in which he described four new genera (*Chiropterotriton, Parvimolge, Magnadigita, Pseudoeurycea*), resurrected *Oedipina* and *Haptoglossa*, and continued to recognize *Bolitoglossa* and *Thorius*. Since that time, there has been relative stability in the generic classification of the group. *Lineatriton* was established by Tanner (1950), *Magnadigita* was placed in the synonymy of *Bolitoglossa* by Wake and Brame (1963), and *Haptoglossa* was placed in the synonymy of *Oedipina* by Brame (1968). The entire assemblage was characterized and the genera defined by Wake (1966), who established the supergenus *Bolitoglossa* for this group. This supergenus, and the supergenera *Hydromantes* and *Batrachoseps*, were included in the tribe Bolitoglossini, subfamily Plethodontinae, of the family Plethodontidae. Many species have been discovered since 1926; herein, we recognize 138.

The most recent comprehensive treatment of the supergenus *Bolitoglossa* (Wake and Lynch, 1976) dealt mainly with ecology, distribution, and biogeography and offered little new morphological or taxonomic analysis. Since the publication of that paper, major new discoveries have been made; here, we attempt to give phylogenetic perspective to the available information.

The present effort is not definitive, for continued new discoveries indicate that our knowledge of the group, even at the generic level, remains incomplete. We are aware of many undescribed species, and a number of described species—including some crucially important ones—are known from only one or a very few individuals. Nevertheless, we believe that the broad outlines of relationship are sufficiently clear to justify the substantial revision we undertake here.

MATERIALS AND METHODS

We have not considered in detail the species of *Bolitoglossa, Oedipina,* and *Thorius,* all large, monophyletic genera, which are either under intense study presently (*Bolitoglossa* by D.B. Wake, P. Alberch, A. Larson, and colleagues, *Thorius* by J. Hanken), or have been analyzed recently (*Oedipina* by Brame, 1968). Instead, we have emphasized apparently polyphyletic and paraphyletic groups, as well as newly discovered species that do not easily fit into any existing genus. In these critical cases, we have analyzed doubly cleared and stained specimens, histological sections, and dissections of fixed material. As a point of departure for the choice and analysis of characters, we have relied on the literature, which will be cited where appropriate.

We have had access to adequate samples of most of the species. Important species for which we have lacked sufficient material but nevertheless can offer useful information include (present generic designation used): *Chiropterotriton barbouri, C. richardi,* and *Parvimolge praecellens.* These are discussed in appropriate places in the following account.

As noted above, one of the new genera has recently been described (Elias and Wake, 1983). We begin this work with an account of the characters that are used in our generic revision. We then describe a newly discovered genus and species and erect two new generic names to encompass previously known species. Finally, we present a preliminary phylogenetic analysis.

CHARACTERS USED FOR ANALYSIS

A necessary first step in the process of phylogenetic reconstruction is the identification of monophyletic taxa (*sensu* Eldredge and Cracraft, 1980). Our goal is to deduce monophyletic groups from a matrix of morphological character states. There are incomplete data for too many species to justify an extensive analysis at the species level. Accordingly, we have relied on the literature and our own previous work to recognize groups of species. We have treated these groups as hypotheses and have investigated whether or not each is a monophyletic taxon. A group that is found to be monophyletic is then treated as a genus. We believe that the generic level of classification should combine species into monophyletic units that are separated from other such units by morphological gaps. Ideally, the gaps will coincide with ecological and behavioral differences as well. Thus, our objective is to define generic-level units that are meaningful in both phylogenetic and ecological terms.

In the analysis that follows, each genus is scored for eighteen characters (Table 1). In certain genera, there is some variation in these characters among, or even within, species. Only if a derived condition is characteristic of every known population and species (i.e., only if it appears in most adults) is the genus as a whole scored as derived. Thus, our character scoring should reflect the most primitive common denominator for each genus discussed and should represent the situation in the common ancestor of the included species. The disadvantage of this conservative approach is that it masks a certain amount of parallelism.

The characters used in our analysis are described below. All of the characters are treated as two-state characters, with primitive (plesiomorphic) and derived (apomorphic) states identified on the basis of outgroup analysis (Eldredge and Cracraft, 1980). Our outgroups are the genera *Hydromantes* and *Batrachoseps,* the other members of the tribe Bolitoglossini; and the members of the tribe Plethodontini. Most of the osteological characters have already been discussed in detail by Wake (1966) and Lynch and Wake (1978). By convention, we code the characters (0) to indicate primitive and (1) to indicate derived states.

1. *Mesopodial mineralization.* Mesopodials are cartilaginous throughout life (0) or are mineralized in adults (1).

2. *Tibial spur.* A well-developed rodlike structure, free from the shank of the bone, is present proximally (0) or is absent or reduced to a low ridge (1).

3. *Carpal fusion.* The ulnare and intermedium are discrete (0) or fused (1).

4. *Tarsal fusion.* Distal tarsals four and five are discrete (0) or fused (1).

5. *Mental glands.* Clusters of individual glands form a small patch located near the tip of the chin in male tropical salamanders (Truffelli, 1954). The patch is either externally visible, and ovoid, circular, or subtriangular, with rounded or low columnar individual internal glands (0), or is externally obscure, with long, tubular individual internal glands that are oriented posteriorly from their openings near the chin (1). The tubular glands extend posteriorly as twisted tubes covered by the skin of the gular area.

6. *Stylus of operculum.* The stylus, or columella, is not well developed in any of the tropical species, but it may be present, with a distinct rodlike shape (0) or reduced to a broad bulge or be entirely absent (1).

7. *Preorbital processes of vomers.* These slender processes, which may or may not bear teeth, are either present between the internal nares and the orbit (0) or absent (1).

8. *Prefrontal bones.* These bones are either present in varying degrees of development (0) or absent (1).

9. *Septomaxillary bones.* These bones are not well developed in any tropical salamanders, but small ossicles may be present (0) or absent (1).

10. *Frontal processes of premaxillary bone.* Where only a single premaxillary bone is present, the frontal processes are either fused together at the point of origin on the dorsal surface of the pars dentalis and for some distance dorsoposteriorly (1) or separated for their entire length (0). We score those few instances in which the processes arise separately and subsequently fuse as 0.

11. *Premaxillary bones.* The pars dentalis of plethodontid salamanders is either divided (0) or fused so that only a single bone is present (1).

12. *Skull roof.* The parietal bones may either meet or approach each other very closely on the midline, thus forming a complete skull roof (0), or be widely separated and joined by a connective tissue sheet, thus forming an incomplete skull roof (1).

13. *Sublingual fold.* A small to large fold of glandular skin underlying the tongue may be present (0) or absent (1).

14. *Limb length.* Limbs are moderate to short in length, so that they overlap slightly or not at all when adpressed (0), or are very long, so that they overlap by more than two costal interspaces (1).

15. *Tarsal arrangement.* Distal tarsal four is discrete from and larger than distal tarsal five and articulates with the fibulare (0), or distal tarsal five is discrete from and larger than four and articulates with the centrale (1). When distal tarsals four and five are fused, the character is scored as 0.

16. *Trunk vertebral shape.* The ratio of centrum length to posterior centrum diameter is low (2.5–4), and the vertebrae are relatively wide and short (0), or the ratio is high (greater than 4), and the vertebrae are relatively narrow and elongate (1).

17. *Number of trunk vertebrae.* There are either 14 (0) or 18 or more (1).

18. *Tail shape.* The tail is either round or ovoid in cross section (0) or strongly compressed laterally, with a dorsal, glandular ridge (1).

The eighteen characters are listed in Table 1, along with the states that characterize each of the 11 genera we recognize in this paper. This table alone can be used to diagnose all of the genera. In most instances the genera are diagnosed by autapomorphies (derived characters unique to a given taxon), combinations of synapomorphies (derived characters shared by two or more taxa), or both. In some instances, determination that a given genus is monophyletic requires an analysis of the distribution of character states over all taxa; such cases are detailed in the Discussion. All 11 genera can be readily diagnosed on the basis of unique combinations of traits, including both apomorphic and plesiomorphic states. *Bolitoglossa* probably should be divided into at least two taxa (Wake and Lynch, 1976), but it is a well-defined (if unwieldy), monophyletic taxon as currently recognized. However, our generic concept does require that we recognize four new generic taxa. One of these, *Nyctanolis,* is a recently discovered monotypic genus that has been described elsewhere (Elias and Wake, 1983). A second newly discovered genus, also monotypic, is described immediately below. The other two new genera result from subdivision of an existing genus and are described below in the context of our generic diagnoses.

DESCRIPTION OF A NEW GENUS AND SPECIES

Bradytriton new genus

TYPE SPECIES. *Bradytriton silus* new species.

DIAGNOSIS. A plethodontid salamander belonging to the subfamily Plethodontinae, tribe Bolitoglossini, supergenus *Bolitoglossa. Bradytriton* is a short-snouted, stout-bodied, short-tailed taxon with small limbs and diminutive, syn-

Table 1. Distribution of character states in genera of neotropical plethodontid salamanders. See text for listing of characters. 0 = primitive state; 1 = derived state.

	Character																	
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Bolitoglossa	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0
Bradytriton	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
Chiropterotriton	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Dendrotriton	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Lineatriton	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0
Nototriton	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0
Nyctanolis	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Parvimolge	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0
Pseudoeurycea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Oedipina	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0
Thorius	1	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0

dactylous hands and feet, readily distinguished from most other members of the supergenus on the basis of those features. It differs from all other members of the supergenus in having a laterally compressed tail with a relatively massive dorsal glandular ridge. *Thorius* and *Parvimolge* have short limbs, but these genera are much smaller and differ in other ways as well: *Thorius* has an incomplete brain case, and both genera frequently have mineralized mesopodial and hyobranchial ossifications as adults. *Nototriton* and *Dendrotriton* have long, slender tails. All *Bolitoglossa* lack sublingual folds. Most *Pseudoeurycea* have long tails and long limbs, and all lack the mesopodial fusions (ulnare-intermedium in manus; fourth and fifth distal tarsal in pes) that characterize *Bradytriton.*

ETYMOLOGY. From *bradys,* Gr., referring to the slow and lethargic movements of the living animals, and *triton,* Gr., a commonly used term for salamanders.

Bradytriton silus new species

Figures 1 through 6

HOLOTYPE. Museum of Vertebrate Zoology (MVZ) 131587, an adult female from Finca Chiblac, 15 km NE Barillas, Depto. Huehuetenango, Guatemala, elevation 1,310 m (4,300 ft), collected by P. Elias, 6 September 1974.

PARATYPES. MVZ 131586, LACM 134566, same data as the holotype; MVZ 131589–131594 (6 specimens), same locality and collector as holotype, collected 7 September 1974; MVZ 134635–134637 (3 specimens), El Rayo, elevation 1,370 m (4,500 ft), 3 km S buildings of Finca Chiblac, 10 km NE Barillas, Huehuetenango, Guatemala, collected by J. Jackson and P. Elias on 1 September 1975; MVZ 134638, same locality and collectors as preceding series, collected on 31 August 1975; MVZ 173063, Finca Chiblac, 10 km NE Barillas, Depto. Huehuetenango, Guatemala, elevation 1,370 m (4,500 ft), collected by H.B. Shaffer and P. Elias on 2 July 1977; MVZ 173064, same data as preceding number, collected between August 1975 and October 1977 by J. Jackson and P. Elias.

DIAGNOSIS (measurements in millimeters). See Generic Diagnosis. A stout species of moderate size (standard length, SL, in four adult males, 39.1–53.3, mean 45.3; seven adult females 44.5–53.0, mean 49.0; Table 2) with a very stout, short tail (SL/tail length in three adult males is 1.3–1.7, mean 1.4; in six adult females, 1.2–1.7, mean 1.4), short limbs (when adpressed, fore and hind limbs leave 2–3, mean 2.3, costal interspaces uncovered in four adult males; 2.5–3, mean 2.9, in seven adult females), and small, syndactylous hands and feet. The relatively broad head (SL/head width in four adult males is 5.9–6.1, mean 6.1; in seven adult females, 5.7–6.6, mean 6.2) is essentially continuous with the body, and there is no neck. Maxillary teeth (41–50, mean 44.0, in four adult males; 40–59, mean 47.9, in seven adult females) and vomerine teeth (16–22, mean 18.5, in four adult males; 17–25, mean 20.6, in seven adult females) are moderate in number. The species is reddish brown in color, with obscure streaking and flecking of lighter and darker pigments.

DESCRIPTION. This stout, short-limbed species has a very short, truncate snout and diminutive hands and feet.

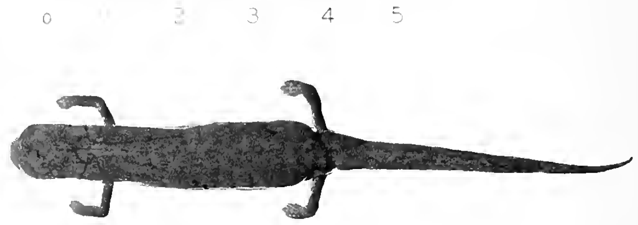

Figure 1. Dorsal view of MVZ 131587, the holotype of *Bradytriton silus* new genus and species.

The nostrils are small. Labial protuberances are poorly developed in females, which have an especially short snout, but are large and wide in adult males; the protuberances produce a broad muzzle rather than the elongate snout typical of other tropical salamanders. Mental glands are present in males but are not externally demarcated; the glands consist of a cluster of moderately long tubules that converge in the region of the mandibular symphysis, where they open individually to the ventral surface of the anterior intermandibular region. The tongue is adetoglossal, with a distinct small pad.

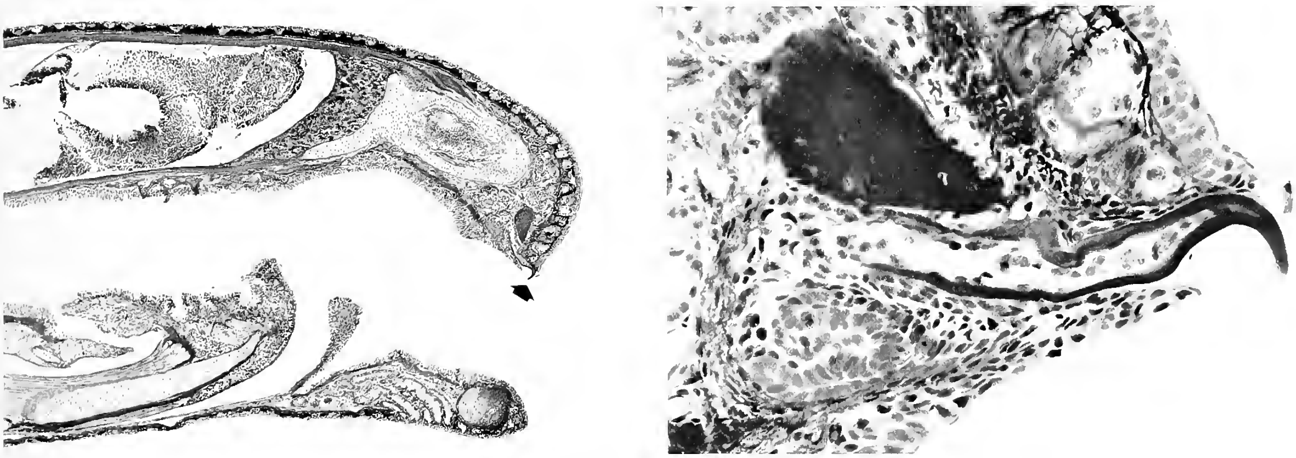

Figure 2. Parasagittal section through the head of a specimen (MVZ 134637) of *Bradytriton silus* new genus and species. The section is near the midline and passes through the mandibular symphysis.

Left. The arrow points to an enlarged premaxillary tooth and indicates the part of the section that is magnified in the view on the right. When the mouth is closed, the premaxillary teeth extend outside the mouth and lie near the ventral and anterior parts of the lower jaw, near the openings of the mental gland. The long, tubular ducts of the mental gland are evident immediately posterior to the mandible. Note that no external ventral swelling is present. Also well displayed in this section is the complex free tongue characteristic of the tribe Bolitoglossini. The hyoglossal muscles are attached to the apparently flexible anterior tip of the basibranchial. Immediately anterior to the tongue is the large sublingual fold, characteristic of all of the tropical salamanders except *Bolitoglossa*.

Right. Enlargement of the premaxillary tooth at the end of the arrow in the left part of this figure. The pedicel of the tooth is attached to the posteroventral border of the premaxillary bone (here oriented so that the border appears to be ventral). The crown is relatively large and is unicuspid. The cusp is strongly hooked.

Table 2. Data for type series of *Bradytriton silus* new genus and species.*

	Sex	Standard length	Head length	Head width	Foot width	Hind limb length	Fore limb length	Tail length	Maxillary tooth number	Premaxillary tooth number	Vomerine tooth number	Limb interval
MVZ 131589	♂	53.3	11.3	8.7	3.3	12.1	9.4	—	50	3	17	3.0
MVZ 134636	♂	46.4	10.3	7.6	3.1	11.0	9.5	36.0	41	5	16	2.0
MVZ 134637	♂	42.3	8.8	6.8	2.3	9.6	8.7	31.6	43	6	19	2.0
MVZ 134638	♂	39.1	9.0	6.6	2.3	8.7	8.0	23.2	42	8	22	2.0
MVZ 131591	♀	53.0	10.4	8.7	3.2	10.7	9.5	30.6	59	8	22	3.0
MVZ 131593	♀	51.5	10.3	8.8	2.5	9.2	9.6	—	48	8	20	3.0
MVZ 131586	♀	50.1	9.7	7.8	2.9	11.0	10.1	40.4	46	9	19	3.0
MVZ 134635	♀	48.8	10.1	7.4	2.7	11.0	9.2	34.1	46	9	25	3.0
MVZ 131587**	♀	48.5	9.5	7.5	2.5	9.4	9.5	36.6	52	6	17	3.0
MVZ 131592	♀	46.6	9.7	8.2	2.9	11.0	9.5	34.5	44	10	23	2.5
LACM 134566	♀	44.5	9.3	6.8	2.5	8.6	8.9	33.3	40	9	18	3.0
MVZ 131590	J	35.6	8.1	6.7	2.2	7.5	7.3	21.5	31	8	16	2.5
MVZ 131594	J	34.4	7.8	6.1	1.4	7.2	7.1	22.3	37	8	18	2.0

* All measurements are in millimeters.

** Holotype.

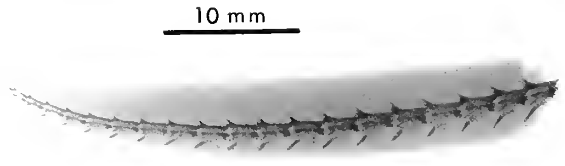

Figure 3. Radiograph of the broken tail of a specimen (MVZ 131586) of *Bradytriton silus* new genus and species. Dorsal to the top. Note the large glandular mass above the vertebral column.

The sublingual fold is well developed. The profile of the rounded head is undifferentiated from the trunk, and there is no apparent neck region. A deep unpigmented groove extends beneath the eye, following its curvature, but does not extend to the lip. The eyes are moderate in size and protrude slightly beyond the margin of the jaw. The postorbital groove is an indistinct furrow that extends posteriorly from the eye and intersects a deep vertical groove at right angles. The latter groove passes behind the base of the mandible and becomes a clearly defined nuchal groove. The gular fold is pronounced. Vomerine teeth are few to moderate in number and are arranged in a single, curved row that extends laterally beyond the lateral margin of the internal nares. Maxillary and vomerine teeth increase in number to some extent with increasing body size. The maxillary tooth row extends back to a point nearly posterior to the eyeball. Premaxillary teeth are 3–8, mean 5.5, in four adult males, 6–10, mean 8.4, in seven adult females; the teeth of males are very large and hooked and protrude under or through the lip (Fig. 2). The trunk is stout and cylindrical. The tail is of moderate length and is strongly tapered near its tip. It has a marked basal constriction and is strongly compressed laterally. The tail appears stout when viewed laterally but seems narrow from a dorsal perspective (Figs. 1, 3). Postiliac glands are distinct. The limbs are short and slender. Hands and feet are diminutive and syndactylous; the greatest foot width is about $^{1}/_{15}$ SL and the foot is barely wider than the lower limb. The digital tips are free, but adjacent digits are fused for most of their length (Fig. 4). There are no subdigital pads. The toes, in order of decreasing length, are 3, 2, 4, 5, 1; the fingers, 3, 2, 4, 1.

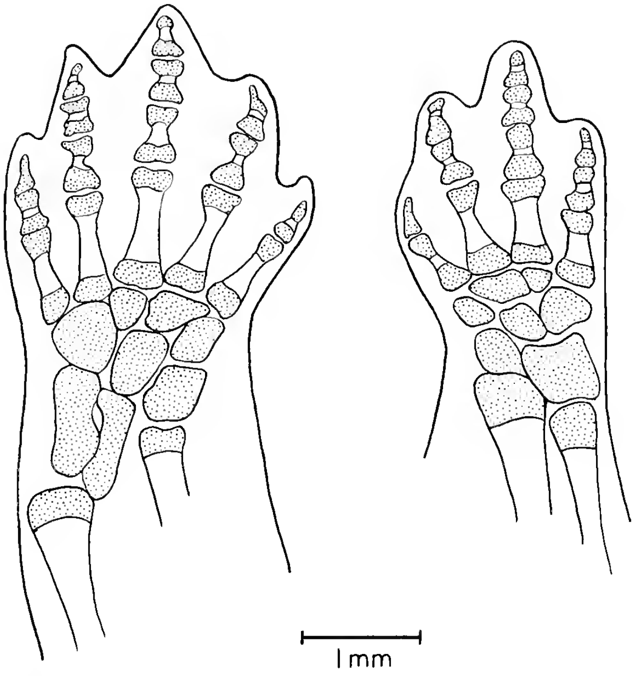

Figure 4. Dorsal views of the left foot (left) and of the right hand (right) of an adult male (MVZ 173064) *Bradytriton silus* new genus and species. Cartilage is stippled. The phalangeal elements are very poorly ossified and are less distinct than illustrated here (see text). Note the syndactylous nature of the digits.

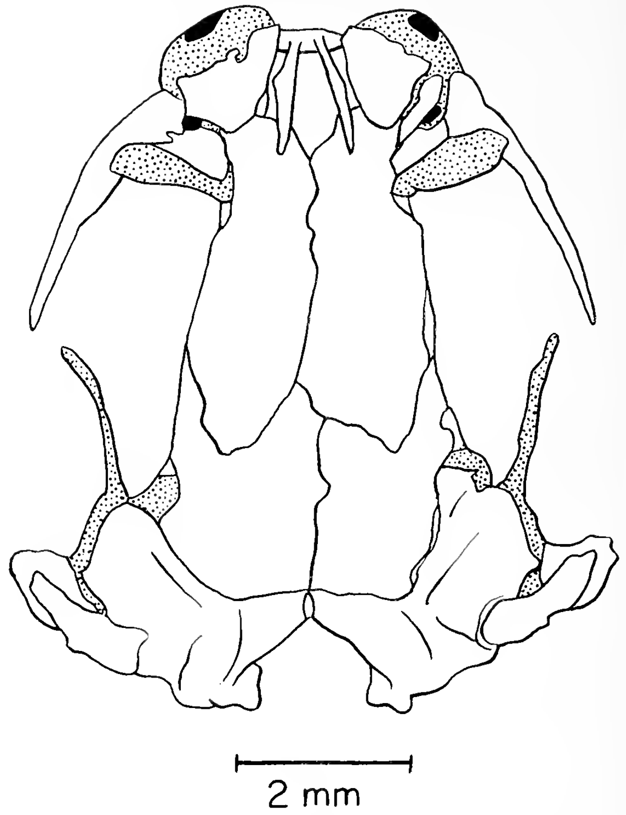

Figure 5. Dorsal view of the skull of an adult male (MVZ 173063) *Bradytriton silus* new genus and species. Bone is outlined, and cartilage is stippled. The external nares and the nasolacrimal foramina are black.

MEASUREMENTS OF THE HOLOTYPE (in millimeters). Head width 7.5; snout to gular fold (head length) 9.2; head depth at posterior angle of jaw 4.6; eyelid width 1.9; anterior rim of orbit to snout 2.0; horizontal orbit diameter 2.4; interorbital distance 2.3; vomerine teeth virtually continuous with parasphenoid tooth patch; snout to fore limb 12.6; distance separating internal nares 1.8; distance separating external nares 1.9; snout projection beyond mandible 0.3; snout to posterior angle of vent (standard length) 48.5;

snout to anterior angle of vent 44.4; axilla to groin 28.1; tail length 36.6; tail width at base 3.4; tail depth at base 4.8; fore limb length (to tip of longest toe) 9.5; hind limb length 9.4; hand width 1.7; foot width 2.5.

COLORATION IN LIFE. The dorsal coloration of this species is reddish brown. This color is broken by irregular flecks of black on the anterior trunk and dominated by black on the head. Brown coloration extends halfway down the lateral surfaces. The cheeks, sides of the tail, and lower flanks are black, overlain with dense white flecks. The legs are brown proximally but grade distally to black with white flecking. The feet are black marked with white flecks dorsally. The eye is chestnut brown.

COLORATION IN ALCOHOL. The dorsal surfaces of the head and trunk are dark gray. This color gives way to lighter gray and then to brown on the tail. Black flecks are superimposed on the brown at the tail tip. The arms and legs are dark gray with some light flecks. The lips, chin, throat, and undersides of the legs are dark gray with light gray flecks. The ventral surface of the trunk is unmarked dark gray. The ventral surface of the tail lightens distally to brown interrupted by darker flecks. The palmar surfaces and the tips of the nasal cirri are pale gray.

HABITAT. This species lives in an area of very humid cloud forest that received 5 to 6 meters of rainfall annually. All specimens were taken within 2 km of the type locality and were found in direct contact with the substratum under cover objects. Sympatric with *Bradytriton* were three species of *Bolitoglossa*, one species of *Nyctanolis*, various hylid and leptodactylid frogs, lizards of the genera *Anolis*, *Sceloporus*, and *Lepidophyma*, and one member of the snake genus *Leptodeira* (Elias, in press).

OSTEOLOGY AND RELATED MORPHOLOGY. Information has been derived from two cleared and stained male specimens, from radiographs of the entire sample, and from histological sections of the head and neck of one male.

The skull (Fig. 5) is short and very broad. The facial portion of the skull is poorly developed and is little expanded in front of the eyes. The anterior cranial elements are surprisingly weak for a moderate-sized species, and the bones are highly variable in shape, position, and number from one individual to the next, and even from one side to the other in the same individual. The premaxillary is relatively broad and has a large pars dentalis. However, the bone virtually "floats" at the anterior end of the skull; in most individuals, it does not contact the maxillaries, and in some it is separated from those bones by a sizeable gap. Even when a contact exists, the articulation is tenuous. The palatal portions of the premaxillary are greatly reduced or absent and do not contact the anterior extensions of the vomers. The frontal processes arise separately from the pars dentalis and are separated for their whole length. They are very narrow and columnar basally but become markedly compressed vertically to form the lateral margins of the gland-filled internasal fontanelle. The processes are generally divergent for their entire length and become flattened and slightly expanded near their distal tips. These tips overlap the expanded facial portions of the frontals in relatively firm (for this species) articulations. The frontal processes terminate distinctly posterior to the posterior tip of the nasals, a little behind the osseous anterior margin of the orbit. The internasal fontanelle is relatively narrow, except near its posterior terminus. In three adult males the nasals are strongly protuberant, extending well anterior to the jaw outline, but they are only slightly to moderately protuberant (Fig. 5) in the other males. The nasals protrude slightly in two females, including the holotype. Nasals are very irregular in size, shape, and degree of ossification but

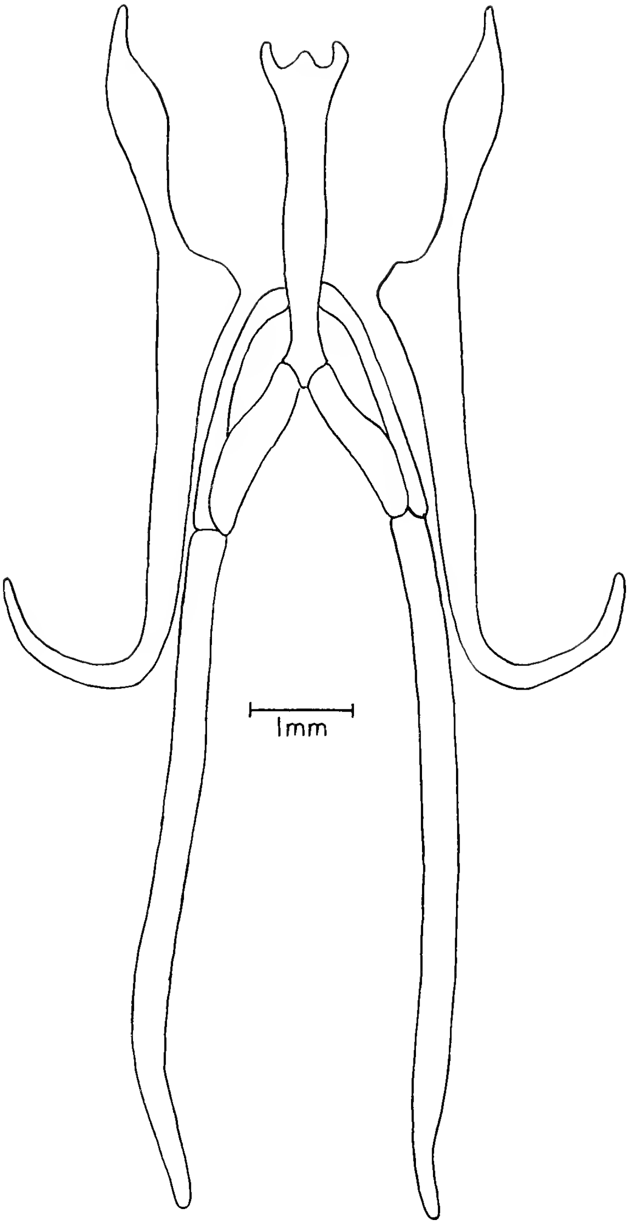

Figure 6. Dorsal view of the hyobranchial apparatus of an adult male (MVZ 173063) *Bradytriton silus* new genus and species. The entire structure is cartilaginous. The paired ceratohyals ordinarily lie closer together but have been moved somewhat laterally for clarity of illustration.

tend to be roughly triangular to quadrangular. The posterior tip is poorly defined, and the anterior margin is very irregular. Tiny fragments of disconnected bone frequently occur around the anterior and lateral margins of the nasal. In one cleared and stained individual, one of these fragments is very large and is situated as if it were an entirely separate bone intercalated between the nasal and the prefrontal (Fig. 5). This fragment is only slightly smaller than the prefrontal. The nasals only slightly overlap the anterior parts of the frontals. They have a variable degree of contact with the maxillary facial processes but a very narrow contact with the prefrontals. The posterolateral margin of the nasals may be slightly evacuated for the passage of the nasolacrimal duct, which passes through a shallow but distinct channel in the lateral part of the prefrontal and enters the nasal capsule through a foramen in the anterior margin of the prefrontal. The foramen may form a half-circle in the prefrontal. The prefrontals are about one-third the size of the nasals. Some small, bony fragments are present in some individuals at the anteroventral end of the prefrontals. The prefrontals are relatively long and narrow and are extensively overlapped by the facial processes of the maxillary. The prefrontals overlap the frontals only slightly. The maxillaries are relatively short and straight with narrow, pointed anterior and posterior projections on the dental portion. The posterior tips extend nearly to the posterior margin of each eyeball. Maxillary teeth are bicuspid and moderate in size. They are borne along all but the tip of the dental portion of the maxilla. The relatively well-developed palatal portion of the maxillaries is separated by a strong articulation from the lateral-most part of the vomerine body. There are no septomaxillary bones.

The large, morphologically specialized premaxillary teeth of males are attached to the premaxillary in such a way that their elongate crowns project directly anteriorly and pierce the lip (Fig. 2). Once through the lip, the unicuspid (apparently only the lingual cusp is retained) makes a sharp 90° turn caudad before terminating in a point. When the mouth is closed, the tooth tip is very close to the opening of the mental gland. This gland, which has a restricted exit at the mandibular symphysis, is a cluster of tubules converging to form a small cluster of apertures (Fig. 2). The glands and teeth constitute a functional complex that serves to transfer the glandular secretion to females during courtship in a manner analogous to vaccination (Arnold, 1977). Teeth of similar shape occur in some species of *Pseudoeurycea* (Taylor, 1941).

The large, strong vomers are in limited contact only at their extreme tips, posterior to the large intervomerine fontanelle. A distinct, narrow process at the anterior end of the vomer extends toward the premaxillary but does not touch that bone; rather, it is appressed against the ventral surface of the nasal capsule and follows that structure to curve upwards at its anterior tip. Immediately medial and anterior to the internal naris, the body of the vomer is strengthened by a dorsal bony ridge that is apparently unique among bolitoglossine salamanders. The large, stout, but relatively short, preorbital process falls far short of the lateral margin of the vomerine body. The process is blunt tipped, and it has a dorsal dimension that is very unusual in that it seems to become continuous with the antorbital cartilage. The vomerine teeth are borne in a single curving row along the base of the vomer body and nearly to the tip of the preorbital process. The bicuspid teeth are about the size of the maxillary teeth.

Frontals are well developed and articulate firmly with each other middorsally, except at their anterior end. The posterior part of each bone is a large, broad lobe that broadly overlaps the parietal. A small, anterior lobe of the parietal abuts the lateral margins of the posterior lobe of the frontal but does not significantly overlap the frontal. The facial portion of the frontal is rather poorly developed. Anteriorly, the frontal is drawn into a narrow point lying ventral or lateral to the frontal processes of the premaxillary.

The parietals are large bones, firmly articulated to each other and to all surrounding bones. The stout, well-developed lateral spurs extend anteroventrally, overlapping the cartilaginous insertion of the ascending process of the palatoquadrate cartilage into the braincase. The semicircular canals produce prominent bulges in the relatively large otic capsules. A small but prominent spinous process is present at the extreme lateral margin of each capsule. A fibrous mass of connective tissue extends from this process to the quadrate. The squamosal lies in a distinct depression in the lateral wall of the capsule. The large parasphenoid is relatively broad and blunt-tipped anteriorly; the orbitosphenoids are relatively widely separated. Posterior vomerine teeth are in two bilateral patches that diverge posteriorly. The patches in two males contain 36–39 and 44–48 small, bicuspid teeth, respectively. The operculum has no stilus, although a slight protrusion is present. The well-developed quadrate is attached to the otic capsules by relatively large, strong squamosals. A small process extends posteriorly from the squamosal and is connected by a ligament to the proximal tip of the ceratohyal.

The lower jaw is rather weak. The prearticular is relatively large, but low, and the dentary is very slender. The arc of the lower jaw is relatively flat and broad.

The hyobranchial apparatus is typical of that of generalized members of the supergenus *Bolitoglossa* in being cartilaginous and lacking a urohyal (Fig. 6). The rather slender ceratohyals have a discrete and well-developed medial process. The very narrow anterior process is drawn into a point that extends upward into the sublingual fold. The long and slender epibranchials are slightly more than twice the length of the basibranchial. The basibranchial is slightly less than twice the length of the second ceratobranchial. The second ceratobranchials are much stouter than the slender first ceratobranchials. The first ceratobranchials are relatively well developed in comparison with those of other tropical plethodontids. The radii of the first basibranchial are continuous with the main part of the element, and there is no sign of a fibrocartilage joint. The broad-based and relatively short radii are joined by a distinct connective tissue strand. The most distinctive feature of the entire hyobranchial apparatus is the very well-developed anterior projection that is unique among the tropical genera (Figs. 2, 6). This broad-based and relatively stout projection is apparently somewhat flexible, for the cartilage cells at its base are surrounded by less intercellular matrix than are the cells either proximal or distal to it. This process apparently represents a primitive condition and is reminiscent of the process seen in *Ensatina* (Lombard and Wake, 1977), although the process in *Ensatina* is less continuous with the basibranchial. The anterior basibranchial process is clearly a less-derived homologue of the lingual cartilage that is present in many tropical plethodontids.

The vertebral column consists of relatively stout vertebrae, with well-developed centra. There are one cervical, fourteen trunk, one sacral, two caudosacral, and a varying number of caudal vertebrae (from 20 to 26 in individuals having complete tails). The atlas has no special features, but the neural arch is barely completed in both cleared and stained adults. The first trunk vertebra is distinctly shorter than the remaining vertebrae and has a high, well-developed neural crest. Lower crests are present on the next few trunk vertebrae. The centrum is large and may be largely filled with mineralized cartilage, for only the terminal concavities are clearly filled by unmineralized intervertebral cartilage. All trunk vertebrae have well-developed, separated, pointed processes (hyperapophyses) on the posterior border of the neural arch. The nerve route pattern is typical of bolitoglossine salamanders (Edwards, 1976): the first trunk vertebra has a single foramen in front of the transverse processes, the second has single foramina both in front of and behind the transverse processes, and the third and succeeding vertebrae (to the end of the tail) have single foramina behind the transverse processes. The transverse processes of the trunk vertebrae are well developed. The dorsal and ventral rib bearers are separated for their entire lengths. The long, relatively straight processes extend beyond the lateral margins of the zygapophyses. They are sharply angled posteriorly in the first few vertebrae but are nearly perpendicular to the column over most of its length. The dorsal bearer is immediately dorsal to the ventral bearer, but it tends to be slightly more posteriorly oriented. Moderately long ribs with distinctly separated heads are present on all but the last trunk vertebra. Transverse processes of the first caudosacral vertebra are stout and blunt-ended and are swept somewhat posteriorly. Transverse processes of the second caudosacral vertebra are short, stout, and blunt-ended; they are nearly perpendicular to the column or are slightly anteriorly oriented. The first caudal vertebra is short and is associated with a distinctly constricted tail base. The relatively short transverse processes located at the extreme anterior end of the centrum are sharply oriented in an anterior direction. The transverse processes of succeeding caudal vertebrae are progressively shorter and barely exceed the anterior zygapophyses in length; they are borne on the extreme anterior end of each vertebra, at the base of the zygapophyses. The sharply tapered tail is deep as a result of a thick glandular layer lying dorsal to the vertebral column but is relatively narrow. Caudal vertebrae generally lack neural crests, although there may be low and irregularly formed crests on the first one or two vertebrae; however, the caudal vertebrae have very well-developed hyperapophyses.

The small hands and feet are highly distinctive (Fig. 4). They are very reduced in size and have relatively little ossified tissue. The digits are fused to one another for most of their lengths but are free at their tips. Indeed, the digits are so poorly developed that it is somewhat artificial to present a phalangeal formula. Some phalanges are entirely cartilaginous, others may have a tiny speck of ossified tissue, and only the proximal phalanx of the longest finger and toe is consistently well ossified. An unusual feature is the cartilaginous tip of many terminal phalanges. In other plethodontid salamanders, these tips are well ossified and often specialized in structure. The poor degree of development suggests that *Bradytriton* does not use its limbs for specialized locomotory activity. A few individuals can be scored as having a phalangeal formula of 1, 2, 3, 2, for the hand and 1, 2, 3, 3, 2, for the foot, based on the presence of tiny specks of radio-opaque material visible in radiographs. Even the metapodial elements, which are cylindrical in shape, are small and poorly ossified, and the first digit of the hand has an especially small element. As a result of the fusion of the ulnare and intermedium, there are seven carpals; similarly, there are eight tarsals as a result of the fusion of distal tarsals 4 and 5. A distinct spur projects from the shank of the tibia for nearly its entire length, and there is a low but distinct tibial crest.

RANGE. *Bradytriton silus* is known only from the immediate vicinity of the type locality on the eastern slopes of the Sierra de los Cuchumatanes in extreme northwestern Guatemala.

ETYMOLOGY. From *silus,* L. for "pug-nosed" referring to the characteristic truncated appearance of the snout.

GENERIC SYNOPSES

Bolitoglossa Duméril, Bibron, and Duméril

Oedipus Tschudi
Eladinea Miranda-Ribeiro
Magnadigita Taylor
Palmatotriton Smith

TYPE SPECIES. *Bolitoglossa mexicana* Duméril, Bibron, and Duméril.

DIAGNOSTIC CHARACTERS. Small to very large salamanders with partially to fully webbed hands and feet, distinguished from members of all other tropical salamander genera in lacking a sublingual fold.

REFERRED SPECIES. *Bolitoglossa adspersa* (Peters); *B. altamazonica* (Cope); *B. alvaradoi* Taylor; *B. arborescandens* Taylor; *B. biseriata* Tanner; *B. borburata* Trapido; *B. capitana* Brame and Wake; *B. cerroensis* Taylor; *B. chica* Brame and Wake; *B. colonnea* (Dunn); *B. compacta* Wake, Brame, and Duellman; *B. cuchumatana* (Stuart); *B. cuna* Wake, Brame, and Duellman; *B. dofleini* (Werner); *B. dunni* (Schmidt); *B. engelhardti* (Schmidt); *B. epimela* Wake and Brame; *B. equatoriana* Brame and Wake; *B. flavimembris* (Schmidt); *B. flaviventris* (Schmidt); *B. franklini* (Schmidt); *B. hartwegi* Wake and Brame; *B. helmrichi* (Schmidt); *B. hypacra* (Brame and Wake); *B. lignicolor* (Peters); *B. lincolni* McCoy and Walker; *B. macrinii* (Lafrentz); *B. marmorea* (Tanner and Brame); *B. medemi* Brame and Wake; *B. meliana* Wake and Lynch; *B. mexicana* Duméril, Bibron and

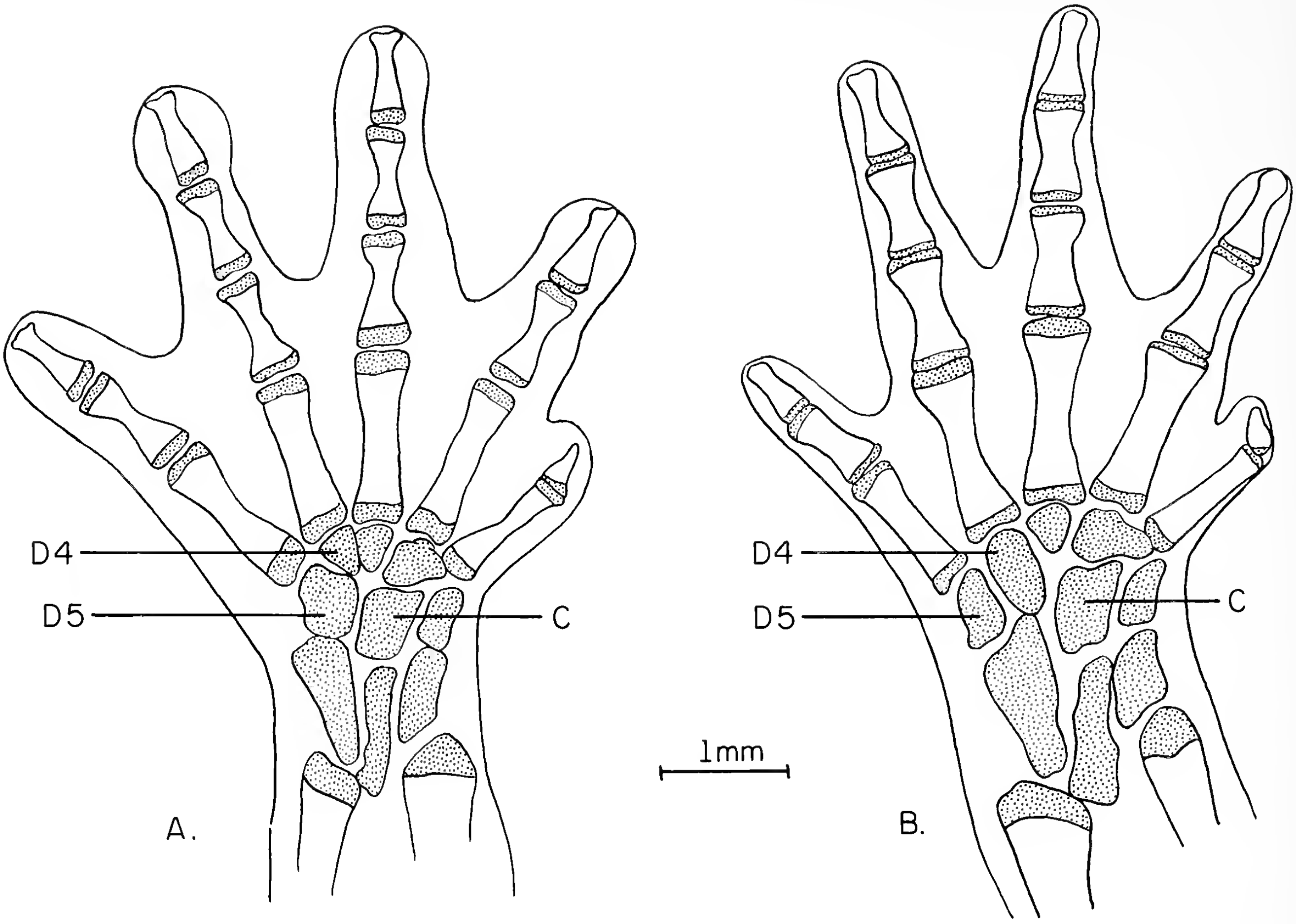

Figure 7. Feet of *Chiropterotriton* and *Pseudoeurycea*.

A. Left foot of an adult *Chiropterotriton multidentatus* (39.6 mm SL) from Hidalgo, Mexico. Cartilage is stippled. Note that distal tarsal 5 is larger than distal tarsal 4 and articulates with the centrale. This arrangement is unique to *Chiropterotriton* within the supergenus *Bolitoglossa*.

B. Left foot of an adult *Pseudoeurycea leprosa* (53.9 mm SL) from Veracruz, Mexico. Cartilage is stippled. Note that distal tarsal 5 is smaller than distal tarsal 4 and that it does not articulate with the centrale; this is the primitive pattern in plethodontid salamanders. The foot of this species is relatively much smaller than that of *C. multidentatus*, for although the feet as illustrated are about the same size, the specimen of *Pseudoeurycea* is much larger. Note that the fifth toe is smaller in *Pseudoeurycea* than in *Chiropterotriton*.

Duméril; *B. minutula* Wake, Brame, and Duellman; *B. morio* (Cope); *B. mulleri* (Brocchi); *B. nicefori* Brame and Wake; *B. occidentalis* Taylor; *B. odonnelli* (Stuart); *B. orestes* Brame and Wake; *B. palmata* (Werner); *B. pandi* Brame and Wake; *B. peruviana* (Boulenger); *B. phalarosoma* Wake and Brame; *B. platydactyla* (Gray); *B. ramosi* Brame and Wake; *B. resplendens* McCoy and Walker; *B. riletti* Holman; *B. robusta* (Cope); *B. rostrata* (Brocchi); *B. rufescens* (Cope); *B. salvinii* (Gray); *B. savagei* (Brame and Wake); *B. schizodactyla* Wake and Brame; *B. schmidti* (Dunn); *B. silverstonei* Brame and Wake; *B. sima* (Vaillant); *B. sooyorum* Vial; *B. striatula* (Noble); *B. stuarti* Wake and Brame; *B. subpalmata* (Boulenger); *B. taylori* Wake, Brame, and Myers; *B. vallecula* Brame and Wake; *B. veracrucis* Taylor; *B. walkeri* Brame and Wake; *B. yucatana* (Peters).

RANGE. *Bolitoglossa* has by far the widest range of any of the tropical salamander genera. It occurs almost continuously from the lowlands of eastern San Luis Potosi, Mexico, in the north, south to the Amazonian lowlands of southern Peru, the mountains near Cochabamba, Bolivia, and southern Minas Gerais, Brazil.

COMMENT. Many species have been added to this large genus during the past two decades, but no revisionary study has been undertaken. A number of undescribed species are known to us. We here place *Bolitoglossa omniumsanctorum* in the synonymy of *B. morio* on the basis of close similarity of the type specimens of *B. omniumsanctorum* to specimens of *B. morio* in size, form, and coloration.

Wake and Brame (1969) and Wake and Lynch (1976) discussed a possible subdivision of this large, cumbersome genus. Wake and Lynch (1976) referred to "alpha" and "beta" sister groups and suggested that these might eventually be recognized as separate genera. The beta group is defined on the basis of an apomorphic character, a tail base specialization (Wake and Dresner, 1967). Members of the alpha group frequently have osteological reductions and foot specializations, but we know of no apomorphic character or combination of characters that would unambiguously define the alpha group. These diagnostic problems, combined with the absence of marked ecological or phenetic differentiation between the two groups, lead us to postpone formal division.

Bradytriton new genus

TYPE SPECIES. *Bradytriton silus* new species.

DIAGNOSTIC CHARACTERS. This is a short-snouted, stout-bodied salamander with small limbs and small, syndactylous hands and feet. It differs from all other tropical salamander genera in having a laterally compressed tail with a well-developed dorsal glandular ridge.

REFERRED SPECIES. *Bradytriton silus* new species.

RANGE. The unique species is known only from the immediate vicinity of the type locality on the northeastern slopes of the Sierra de los Cuchumatanes in northwestern Guatemala.

Chiropterotriton Taylor

TYPE SPECIES. *Oedipus multidentatus* Taylor.

DIAGNOSTIC CHARACTERS. Small to moderately large salamanders with relatively broad, partially webbed hands and feet and broad-tipped fingers and toes. *Chiropterotriton* differs from all other tropical salamander genera in its arrangement of tarsal cartilages: in *Chiropterotriton,* distal tarsal five is larger than distal tarsal four and articulates with the centrale; in other genera, four is larger than five, and five is excluded from articulation with the centrale (Fig. 7).

REFERRED SPECIES. *Chiropterotriton arboreus* (Taylor); *C. chiropterus* (Cope); *C. chondrostega* (Taylor); *C. dimidiatus* (Taylor); *C. lavae* (Taylor); *C. magnipes* Rabb; *C. mosaueri* (Woodall); *C. multidentatus* (Taylor); *C. priscus* Rabb.

RANGE. The genus is restricted to eastern Mexico, from west-central Tamaulipas in the north to the mountains of northern Oaxaca in the south.

COMMENT. Most species of this genus have been studied in some detail by Rabb (1955, 1958, 1965). The major unstudied unit is that comprising *C. chiropterus* and *C. lavae.*

Dendrotriton new genus

TYPE SPECIES. *Oedipus bromeliacia* Schmidt.

DIAGNOSIS. Small, slender, long-tailed, arboreal salamanders with long legs, broad hands and feet, and long, broad-tipped digits. *Dendrotriton* differs from *Oedipina* by its short trunk (14 vs. 18 or more trunk vertebrae) and long limbs; from *Nyctanolis* in having a single premaxillary; from *Chiropterotriton* in having a larger fourth than fifth tarsal; from *Bolitoglossa* in possessing a sublingual fold; from *Bradytriton, Nototriton, Parvimolge, Oedipina* and *Thorius* by its lack of carpal and tarsal fusions; from *Lineatriton* by its short vertebrae and long legs; and from *Pseudoeurycea* by its lack of prefrontals and tibial spurs.

REFERRED SPECIES. *Chiropterotriton bromeliacia* (Schmidt); *C. cuchumatanus* Lynch and Wake; *C. megarhinus* Rabb; *C. rabbi* Lynch and Wake; *C. xolocalcae* (Taylor).

ETYMOLOGY. From *dendron,* Gr. for tree, referring to the arboreal habits of all known species, and *triton,* Gr., a commonly used term for salamanders.

RANGE. Southwestern Chiapas, Mexico, through western Guatemala.

COMMENT. This group has recently been studied in detail by Lynch and Wake (1975), who presented photographs of all five species.

Lineatriton Tanner

TYPE SPECIES. *Spelerpes lineolus* Cope.

DIAGNOSTIC CHARACTERS. A very slender, elongate, fossorial form with diminutive limbs, hands and feet, and an extremely long tail. *Lineatriton* is distinguished from all other tropical salamander genera in having very elongated, narrow vertebrae. *Oedipina* has a similar body form and ecology but differs from *Lineatriton* in having 18 or more, rather than 14, trunk vertebrae.

REFERRED SPECIES. *Lineatriton lineola* (Cope).

RANGE. *Lineatriton* is restricted to two disjunct areas of the Gulf slope of Mexico: along the lower slopes of the mountains of west-central Veracruz and the area around Los Tuxtlas in eastern Veracruz.

COMMENT. This is one of the most distinctive of the tropical genera and is apparently monotypic. It has been little studied since the work of Tanner (1950).

Nototriton new genus

TYPE SPECIES. *Spelerpes picadoi* Stejneger.

DIAGNOSIS. Small, long-tailed salamanders of arboreal, terrestrial, or semifossorial habitats. The species have moderately long to short legs and small hands and feet. The intermedium and ulnare of the manus and distal tarsals four and five of the pes are fused. The genus is distinguished from other genera with similar fusions as follows: from *Oedipina* by having only 14 rather than 18 or more trunk vertebrae; from *Bradytriton* by having a long, slender tail and slender body; from *Parvimolge* by having the tail longer than the body, by having frontal processes fused together at their base (all species but *richardi*), and by lacking mesopodial and hyobranchial mineralizations; from *Thorius* by having a complete skull roof over the brain case; from *Bolitoglossa* by having carpal fusions and a sublingual fold.

REFERRED SPECIES. *Chiropterotriton barbouri* (Schmidt); *Bolitoglossa diminuta* Robinson; *Chiropterotriton nasalis* (Dunn); *C. picadoi* (Stejneger); *C. richardi* (Taylor); *C. veraepacis* Lynch and Wake.

ETYMOLOGY. From *notos,* L., referring to the southerly distribution of the genus, and *triton,* L., Gr., a commonly used term for salamanders.

RANGE. *Nototriton* ranges from eastern Guatemala to the Meseta Central of Costa Rica.

COMMENT. Most of *Nototriton* consists of what has been called the *picadoi* group (Wake and Lynch, 1976) or the *nasalis* group (Lynch and Wake, 1978) of *Chiropterotriton*. The species *richardi* may not be referable to this genus; it was originally described as a member of the genus *Parvimolge* and has been considered problematic by Rabb (1955), Wake (1966), Wake and Lynch (1976), and Lynch and Wake (1978). It is more appropriately placed in *Nototriton* than elsewhere, but it differs from other members of the genus in possessing an unusual combination of ancestral and derived characters (Lynch and Wake, 1978). Table 2 was constructed by ignoring *N. richardi*, but we have nonetheless tentatively assigned the species to this genus because it does not come as close to fitting into any other genus. Further, we are reluctant to establish a new genus for such a poorly known form.

The species described as *Bolitoglossa diminuta* by Robinson (1976) is also most appropriately placed in *Nototriton*. Radiographs of the holotype reveal that it has frontal processes of the premaxillary that are fused, and it has a very long tail for its small body size (53% of total length). It was reported to lack a sublingual fold, and we have been unable to see one; however, the holotype, a mature female, is very small (31.1 mm SL), and it may be impossible to determine the status of this character without histological sections. *Nototriton richardi* has a very reduced sublingual fold. It was on the basis of the apparent absence of this fold in the holotype of *B. diminuta* that the senior author urged Robinson to describe the species as a *Bolitoglossa*, even though Robinson had originally intended to place it in the genus *Chiropterotriton*.

Nyctanolis Elias and Wake

TYPE SPECIES. *Nyctanolis pernix* Elias and Wake.

DIAGNOSTIC CHARACTERS. This is a large, long-legged, long-fingered, long-toed, long-tailed taxon that differs from all other tropical salamander genera in having paired premaxillary bones.

REFERRED SPECIES. *Nyctanolis pernix* Elias and Wake.

RANGE. The unique species is known from the northeastern slopes of the Sierra de los Cuchumatanes in NW Guatemala; near the Lagos de Montebello in nearby Chiapas, Mexico; and from the Sierra de las Minas in eastern Guatemala.

Oedipina Keferstein

Oedipina Keferstein
Ophiobatrachus Gray
? *Haptoglossa* Cope
Oedopinola Hilton

TYPE SPECIES. *Oedipina uniformis* Keferstein.

DIAGNOSTIC CHARACTERS. Slender, elongate salamanders of moderate to large size with very small limbs, hands, and feet, and a very long tail. *Oedipina* is distinguished from all other tropical salamander genera, including *Lineatriton*, the only genus that resembles it externally, by having 18 to 22 (rather than 14) trunk vertebrae.

REFERRED SPECIES. *Oedipina alfaroi* Dunn; *O. altura* Brame; *O. carablanca* Brame; *O. collaris* (Stejneger); *O. complex* (Dunn); *O. cyclocauda* Taylor; *O. elongata* (Schmidt); *O. grandis* Brame and Duellman; *O. ignea* Stuart; *O. parvipes* (Peters); *O. paucidentata* Brame; *O. poelzi* Brame; *O. pseudouniformis* Brame; *O. stuarti* Brame; *O. taylori* Stuart; *O. uniformis* Keferstein.

RANGE. *Oedipina* ranges from south-central Chiapas, Mexico, through all of Central America and western Colombia to northwestern Ecuador.

COMMENT. This is an exceptionally well-defined genus. Since the revision by Brame (1968), only one additional species, *O. grandis*, has been described, and there have been no other taxonomic changes.

Parvimolge Taylor

TYPE SPECIES. *Oedipus townsendi* Dunn.

DIAGNOSTIC CHARACTERS. Diminutive salamanders with relatively stocky bodies, short legs with small hands and feet, and short, stout tails. It is distinguished from other genera with small species as follows: from *Bolitoglossa* in having a sublingual fold; from *Dendrotriton* and *Chiropterotriton* in having distal tarsals four and five fused and the intermedium and ulnare fused; from *Nototriton* in having a short tail and lacking fused frontal processes of the premaxillary; from *Thorius* in having a complete skull roof over the braincase.

REFERRED SPECIES. *Parvimolge townsendi* (Dunn).

COMMENT. Two other species, *praecellens* and *richardi*, have been included in the genus. Neither seems to be closely related to *townsendi*, and we here refer them to the genera *Pseudoeurycea* and *Nototriton*, respectively.

Pseudoeurycea Taylor

TYPE SPECIES. *Spelerpes leprosus* Cope.

DIAGNOSTIC CHARACTERS. A diverse group of moderate-sized to very large salamanders with moderate to long limbs, well-developed hands and feet in which the middle digits are markedly longer than the outer ones (Fig. 7), and a tail about as long as the body. The species are very generalized in morphology. The genus differs from *Nyctanolis* in having a single premaxillary and shorter limbs and tail; from *Dendrotriton* in having prefrontals and tibial spurs; from *Bolitoglossa* in having a sublingual fold; from *Chiropterotriton* in having a fourth distal tarsal that articulates with the fibulare and is larger than the fifth (Fig. 7); from all other genera in having separate distal tarsals four and five.

REFERRED SPECIES. *Pseudoeurycea altamontana* (Taylor); *P. anitae* Bogert; *P. bellii* (Gray); *P. brunnata* Bumzahem and Smith; *P. cephalica* (Cope); *P. cochranae* (Taylor); *P. conanti* Bogert; *P. exspectata* Stuart; *P. firscheini* Shannon and Werler; *P. gadovii* (Dunn); *P. galeanae* (Taylor); *P. goebeli* (Schmidt); *P. juarezi* Regal; *P. leprosa* (Cope); *P. melanomolga* (Taylor); *P. mystax* Bogert; *P. nigromaculata* (Taylor); *P. praecellens* (Rabb); *P. rex* (Dunn); *P. robertsi* (Taylor); *P. scandens* Walker; *P. smithi* (Taylor); *P. unguidentis* Smith and Taylor; *P. werleri* Darling and Smith.

RANGE. The genus ranges from eastern Sonora, Mexico, in the northwest, and west-central Tamaulipas, Mexico, in the northeast, through most of eastern and south-central Mexico into western and southern Guatemala.

COMMENT. Few characters bind this assemblage of generalized species together. The genus lacks any autapomorphies and is mainly defined by exclusion. A few species stand out from the rest as distinct morphological entities (e.g., *P. bellii, P. praecellens, P. werleri*). The *gadovii, rex,* and *leprosa* groups are the core of the genus and appear to be closely interrelated (Maxson and Wake, 1981). We here assign *praecellens* to *Pseudoeurycea.* Rabb (1955) placed it in the genus *Parvimolge* with some hesitation. It differs from *P. townsendi* in that it is larger and stouter and has prefrontal bones. Rabb (1955) reported that *P. praecellens* had some mineralization of the hyobranchial apparatus, as in *P. townsendi*; however, we have been unable to see this feature in our radiographs of the unique holotype. The species fits reasonably well in *Pseudoeurycea,* and Rabb suggested that it might prove to be a relative of *P. cephalica.*

Thorius Cope

TYPE SPECIES. *Thorius pennatulus* Cope.

DIAGNOSTIC CHARACTERS. Diminutive, slender salamanders with short limbs and small hands and feet. *Thorius* is distinguished from all other tropical salamanders by two characters: the suborbital groove intersects the lip, and the skull is incompletely ossified, leaving the braincase uncovered by bone (the parietal bones have an especially large gap separating them).

REFERRED SPECIES. *Thorius dubitus* Taylor; *T. macdougalli* Taylor; *T. maxillabrochus* Gehlbach; *T. minutissimus* Taylor; *T. narisovalis* Taylor; *T. pennatulus* Cope; *T. pulmonaris* Taylor; *T. schmidti* Gehlbach; *T. troglodytes* Taylor.

RANGE. The genus ranges from the eastern margins of the Mexican Plateau into the mountains of northern and central Oaxaca, and in the Sierra Madre del Sur of southern Oaxaca and Guerrero, Mexico.

COMMENT. The genus has recently been studied in detail by Freeman (1977) and Hanken (1980), but the taxonomic results of these unpublished theses are not yet available. All of the described species (except perhaps *T. maxillabrochus*) are valid, but there are numbers of additional undescribed species.

DISCUSSION

The supergenus *Bolitoglossa* was redefined by Elias and Wake (1983) on the basis of hyobranchial and tail base characteristics. All genera considered here have the features of the supergenus. Our main departure from Wake (1966) is that two formerly diagnostic features are deemphasized. First, *Nyctanolis* has two premaxillary bones; thus, the supergenus *Bolitoglossa* can no longer be characterized by the presence of a single, fused bone. Second, *Nyctanolis* and some species of *Pseudoeurycea* have a lateral parietal spur that is only poorly developed: in *Nyctanolis* the spur may be little more than a low ridge on the underside of the bone, and in some *Pseudoeurycea* the "spur" is really only a small lateral lobe. Still, at least some form of parietal "spur" is present in all members of the supergenera *Batrachoseps* and *Bolitoglossa.*

With the new genera, the supergenus *Bolitoglossa* includes 11 genera. *Nyctanolis, Bradytriton, Parvimolge,* and *Lineatriton* are monotypic; the other genera include from five (*Dendrotriton*) to over sixty (*Bolitoglossa*) species. Additional undescribed species that are known to us will increase the number of species in such large genera as *Bolitoglossa, Pseudoeurycea,* and *Thorius* but will not affect the monotypic genera.

The genera *Bolitoglossa, Lineatriton, Oedipina, Pseudoeurycea,* and *Thorius* are essentially unchanged by our analysis. The content of *Parvimolge* is reduced to a single species by transfer of the species *praecellens* to *Pseudoeurycea.* The genus most strongly affected is *Chiropterotriton.* As a result of the shift of the old *bromeliacia* species group (Lynch and Wake, 1975) to the new genus *Dendrotriton* and of the old *picadoi* (Wake and Lynch, 1976) or *nasalis* (Lynch and Wake, 1978) species group to the new genus *Nototriton, Chiropterotriton* has been reduced to a group of nine species that inhabit eastern Mexico. The species formerly known as *Bolitoglossa diminuta* is included in *Nototriton.* The other two new genera, *Nyctanolis* and *Bradytriton,* are based on newly discovered species.

Hecht and Edwards (1976a, 1976b) and Hecht (1976) discuss the relative information content of different types of shared derived character states (synapomorphies) for the reconstruction of phylogeny. Ordered by increasing significance (basically, the degree of confidence one has in their interpretation) in phylogenetic reconstruction are five classes of synapomorphies:

"(I) Shared and derived character states which are the result of loss. Such loss characters are the zero state because there is no developmental evidence.
(II) Shared and derived character states which are the results of simplification or reduction of complex structures as indicated by comparative or developmental anatomy.
(III) Shared and derived character states which are the result of growth and developmental processes dependent on size, age, and hormonal and other physiological relationships. Characters related to allometric functions are the best examples.
(IV) Shared and derived character states which are highly integrated functionally and are subject to directional selection.
(V) Shared and derived character states which are unique and innovative in structure (the most important type of information)." (From Hecht and Edwards, 1976a.)

Our analysis in this paper is based on the 18 characters outlined earlier. The apomorphic characters we have chosen include seven that are autapomorphic (Table 1). These are not useful in phylogenetic analysis but are included because they aid in diagnosing genera. The 11 remaining characters vary in degree of utility. Six involve morphological transformation, and five involve losses of elements. We interpret our loss characters as falling into the third category of Hecht and Edwards (1976) rather than the first, for we have some ontogenetic information concerning the way in which four of the five characters are lost. We believe that loss of septomaxillaries, prefrontals, preorbital processes of vomers, and columellae (or stylar processes of the opercula) are all paedomorphic characters (Lynch and Wake, 1978; Alberch et al., 1979; Alberch and Alberch, 1981; Elias, in press), but whether they should all be counted as independent characters or considered to be parts of a single "global" paedomorphic process is unresolved.

The six remaining characters (1, 3, 4, 5, 10, 11) all involve transformations. Characters 10 and 11 relate to ontogenetic phenomena and fall into Hecht and Edwards's third category. Transformation characters 1, 3, 4, and 5 are parts of integrated, functionally significant systems; they fall in the fourth category of Hecht and Edwards.

Other authors have used additional characters in generic diagnoses of tropical salamanders. Some of these characters (e.g., a posteriorly directed spur on the squamosal in *Thorius*) are autapomorphies and of little use in phylogenetic analysis. Others occur in all members of one genus but also appear irregularly in one or a few species in some other genera (e.g., the complex tail base present in some *Pseudoeurycea*). Other characters, such as the shape and degree of ossification of the intervertebral articulation (used by Taylor, 1944), are subject to extreme ontogenetic variation (Wake, 1970), and we have not had sufficient material to perform a complete analysis. Still other characters, such as external shape of hands and feet, shape of terminal digits, length of ribs, and fusion or nonfusion of transverse processes, have proven impossible to codify consistently for all neotropical species, but these may well have utility for finer analysis of intra- and intergeneric relationships in the future. The hyobranchial apparatus (features of the tip of the first basibranchial, including length and shape of radii and detailed structure of the lingual cartilage and associated musculature) holds much promise as a source of additional characters (Tanner, 1952; Lombard and Wake, 1977). However, this structure requires detailed histological study, and we have examined too few species to discern broad patterns. Future studies should involve comparative ontogenetic analyses, for heterochronic modes of evolution have been strongly implicated in salamanders (Wake, 1966; Alberch et al., 1979; Alberch and Alberch, 1981).

Biochemical, immunological, and cytological characters are useful in analyzing phylogenetic relationships in the supergenus *Bolitoglossa*. Recently Maxson and Wake (1981) used immunological approaches to study albumin evolution in *Pseudoeurycea* and *Chiropterotriton* (*sensu lato*). Extensive evolution of albumin has taken place in these groups, and immunological methods will be most useful at the intrageneric level of comparison. In reference to the present generic review, the principal result of interest from the immunological work is the finding that *Chiropterotriton* (antisera from *C. multidentatus*) and *Dendrotriton* (antisera from *D. bromeliacia*) are more similar to *Pseudoeurycea* (antisera from five species) than they are to each other. This finding corroborates our conclusion that the two genera are distinct. No antisera were prepared for species of *Nototriton*, but one-way tests were made to some species of the genus. Immunological distances between species of *Chiropterotriton* and *Dendrotriton* are about equivalent to those between *Chiropterotriton* and *Nototriton*, but immunological distances between *Dendrotriton* and *Nototriton* are considerably less. Distances within *Dendrotriton* (maximum 21) are much less than between *Dendrotriton* and *Nototriton* (minimum 64).

Some data on chromosomes are available (Leon and Kezer, 1978; J. Kezer and S. Sessions, pers. comm.). All members of the supergenus *Bolitoglossa* so far examined have a haploid chromosome number of 13, as do members of the genus *Batrachoseps*. All other plethodontids examined have a haploid number of 14. The species of *Dendrotriton* (*D. bromeliacia, D. cuchumatanus, D. rabbi*) and *Nototriton* (*N. picadoi, N. veraepacis*) so far examined have a distinct heteromorphism (presumably XY) in the thirteenth pair of chromosomes. This pattern has been found in some species of *Thorius* and *Oedipina* but not in *Chiropterotriton, Pseudoeurycea, Lineatriton, Bolitoglossa,* or *Parvimolge* (chromosomes of *Nyctanolis* and *Bradytriton* have not been examined). These data lend further support to our decision to separate *Dendrotriton* and *Nototriton* from *Chiropterotriton*.

From the 18 characters analyzed we are unable to conclusively demonstrate the monophyletic status of 3 of the 11 bolitoglossine genera: *Dendrotriton, Nototriton,* and *Pseudoeurycea* (Table 1). A genus appearing in Table 1 must have at least one apomorphic character (a synapomorphy for the species of the genus) that is not shared with any other given genus in order for us to consider it to be monophyletic.

All of the apomorphies shown for *Dendrotriton* in Table 1 are shared with *Oedipina*; nevertheless, in other characters, which proved impossible to score for all neotropical genera, *Dendrotriton* shows derived states not found in *Oedipina*. Species of *Dendrotriton*, all of which are arboreal, show such derived features as relatively long legs, with long, well-developed digits and expanded terminal phalanges. *Oedipina*, all of which are semi- to fully fossorial, have very short legs, with short, erratically developed digits and unspecialized phalanges. The limb states of the two genera are derived in opposite directions from the ancestral state. Thus, despite the absence of defining synapomorphies in our formal tabulation, we consider *Dendrotriton* to be a well-defined, monophyletic assemblage.

The situation with *Pseudoeurycea* is far more complex. This genus is something of a "waste-basket," notwithstanding arguments of Baird (1951) to the contrary. It has only a single apomorphy (fused premaxillaries, character 11, Table 1), and this is shared with all genera of the supergenus except *Nyctanolis*. All of the other genera are easily distinguished from *Pseudoeurycea* on the basis of a variety of synapomorphies and autapomorphies. The species of *Pseudoeurycea* are relatively diverse in external structure and behavior but are basically similar in their generalized osteology, such that there is no clear osteological basis for subdividing the genus into monophyletic assemblages. The generotype is *P. leprosa*; it and some allied species have a plesiomorphic character (septomaxillary bones) and an apomorphic character (a complex tail base, not coded here, but rather similar to the tail base seen in *Bolitoglossa* beta, Wake and Lynch, 1976). It may eventually be possible to formally recognize this group taxonomically, but the remaining species in the present genus *Pseudoeurycea* would still constitute a very disparate assemblage. Maxson and Wake (1981) have shown that species of *Pseudoeurycea* are greatly divergent in albumin structure. One group that is not well defined morphologically can be defined reasonably well on a biochemical basis (the combined *gadovii* and *rex* groups of Wake and Lynch, 1976, together with some members of other groups). However, an electrophoretic analysis in progress (Yang and Wake, unpublished data) discloses that most species are very distinct from one another and that groups of species are not readily apparent. *Pseudoeurycea* may be a paraphyletic taxon, the members of which have retained relatively conservative morphologies. In this respect, the genus presents a taxonomic problem similar to that encountered in the genus *Plethodon* (Larson et al., 1981), another taxon based largely on plesiomorphic characteristics. We do not think that *Pseudoeurycea*, as presently constituted, represents the remnants of the ancestral stock of all tropical salamanders, for in many respects members of *Nyctanolis* and *Chiropterotriton* are more generalized osteologically. For example, *C. priscus* has relatively large, well-developed septomaxillary bones, primitive elements that occur only occasionally in the few species of *Pseudoeurycea* that have them. Thus, our character scorings must be used cautiously when making phylogenetic interpretations.

Notototriton, although it is readily distinguished from most genera, has no apomorphies that are not shared with *Oedipina*. This situation is superficially similar to the problem of *Dendrotriton* versus *Oedipina*, but the three synapomorphies shared by *Nototriton* and *Oedipina* are a different set. Further, unlike *Dendrotriton*, *Nototriton* may be a paraphyletic group that includes lineages of a pre-*Oedipina* stock (see Lynch and Wake, 1978). For example, *N. richardi*, a poorly known species of which fewer than ten specimens have been collected, appears to be more primitive than other *Nototriton* in some respects but more derived in others. It could be placed in *Oedipina*, but it lacks an increased number of trunk vertebrae (character 17), the synapomorphy that most strongly distinguishes the species of *Oedipina* from all other tropical plethodontids. The remaining species of *Nototriton* form a well-defined assemblage (see Lynch and Wake, 1978). As recognized here, *Nototriton* is a diverse group consisting of several rare, secretive, and poorly known species. At this time we are unable either to define autapomorphies for the genus or to subdivide it into clearly monophyletic sublineages. By joining *Oedipina* and *Nototriton* to form a single genus, we could claim monophyly for the group as a whole, but this would severely blur the limits of the present genus *Oedipina*, one of the most tightly knit, well-diagnosed, and highly apomorphic genera of salamanders. Species of *Nototriton* share a number of structural and ecological similarities, and they are sharply distinguished from *Oedipina* by the synapomorphies of the latter group. Accordingly, we choose to recognize both *Oedipina* and *Nototriton*, although the latter genus may ultimately not prove to be a monophyletic assemblage.

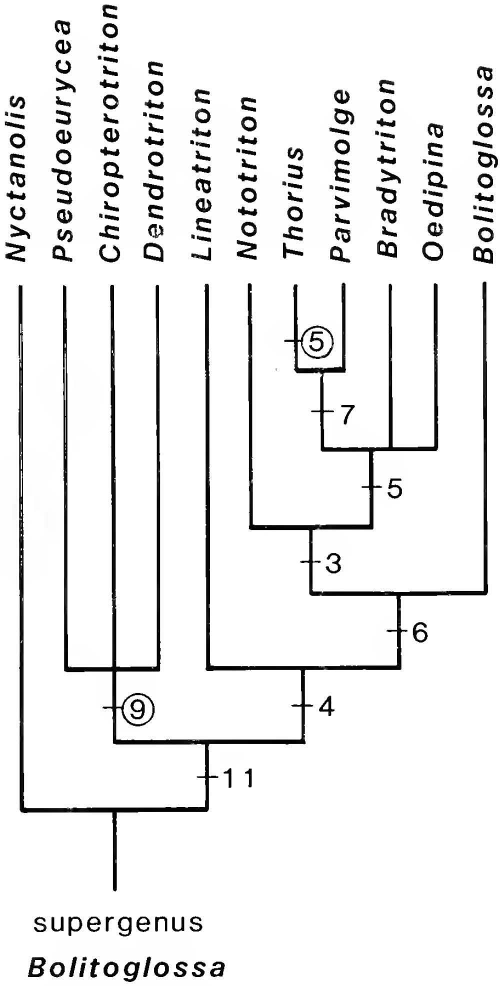

Figure 8. Maximum parsimony cladogram of genera in the tribe Bolitoglossini. The numbered characters (Table 1) are present in their derived condition in all taxa above the point in the dendrogram where the lines occur. Reversals are circled. The tree treats character 9 as if it were a synapomorphy in its reversed form (i.e., resembling the presumed primitive condition). Parallelisms are not illustrated.

We used the data in Table 1 to compute Wagner trees, using the method of cladistic inference by parsimony (Farris, 1970), but with one modification. We fixed the root of the tree *a priori* by declaring *Nyctanolis* to be the first derivative branch. We believe that the premaxillary character is considerably more substantial than any other in the matrix (because it is conservative and relatively well understood; see Wake, 1966), and we accordingly used the rooting method to weight this character heavily. The resulting tree is presented in Figure 8.

There are reasons for questioning the validity of this maximum parsimony tree. Although there are six stems characterized by synapomorphies, two of these are reversed later in the dendrogram. Only three of the six synapomorphic characters (3, 4, 5) are "high-quality" characters, i.e., characters that fall into Hecht and Edwards's (1976a) category 4 and constitute parts of integrated systems. The significance of character 5 is unclear; the long, tubular mental glands of certain of the genera (e.g., *Oedipina, Bradytriton*) are unusual but may represent extreme cases of subtler variation that would require histological documentation. Note that the dendrogram requires a reversal of this character in the stem leading to *Thorius*. It seems more likely that tubular glands have evolved in parallel, a hypothesis that is supported by the observation that some species of the unrelated North American genus *Eurycea* have such glands. Characters 3 and 4 involve fusions of carpals and tarsals. Although these characters may be more complex than those that involve loss of elements, they nevertheless require little more than simple developmental modifications. We know that character 3 has evolved independently in extra-tropical plethodontids (e.g., *Aneides hardii* and some species of *Batrachoseps*; Wake, 1966). However, among plethodontids character 4 (tarsal fusions) appears to be unique to the genera reported here. It is possible that distal tarsals 4 and 5 are fused in *Batrachoseps*, rather than 5 being lost as Wake (1966) has suggested.

Because we have fixed the root of the tree with *Nyctanolis*, character 11 will be a common feature of most possible dendrograms. Characters 6 and 7 fall into Hecht and Edwards's third weighting category, for we have some ontogenetic information concerning them (unpublished and Elias, in press). We think that both characters 6 and 7 reflect parallel evolution, for both characters refer to features that appear relatively late in the development of related species. Character 7 (loss of preorbital processes of the vomer) has evolved independently in some species of *Batrachoseps* (Marlow et al., 1979). Scoring for character 6 (loss of stylus of the operculum) requires a certain degree of subjectivity, because the process, where it appears at all, is invariably very small in members of the supergenus *Bolitoglossa*.

The final significant character in Figure 8 is the presence or absence of septomaxillary bones (character 9). Most members of the supergenus *Bolitoglossa* lack septomaxillaries, and a questionable feature of this tree is that it contains a stem for which the synapomorphy is a postulated reversal (reappearance of septomaxillaries). This reversal unites *Pseudoeurycea, Chiropterotriton*, and *Dendrotriton*, three genera that share no additional synapomorphies and have little else in common. Because the first two of these genera are extensively plesiomorphic, no system of analysis can deal with them easily.

Septomaxillary bones are not well developed in any tropical salamander. They appear regularly in some *Chiropterotriton* (Rabb, 1956; Wake, 1966) but are absent in others (e.g., *C. dimidiatus*). Septomaxillary bones are extremely small and variably present in four of the five species of *Dendrotriton* (Lynch and Wake, 1975, 1978). Septomaxillaries also occur in at least some individuals of several species of *Pseudoeurycea* (*P. cephalica, P. leprosa, P. werleri*, and *P. nigromaculata*) and occasionally in other bolitoglossine genera. Wake (1966) reports their presence in individuals of *Parvimolge townsendi, Oedipina uniformis, Thorius pennatulus*, and three species of *Bolitoglossa*. We hypothesize that tropical salamanders as a group have undergone osteological reduction, and that such reduction may have characterized the ancestral stock. Loss of the septomaxillaries can be interpreted as a manifestation of a general paedomorphic trend in the group (Wake, 1966; Alberch and Alberch, 1981). Because these bones are so well developed in *Chiropterotriton* relative to other members of the supergenus *Bolitoglossa*, we consider it unlikely that a reversal of this character (i.e., re-evolution of septomaxillaries following their loss in an ancestor) has occurred in the genus. *Chiropterotriton* is the only tropical genus in which the presence of septomaxillaries is universal in adults of most species (all but the paedomorphic *C. dimidiatus*). The loss of septomaxillaries in certain *Chiropterotriton* species parallels the loss of the bones in other genera, and the same underlying mechanism could be involved in all cases.

Paedomorphosis is not necessarily a unidirectional process, and some reversals are to be expected. Thus, septomaxillaries may have reappeared in *Dendrotriton* and *Pseudoeurycea*, following their loss in the respective ancestral stocks. The bones occur irregularly even in those species where they are found at all. The rare appearance of septomaxillaries in other genera is likely to be atavistic, i.e., based on a reversal of an original paedomorphic event.

Summarizing our arguments, linkage of *Chiropterotriton, Dendrotriton*, and *Pseudoeurycea* on the basis of a postulated shared reversal of a single character is not warranted. If the septomaxillary character is omitted from the Wagner analysis, the resulting dendrogram includes a stem uniting these same three genera. This time the stem is based on another shared reversal, separation of tarsal elements (character 4). We consider such a reversal to be unlikely but not impossible. Instances are known in which species with fused tarsals show polymorphism for the trait, so reversals could occur (Wake, 1966; Wake and Brame, 1969; Alberch and Alberch, 1981). We conclude that parsimony methods must be used cautiously where extensive parallelism pervades an evolutionary radiation.

An alternative method of analyzing our data is illustrated in Figure 9. This dendrogram is based on the zoogeographic and phyletic arguments of Wake and Lynch (1976, fig. 32), who recognized a "Mexican Group" of genera including *Pseudoeurycea, Chiropterotriton* (*sensu stricto*), *Parvimolge, Lineatriton*, and *Thorius*. Using the present suite of osteological characters, we can find no justification for recognition of a clade including these five genera; so we have indicated a five-way division separating them at the second level of the dendrogram and grouping them to the left of the figure. Although this dendrogram has relatively little internal structure, it does distinguish two groups of three and four genera, respectively.

The dendrogram in Figure 9 differs from that in Figure 8 in several respects. The former dendrogram contains fewer unique synapomorphies (three rather than six) and more parallelisms (ten rather than five), but it has no reversals. A five-way division occurs above the first synapomorphy. The three characters involved in unique synapomorphies (1, 7, 11) fall

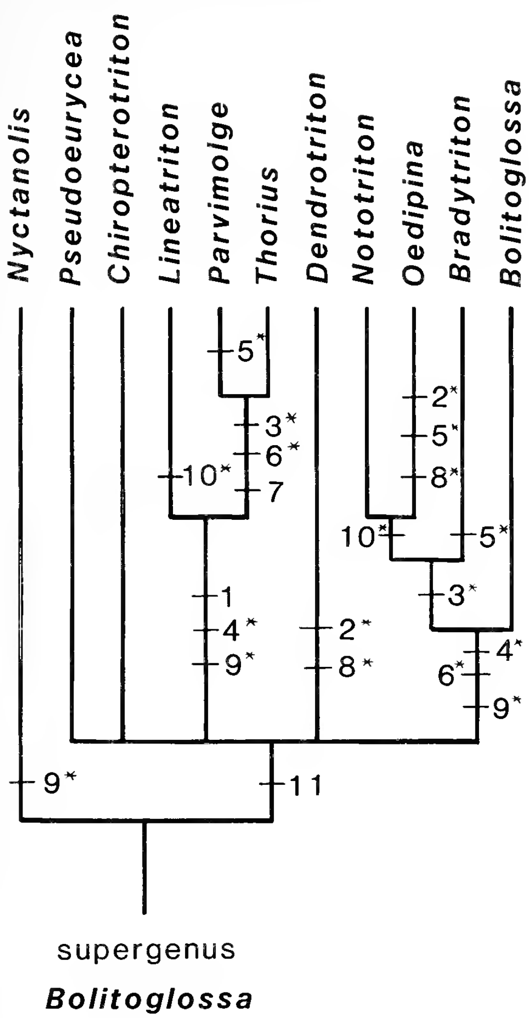

Figure 9. An alternative tree of the genera in the tribe Bolitoglossini. There are no reversals in this tree, but all parallelisms (asterisks) are indicated.

into Hecht and Edwards's (1976a) third and fourth categories, the kinds of characters that they consider to have relatively high systematic value. The stem uniting *Lineatriton, Parvimolge,* and *Thorius* has three synapomorphies. For illustrative purposes, we have indicated all parallelisms in Figure 9, and it can be seen that two of these three synapomorphies evolved in parallel with other stems. The stem uniting *Bradytriton, Nototriton, Oedipina,* and *Bolitoglossa* also has three synapomorphies (4, 6, 9), but none of them is unique.

The tropical plethodontid genera constitute a highly derived lineage. The species are so specialized, in fact, that little further morphological innovation seems possible. Rather, variation on similar themes has occurred repeatedly, with the result that characters useful in the taxonomy of other salamander groups have been subject to extensive parallel evolution. We have long known that such features as elongation of body and tail, diminution in body size, changes in relative limb length and foot size, and increased digital webbing have evolved several times in the group (Wake, 1966; Wake and Lynch, 1976; Alberch and Alberch, 1981). Apparently the evolution of other morphological traits is also complex, and close evolutionary interlinking of seemingly unrelated traits is a possibility (see Alberch et al., 1979; Alberch and Alberch, 1981). The incorporation of biochemical and immunological approaches to phyletic analysis holds promise for unraveling the complex history of this group, but the long evolutionary history of the neotropical salamanders poses serious problems for all known analytical techniques. At one time, the tropical salamanders were considered to form a reasonably compact congeneric group (Dunn, 1926). The intervening years have seen a steady erosion of this concept as new salamanders have been discovered and novel analytical techniques have been applied. Based primarily on its possession of a common tongue projection mechanism (Lombard and Wake, 1977), the supergenus *Bolitoglossa* does appear to be monophyletic, but the group is more ancient and highly diverse than was thought previously. The present effort is but one more developmental stage in our attempt to understand the complex history of the tropical salamanders.

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LITERATURE CITED

Alberch, P., and J. Alberch. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). J. Morph. 167: 249–264.

Alberch, P., S.J. Gould, G.F. Oster, and D.B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

Arnold, S.J. 1977. The evolution of courtship behavior in new world salamanders with some comments on old world salamandrids. Pages 141–183 *in* D.H. Taylor and S.E. Guttman (eds.), *The reproductive biology of amphibians,* Plenum Press, New York City.

Baird, I.L. 1951. An anatomical study of certain salamanders of the genus *Pseudoeurycea.* Univ. Kansas Sci. Bull 34, pt. 1:221–265.

Brame, A.H., Jr. 1968. Systematics and evolution of the Mesoamerican salamander genus *Oedipina.* J. Herpet. 2:1–64.

Cope, E.D. 1869. A review of the species of the Plethodontidae and Desmognathidae. Proc. Acad. Nat. Sci. Philadelphia 1869:93–118.

Dunn, E.R. 1926. The salamanders of the family Plethodontidae. Smith College, Northampton, Mass., viii + 441 pp.

Edwards, J.L. 1976. Spinal nerves and their bearing on salamander phylogeny. J. Morph. 148:305–328.

Eldredge, N., and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process.* Columbia Univ. Press, New York City, viii + 349 pp.

Elias, P. Salamanders of the northwestern highlands of Guatemala. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co., in press.

Elias, P., and D. B. Wake. 1983. *Nyctanolis pernix,* a new genus and species of plethodontid salamander from northwestern Guatemala and Chiapas, Mexico. Pages 1–12 *in* A.G.J. Rhodin and K. Miyata (eds.), *Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams,* The Museum of Comparative Zoology, Cambridge, Mass.

Farris, J.S. 1970. Methods for computing Wagner trees. Systematic Zoology 19:83–92.

Freeman, H.L. 1977. Systematics and evolutionary trends of the Mexican salamander genus *Thorius* Cope, 1869 (Amphibia, Plethodontidae). Ph.D. thesis, Rutgers Univ.

Hanken, J. 1980. Morphological and genetic investigations of miniaturization in salamanders (genus *Thorius*). Ph.D. dissertation, Univ. California, Berkeley.

Hecht, M.K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. Vol. 9, pp. 335–363, *in* M.K. Hecht, W.C. Steere, and B. Wallace (eds.), *Evolutionary biology,* Plenum Press, New York City.

Hecht, M.K., and J.L. Edwards. 1976a. The determination of parallel or monophyletic relationships: The proteid salamanders—a test case. Am. Nat. 110:653–677.

———. 1976b. The methodology of phylogenetic inference above the species level. Pages 3–51 *in* M.K. Hecht, P.C. Goody, and B.M. Hecht (eds.), *Major patterns in vertebrate evolution,* Plenum Press, New York City.

Larson, A., D.B. Wake, L.R. Maxson, and R. Highton. 1981. A molecular phylogenetic perspective on the origins of morphological novelties in the salamanders of the Tribe Plethodontini (Amphibia, Plethodontidae). Evolution 35:405–422.

Leon, P.C., and J. Kezer. 1978. Localization of 5S RNA genes on chromosomes of plethodontid salamanders. Chromosoma 65:213–230.

Lombard, R.E., and D.B. Wake. 1977. Tongue evolution in the lungless salamanders, family Plethodontidae. II. Function and evolutionary diversity. J. Morph. 153:39–80.

Lynch, J.F., and D.B. Wake. 1975. Systematics of the *Chiropterotriton bromeliacia* group (Amphibia: Caudata), with description of two new species from Guatemala. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co. 265:1–45.

———. 1978. A new species of *Chiropterotriton* (Amphibia: Caudata) from Baja Verapaz, Guatemala, with comments on relationships among Central American members of the genus. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co. 294:1–22.

Marlow, R.W., J.M. Brode, and D.B. Wake. 1979. A new salamander, genus *Batrachoseps,* from the Inyo Mountains of California, with a discussion of relationships in the genus. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co. 308:1–17.

Maxson, L.R., and D.B. Wake. 1981. Albumin evolution and its phylogenetic implications in the plethodontid salamander genera *Pseudoeurycea* and *Chiropterotriton.* Herpetologica 37:109–117.

Rabb, G.B. 1955. A new salamander of the genus *Parvimolge* from Mexico. Breviora, Mus. Comp. Zool, 42: 1–9.

———. 1956. A new plethodontid salamander from Nuevo Leon, Mexico. Fieldiana-Zoology, Chicago 39:11–20.

———. 1958. On certain Mexican salamanders of the plethodontid genus *Chiropterotriton.* Occ. Pap. Mus. Zool. Univ. Michigan 587:1–37.

———. 1965. A new salamander of the genus *Chiropterotriton* (Caudata: Plethodontidae) from Mexico. Breviora, Mus. Comp. Zool., 235:1–8.

Robinson, D.C. 1976. A new dwarf salamander of the genus *Bolitoglossa* (Plethodontidae) from Costa Rica. Proc. Biol. Soc. Wash. 89:289–294.

Smith, H.M., and R.B. Smith. 1976. Synopsis of the herpetofauna of Mexico, vol. IV: Source analysis and index for Mexican amphibians. John Johnson, North Bennington, Vermont.

Tanner, W.W. 1950. A new genus of plethodontid salamander from Mexico. Great Basin Natur. 10:37–44.

———. 1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. Univ. Kans. Sci. Bull. 34, pt. 2:583–677.

Taylor, E.H. 1940. New salamanders from Mexico, with a discussion of certain known forms. Univ. Kans. Sci. Bull. 26:407–439.

———. 1941. New plethodont salamanders from Mexico. Herpetologiea 2:57–65.

———. 1944. The genera of plethodont salamanders in Mexico, pt. 1. Univ. Kans. Sci. Bull. 30:189–232.

Trufelli, G.T. 1954. A macroscopic and microscopic study of the mental hedonic gland-clusters of some plethodontid salamanders. Univ. Kans. Sci. Bull. 36, pt. 1:3–39.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Memoirs, So. Calif. Acad. Sci. 4:1–111.

———. 1970. Aspects of vertebral evolution in the modern Amphibia. Forma et Functio 3:33–60.

———. 1972. Emmett Reid Dunn and the development of scientific studies of salamander biology. Pages iii–x *in* Introduction to reprint of E.R. Dunn, Salamanders of the family Plethodontidae, facsimile reprints. Society for the Study of Amphibians and Reptiles, Athens, Ohio.

Wake, D.B., and A.H. Brame, Jr. 1963. The status of the plethodontid salamander genera *Bolitoglossa* and *Magnadigita.* Copeia 1963:382–387.

———. 1969. Systematics and evolution of neotropical salamanders of the *Bolitoglossa helmrichi* group. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co. 175:1–40.

Wake, D.B., and I.G. Dresner. 1967. Functional morphology and evolution of tail autonomy in salamanders. J. Morph. 122:265–306.

Wake, D.B., and J.F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Sci. Bull. Nat. Hist. Mus. Los Angeles Co. 25:1–65.

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THE CRANIAL MORPHOLOGY OF THE FOSSIL BEAVER *DIPOIDES SMITHI* (RODENTIA: MAMMALIA)

Hugh M. Wagner

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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THE CRANIAL MORPHOLOGY OF THE FOSSIL BEAVER *DIPOIDES SMITHI* (RODENTIA: MAMMALIA)

Hugh M. Wagner[1]

ABSTRACT. The cranial morphology of the genus of fossil beaver, *Dipoides,* has never been described or compared with that of other fossil and extant beavers. An extremely well-preserved skull recovered from north-central Oregon in 1974 allows for identification of nearly all features of the cranium. Variation in skull morphology in rodents is generally recognizable at the generic level, and intraspecific variation is usually reflected in differences in the dentition. The skull of *Dipoides* closely resembles that of *Eucastor* and *Castoroides* and differs noticeably from that of *Castor.* The regions of the skull with similarities to *Dipoides, Eucastor,* and *Castoroides* are (1) the bones of the lacrimal region; (2) the arrangement of foramina in the basicranium and interorbital region; and (3) the development of the alisphenoid wing of the internal pterygoid fossa. *Castor* differs in these three areas. Close examination of the crania of these four genera confirms that *Eucastor, Dipoides,* and *Castoroides* represent one group of beavers that has been phyletically distinct from that leading to the extant beaver, *Castor,* since the early Miocene.

INTRODUCTION

Species in the genus *Dipoides* Jäger, 1835, are small beavers that lived during the Hemphillian Mammal Age in North America. The genus appears to have evolved from *Eucastor* Leidy, 1858, during the late Miocene, approximately 8.5 mya (Wagner, 1981).

The genus *Dipoides* was first described by G.F. Jäger in 1835 from late Miocene deposits of Germany. Subsequently, other species of *Dipoides* have been described from late Miocene deposits of Eurasia and North America. R.A. Stirton (1935) reviewed the Tertiary beavers, presenting a phylogeny based on dental characters, with *Dipoides* in the lineage leading to *Castoroides* Foster, 1838. Later, Olson (1940) undertook a comparative study of the cranial foramina of the Castoridae. He described and compared the cranial foramina of *Paleocastor* Leidy, 1869, *Eucastor, Castoroides,* and *Castor* Linneaus, 1758, noting evolutionary trends in foramina within the Castoridae. *Dipoides* was not included in that study.

J.A. Shotwell (1955) reviewed the genus *Dipoides,* basing his taxonomic conclusions on the dental morphology, primarily P_4. He concluded with the description of a new species, *D. smithi* Shotwell, 1955, from McKay Reservoir in north-central Oregon. Stirton (1965) described the cranial morphology of *Castoroides ohioensis* Foster, 1838, in detail, increasing the knowledge of this giant castorid. The specimen of *D. smithi* that I describe in the present paper was recovered from the type locality of the species at McKay Reservoir (Fig. 1) in 1974 and provides new evidence concerning the cranial morphology of the genus and helps clarify its relationship to other genera of castorids.

METHODS AND MATERIALS

The abbreviations used in the text and tables are CNHM (Chicago Natural History Museum), UO (University of Oregon), and UCMP (University of California Museum of Paleontology). All measurements are in millimeters. The comparative specimens are:

Eucastor cf. *E. tortus* Leidy, 1858, CNHM P15787, Big Springs Canyon local fauna, Bennett County, South Dakota, Ogallala Group, Clarendonian.

Castoroides ohioensis Foster, 1838, CNHM P3800, Gravel Pit near Bellflower, McClean County, Illinois Pleistocene.

Castor canadensis Kuhl, 1820, UCMP 126–158, South Dakota, Recent.

Dipoides smithi Shotwell, 1955, UCMP 113422, McKay Reservoir local fauna, Umatilla County, Oregon, ? Shutler Formation, Hemphillian (Figs. 2, 3 and 4).

SYSTEMATICS

Family Castoridae Gray, 1921

Subfamily Castoroidinae Trouessant, 1888

Genus *Dipoides* Jäger, 1835

Dipoides smithi Shotwell, 1955

Figures 2, 3, and 4

REFERRED MATERIAL. UCMP 113422, nearly complete skull lacking only the projection of the premaxillaries

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[1] Department of Physics, University of California, Irvine, California 92717, and Research Associate, Vertebrate Paleontology, Natural History Museum of Los Angeles County.

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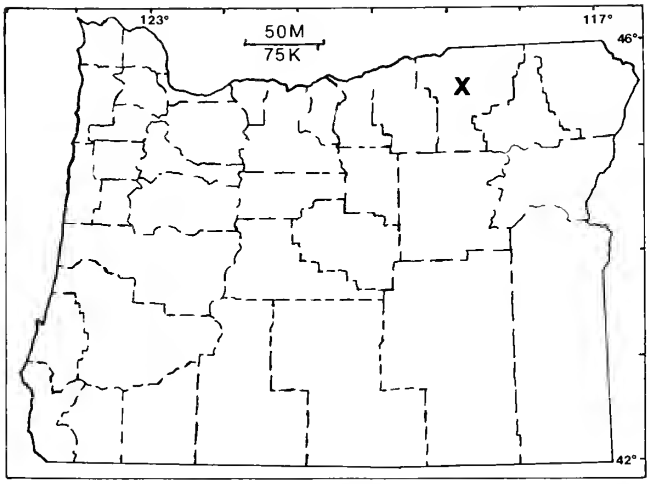

Figure 1. The skull of *Dipoides smithi* was recovered from UCMP locality V74163 at McKay Reservoir in Umatilla County in north-central Oregon, designated by an X.

and incisors (Figs. 2 and 3); UCMP 113433, left dentary fragment with P_4, M_{1-2} (Fig. 4), both from locality UCMP V74163 = U02222, McKay Reservoir, Umatilla County, Oregon, ? Shutler Formation, Hemphillian.

DESCRIPTION AND COMPARISON. The dental morphology of UCMP 113422 agrees with the diagnosis of *D. smithi* (Shotwell, 1955). Upper molars and premolars lack parastria and have S-shaped occlusal patterns characteristic of this species. In the sample of P_4's of *D. smithi* from McKay Reservoir, 16 percent of 24 P_4's had complete or vestigial parastriids and paraflexids.

The incisors and most of the ventral region of the premaxillary bone are absent in this specimen. The dorsal surface of the skull is long and relatively flat. Over the orbits the frontal bone forms a broad, flat surface (Fig. 2). The nasal region is straight, with neither the lateral nor dorsal inflation of *Castor canadensis.* A small protuberance exists on the dorsal lip of the fossa for the masseter profundis anterior muscle at the premaxillary-maxillary suture. This protuberance is similar to that in *Castoroides ohioensis*; *Eucastor* has only a slight one and *Castor* lacks one. Frontoparietal crests arise above the orbits and extend posteriorly along the frontal-parietal suture, where they join to form a strong median sagittal crest between the parietal bones. The lambdoidal crests are well developed, extending laterally nearly to the tip of the mastoid processes.

The anterior and posterior temporal foramina are both present on the parietal-squamosal suture and in the same position as in *Eucastor* and *Castoroides.* Approximately ninety percent of the surfaces of the parietal bones are covered with rugosities. *Eucastor* and *Castoroides* also have similar rugosities although not as extensive anteriorly as in this specimen of *Dipoides.* In *Castor,* such rugosities are not as well developed. The dorsal surface of the cranium in *Dipoides* is more inflated than in *Eucastor* but not as inflated as in *Castor.* The occipital plate intersects a plane extended posterior from the palate at approximately seventy degrees. By comparison, in *Eucastor, Castoroides,* and *Castor,* the occipital plate intersects the same plane at nearly ninety degrees. A small mastoid foramen pierces the mastoid bone slightly lateral to the mastoid-supraoccipital suture. In size and position the mastoid foramen is very similar to that in *Castoroides.* In *Castor,* this foramen is much larger and situated on the mastoid-supraoccipital suture. The occipital condyles appear very similar to those in *Castor* and do not show the transverse flattening of those of *Castoroides.*

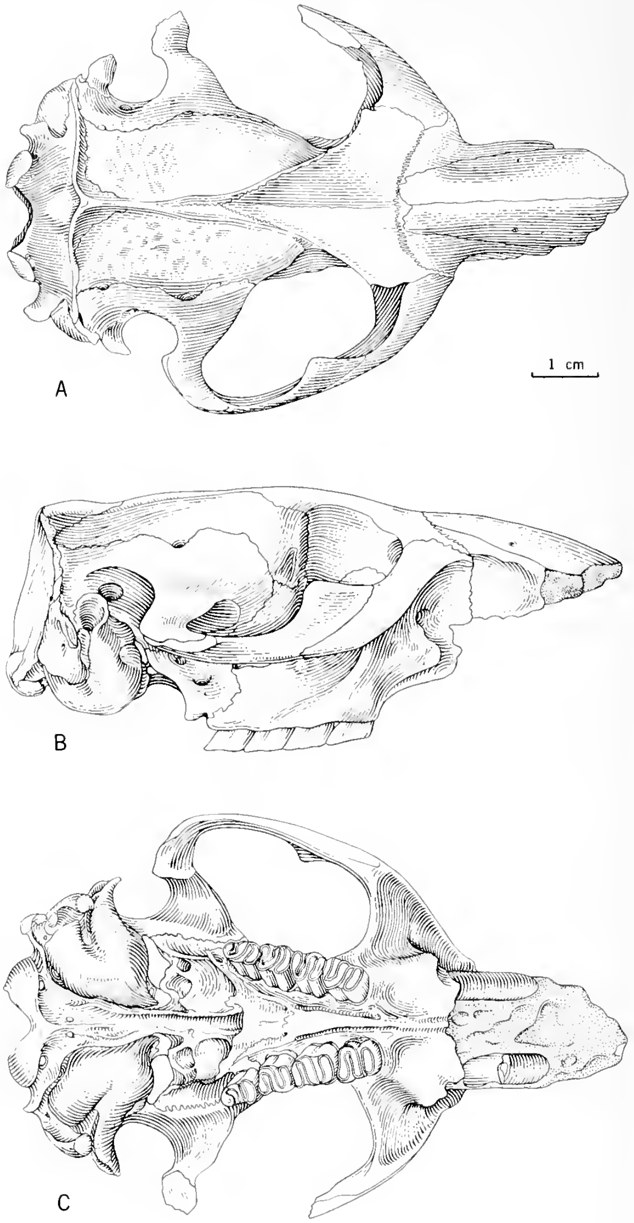

Figure 2. *Dipoides smithi*: Shotwell, 1955, UCMP 113422, McKay Reservoir local fauna, UCMP locality V74163, nearly complete skull lacking the incisor region; A, dorsal view; B, right lateral view; C, ventral view; scale indicated.

Anterior and ventral to the infraorbital foramen there is a very prominent masseter superficialis process (Fig. 3, B). A prominent flange or sheath of bone extends dorsally from the lateral edge of this process, closing off the ventral region of the infraorbital foramen from the masseter lateralis profundus anterior fossa (Fig. 3, B). This flange bends posteriorly toward its dorsal limit and does not extend above the infraorbital foramen. The morphology of the masseteric superficialis process and infraorbital complex in *Dipoides* is nearly identical to that of *Castoroides*. In *Eucastor* the masseteric superficialis process is not well developed, and the structure of the infraorbital region resembles that of *Castor*.

The zygomatic arch is wide, but not to the extreme seen in *Castor* or *Castoroides*. The orbit of *Dipoides* is proportionally larger than in *Castor* and *Castoroides* and appears to be directed more laterally than in *Castor*. The structure of the zygomatic arch and lacrimal region is similar to that in *Castoroides* and *Eucastor* and differs from that in *Castor*. The contribution that the jugal bone makes to the zygomatic arch of *Dipoides, Eucastor,* and *Castoroides* is less than in *Castor*. In the former three genera, the jugal-maxilla suture is on the lateral surface of the zygomatic arch as contrasted to *Castor* where this suture is in the lacrimal area. The anterior margin of the orbit is composed of the maxilla, because the jugal does not extend into the lacrimal region. In *Castor*, however, the jugal-maxilla suture extends anteriorly on the dorsal surface of the zygomatic arch, and the jugal meets the lacrimal in the anterior region of the orbit.

Dipoides has a simple lacrimal region in which only the frontal and maxilla meet on the dorsal surface of the skull. The lacrimal bone does not have a dorsal component in this specimen. The structure of the lacrimal region in *Dipoides* and *Castoroides* is similar by having only the two dorsal elements. *Eucastor* differs slightly from *Dipoides* and *Castoroides,* because a small portion of the lacrimal bone is visible on the dorsal surface at the maxillary-frontal suture. *Castor* has a much more complicated dorsal lacrimal area in which the jugal, maxillary, lacrimal, and frontal bones all meet.

The pattern of foramina within the inner orbit of *Dipoides* is very similar to that in *Eucastor* and distinctly different from the pattern in either *Castoroides* or *Castor*. However, the resemblance to *Castoroides* is greater than to *Castor*. The sphenoid foramen is the anterior foramen, piercing the maxillary in an anterior direction. Directly behind the sphenoid foramen is a slightly smaller one that enters the cranium medially. This foramen completely penetrates the cranium as does the presphenoid canal of Olson (1940) (alisphenoid-rotundum foramen of Stirton (1965)). This foramen appears to be an anterior presphenoid canal. Directly above the anterior presphenoid canal on the orbitosphenoid-frontal suture is the ethmoid foramen. Posterior and ventral to the ethmoid foramen is a well-developed optic foramen entirely enclosed in the orbitosphenoid bone. A large posterior presphenoid canal is situated posterior to the optic foramen in a deep sulcus at the anterior end of the sphenoidal fissure. Near the anteroposterior margin of the alisphenoid wing of the internal pterygoid fossa is the masticatory-buccinator

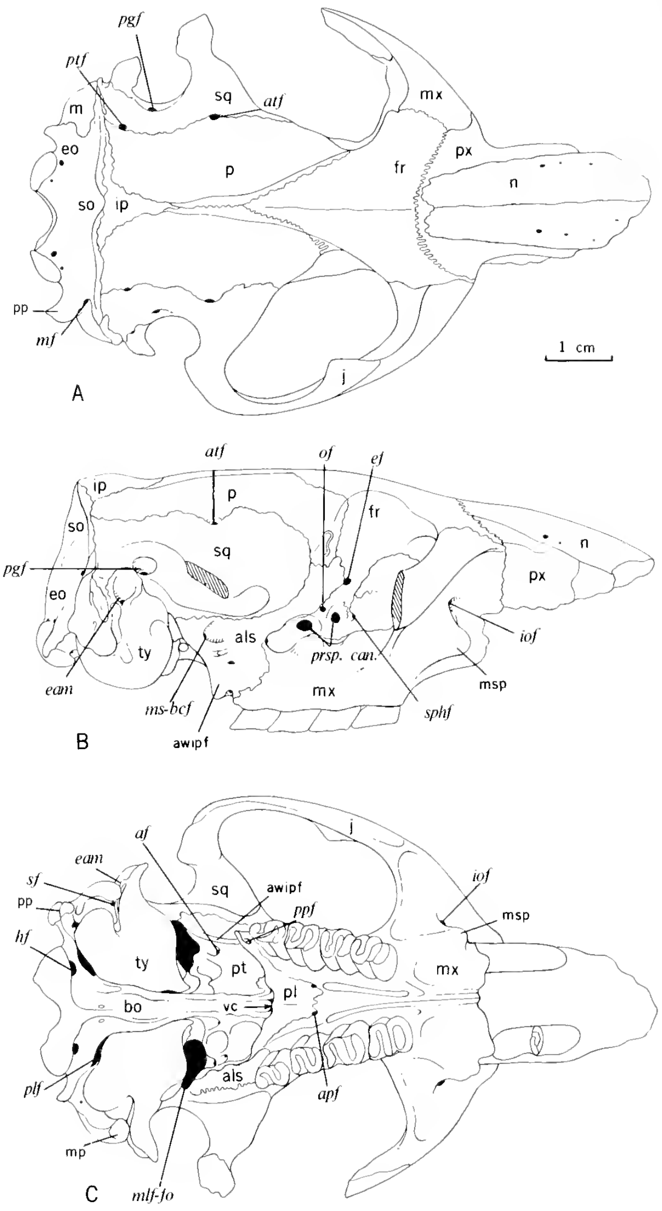

Figure 3. *Dipoides smithi*, Shotwell, 1955, skull with structures labeled, UCMP 113422; A, dorsal view; B, right lateral view; C, ventral view; scale indicated roman type represents bones and structure, italics are foramina. Abbreviations: *af,* alisphenoid foramen; als, alisphenoid; *apf,* anterior palatine foramen; *atf,* anterior temporal foramen; awipf, alisphenoid wing of internal pterygoid process; bo, basioccipital; *eam,* external auditory meatus; *ef,* ethmoid foramen; eo, exoccipital; fr, frontal; *hf,* hypoglossal foramen; *iof,* infraorbital foramen; ip, interparietal; j, jugal; m, mastoid; *mf,* mastoid foramen; *mlf-fo,* median lacerate foramen-foramen ovale; mp, mastoid process; *ms-bcf,* masticatory-buccinator foramen; msp, masseteric superficialis process; mx, maxillary; n, nasal; *of,* optic foramen; p, parietal; *pgf,* postglenoid foramen; pl, palatine; pp, paroccipital process; *prsp. can.,* presphenoid canal; ps, premaxillary; pt, pterygoid; *ptf,* posterior temporal foramen; *sf,* stylomastoid foramen; so, supraoccipital; *sphf,* sphenoidal foramen; sq, squamosal; ty, tympanic; vc, ventral choana.

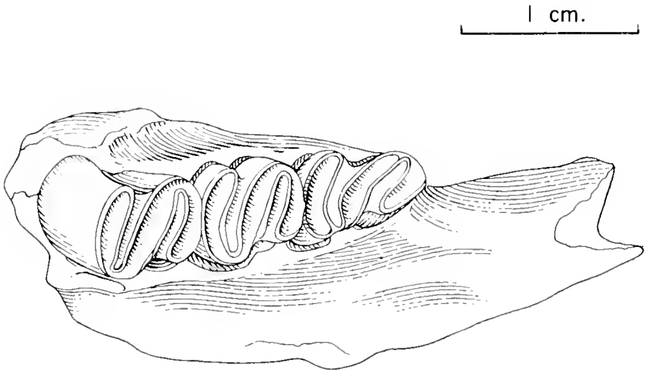

Figure 4. *Dipoides smithi,* UCMP 113433, UCMP V74163, collected near the skull figured in this paper. Left dentary fragment with P_4,M_{1-2} showing normal occlusal wear. This specimen has the more typical P_4 of *D. smithi,* where no paraflexid is present.

foramen. Below the masticatory-buccinator foramen, a portion of the alisphenoid canal is visible, as it passes through the alisphenoid bone. Anteroventral to the alisphenoid canal is a large foramen that appears to enter the pulp cavity of M^3. The pattern of foramina anterior to and including both presphenoid canals in *Dipoides* is very similar to that in *Eucastor* and *Castor. Eucastor* resembles *Dipoides* by having the multiple presphenoid canals. By contrast, in *Castoroides,* the presphenoid canal is single and proportionally much smaller and more posterior in its position.

Posterior to the presphenoid canal, the morphology of the alisphenoid in *Dipoides* does not resemble that in *Castor* but is very similar to that in *Castoroides.* In *Dipoides* and *Castoroides,* the alisphenoid forms a smooth lateral surface of the sphenoid fissure from the anterior sulcus of the presphenoid canal posterior to the masticatory-buccinator foramen. The masticatory-buccinator foramen is directed posteriorly through the margin of the alisphenoid. In *Castor,* part of the alisphenoid forms a strap-like structure, forming the lateral surface of the alisphenoid canal. The masticatory-buccinator foramen and alisphenoid foramen share a common orifice that is at the posterior end of the straplike structure of the alisphenoid. This common foramen is directed anteriorly, entering directly into the sphenoid fissure. The alisphenoid foramen pierces the broad alisphenoid wing of *Dipoides* and *Castoroides,* and a branch of the trigeminal nerve (V_2) enters the skull through a bone canal enclosed in the alisphenoid wing of the internal pterygoid. *Castor* differs in that the alisphenoid foramen does not pass through the alisphenoid wing, but the trigeminal nerve enters via the alisphenoid foramen. This region of the skull of the specimen of *Eucastor* was not well enough preserved to allow comparison.

The postglenoid foramen is large and nearly equal in size

Table 1. A comparison of cranial characters in *Eucastor* cf. *E. tortus,* CNHM P15787; *Dipoides smithi,* UCMP 113422; *Castoroides ohioensis,* CNHM P3800; and *Castor canadensis,* UCMP 126-158.

Characters	*E.* cf. *E. tortus*	*D. smithi*	*C. ohioensis*	*C. canadensis*
Protuberance on dorsal lip of anterior masseteric fossa	slight	slight	well-developed	absent
Temporal foramina present	yes	yes	yes	yes
Rugosities present on parietal bone	slight	well-developed	well-developed	slight
Inflation of cranium	slight	slight	slight	well-developed
Mastoid foramen	small	small	small	large
Masseteric superficialis process well developed	no	yes	yes	yes
Masseteric superficialis process anterior to anterior masseteric fossa	no	yes	yes	no
Lateral vertical flange on infraorbital foramen	yes	no	no	yes
Parallel tooth row on maxillary	yes	no	no	yes
Dorsal choana or invagination on pterygoid or basioccipital bones	no	no	yes	yes
Posterior carotid foramen	absent	absent	present	present
Alisphenoid foramen pierces medial alisphenoid wing of internal pterygoid fossa	not known	yes	yes	no
Jugal extends into lacrimal region	no	no	no	yes
Multiple presphenoid canals	yes	yes	no	yes
Bulla highly inflated	yes	yes	no	yes
Mastoid process extends beyond external auditory meatus	no	no	no	yes

to the external auditory meatus. The external auditory meatus is posterior and ventral to the postglenoid foramen and is appressed posteriorly against the mastoid process and directed laterally. Its anterior lip has the greatest lateral extension. The condition of the postglenoid foramen and external auditory meatus is very similar to that of *Castoroides. Castor* and *Eucastor* differ, having a much smaller postglenoid foramen; the meatus has a more dorsolateral orientation, and its ventral lip has the greatest lateral extension. In *Dipoides* and *Castor,* the meatus projects laterally beyond the mastoid process. In *Castoroides,* it does not.

The internal pterygoid fossa is broad, bounded laterally by the alisphenoid wing and medially by the palatal wing of the pterygoid, which is a septum supporting the hamular process. The alisphenoid foramen is present just anterior to the conjoined median lacerate foramen and foramen ovale on the alisphenoid wing of the internal pterygoid fossa (Fig. 3, C). The surface of the pterygoid fossa has depressions. The ventral choana is triangular in outline, bounded laterally by the palatal wings of the pterygoid. In *Castoroides* the outline of the ventral choana is similar to that of *Dipoides,* but in *Castor* it is nearly circular.

There is a rugosity on the anterior median border of the bulla, resembling that of *Castor,* where the hamular process meets the tympanic. In *Castor* these rugosities extend farther posteriorly, so it seems probable that the hamular processes of *Dipoides* were not as long as in *Castor.* The overall structure of the internal pterygoid fossa in *Dipoides* resembles that in *Castoroides,* in which the alisphenoid wing of the internal pterygoid fossa is expanded, and the alisphenoid foramen enters the skull through the medial surface of the alisphenoid. This region of the skull of *Eucastor* was not preserved well enough to allow comparison.

Dipoides does not possess the dorsal choana (mesopterygoid fossa) of *Castoroides* (see Stirton, 1965). This fossa is unique to *Castoroides. Castor* does have a shallow invagination in the basioccipital, but this invagination is posterior to the mesopterygoid fossa of *Castoroides.*

A small anterior carotid foramen in *Dipoides* pierces the lateral margin of the basisphenoid anterior to the medial extension of the bulla. It is similar in position to that of *Castor.* In *Dipoides* and *Eucastor,* the posterior carotid foramen is not visible along the medial margin of the bulla anterior to the posterior lacerate foramen as it is in *Castor* and *Castoroides.* A large posterior lacerate foramen is present along the posteromedial border of the bulla. Directly posterior to the posterior lacerate is a large hypoglossal foramen. A small stylomastoid foramen is present, wedged between the base of the mastoid process and the boney tube of the tympanic leading to the external auditory meatus. The paroccipital process extends posteriorly almost as far as do the occipital condyles (see Table 1). The very tip of the paroccipital process is hooked ventromedially.

The bullae are very inflated. Their ventral extension does not reach as far ventrally as the greatest depth of the skull at the tooth row (see Fig. 2, B; Table 2). In *Castor,* the bulla, though exhibiting no greater inflation, extends ventrally to a level in line with the tooth row, which is considerably more ventral than in *Dipoides, Eucastor,* or *Castoroides.*

Table 2. Measurements of cranial and dental characters of *Dipoides smithi,* UCMP 113422 (in millimeters).

Posterior margin lambdoidal crest to anterior tip of nasals	90.5*
Dorsal width of rostrum anterior to zygomatic arch	17.0
Least width between orbital fossae	14.7
Greatest width between external auditory meatus	45.7
Greatest width between mastoid processes	23.3
Greatest width of zygomatic arches	64.9
Greatest width between masseteric superficialis processes	23.3
Length from dorsal margin of foramen magnum to greatest height of occiput	15.2
Depth of skull between dorsal surface of skull and occlusal surface of M^2	36.8
Depth of skull between sagittal crest and bulla	30.6
Least width of palate between P^4's	5.2
Least width of palate between M^3's	14.4
Length from anterior border of P^4 to posterior border of M^3	21.9
Length of occlusal surface of P^4	5.8
Width of occlusal surface of P^4	5.5
Length of occlusal surface of M^1	4.9
Width of occlusal surface of M^1	4.5
Length of occlusal surface of M^2	5.0
Width of occlusal surface of M^2	4.4
Length of occlusal surface of M^3	5.1
Width of occlusal surface of M^3	3.8

* Approximate.

In ventral view, the skull of *Dipoides* closely resembles those of *Eucastor* and *Castor* in general outline. The incisors form a crescentic arc that terminates above P^4. The dilator naris fossa is deep in *Dipoides,* with a well-developed, grooved median ridge present on the maxilla. In *Eucastor,* the dilator naris fossa is deep, as in *Dipoides*; however, in the former, the maxilla slopes steeply toward the maxillary-premaxillary suture, and in the latter a relatively flat platform is present. The masseteric superficialis process of *Dipoides* and *Castoroides* is posterior to the anterior flaring of the maxillary. The cheek tooth row diverges posteriorly from the midline of the skull. *Castoroides* has a similar appearance with closely placed P^4's and widely separated M^3's; whereas in *Eucastor* and *Castor,* the cheek tooth rows are nearly parallel. The tooth wear in *Dipoides* forms a flat transverse plane differing from that in *Castor* wherein the upper tooth surface is concave with the labial margin having greater elevation than the lingual edge. There are two nearly parallel medial grooves that run from the premaxillary-maxillary suture posterior to M^1. These grooves resemble those in *Eucastor* and *Castor,* though in *Dipoides* they are deeper. The anterior palatine foramina are present on the suture between the M^2's. The posterior palatine foramen is situated directly posterior to M^3. A ridge is present posterior to the posterior palatine foramen forming the posterolateral margin of the palate. The posterior margin of the palate forming the roof of the mouth of *Dipoides* describes a smooth concave margin. *Eucastor* differs markedly from this condition in having an invagination in the palatine bone that extends anteriorly to the anterior margin of M^3. *Castor* and *Castoroides* resemble *Dipoides* in this feature.

DISCUSSION

A detailed examination of the cranial morphology of *Dipoides smithi* reveals close similarities to *Eucastor* cf. *E. tortus* and *Castoroides ohioensis.* The similarities in the positions of the foramina in the orbital region and basicranium and in the bone development of the skull in these three species indicate a close phyletic relationship supporting Stirton's (1935) conclusions based on dental morphology. The similarities of the skull in *Dipoides, Eucastor,* and *Castoroides* are (1) the relationship of bones of the lacrimal region; (2) the arrangement of foramina in the basicranium and interorbital region; and (3) the development of the alisphenoid wing of the internal pterygoid fossa. *Castor* differs markedly from other genera in all three characteristics.

In *Dipoides* and *Castoroides,* the dorsal surface of the lacrimal region is composed of the maxilla, premaxilla, and frontal bones. *Eucastor* has a lacrimal component. The most anterior extension of the jugal does not reach the lacrimal region. The jugal does contribute to this region of the skull in *Castor,* a definite difference from the other mentioned taxa.

In the *Eucastor, Dipoides, Castoroides* group, *Eucastor* and *Dipoides* differ in the morphology of the infraorbital foramen from *Eucastor* to *Dipoides.* The structure of the infraorbital foramen in *Dipoides* and *Castoroides* is derivable from the condition found in *Eucastor.* The multiple presphenoid canals in *Eucastor, Dipoides,* and some specimens of *Castor* appear to be a primitive trait evolved prior to *Eucastor* and retained in *Eucastor, Dipoides,* and *Castor* but lost in *Castroides.*

The nonparallel upper cheek tooth rows of *Dipoides* and *Castoroides* are derived compared with *Eucastor* and *Castor.* Similar nonparallel tooth rows are seen in some South American histricomorph rodents. It is probable that this represents a modification related to a different masticatory adaptation. For example, the South American rodents that exhibit this type of modification are primarily aquatic forms, with teeth composed of lophs for grinding, very similar to the castorid genera.

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Appreciation is expressed to the Oregon Museum of Science and Industry (OMSI) for providing me the opportunity to prospect and collect fossil specimens from eastern Oregon during the summer of 1974, in conjunction with the Paleontological Research Team, during which time the specimen of *Dipoides smithi* described in this paper was collected. All members of the Paleontology Research Team, sponsored by OMSI, deserve credit for their participation, sharp eyes, and enthusiasm during the field season. It was a pleasure having Bruce Batten, Steve Damiani, Kathy Harvey, Roy West, and Kathy Wolfram as students and companions during the six-week program. The near perfectly preserved skull of *Dipoides smithi* recovered from McKay Reservoir was found by Bruce Batten. The illustrations of *D. smithi* were drawn by Jaime P. Lufkin, an artist from the Museum of Paleontology, University of California, Berkeley.

I thank the curators of the Museum of Paleontology, University of California, Berkeley, The University of California Museum of Vertebrate Zoology, and the Natural History Museum of Los Angeles County for the loan and use of comparative collections. I also thank Lawrence G. Barnes for the helpful and constructive comments offered in his review of this manuscript.

LITERATURE CITED

Jäger, G.F. 1835. Ueber die fossilen Säugethiere, welche in Württemberg gefunded worden sind. Le Abth: 17–18.

Olson, E.C. 1940. Cranial foramina of North American beavers. Jour. Paleontology 14:495–501.

Shotwell, J.A. 1955. Review of the Pliocene beaver *Dipoides.* Jour. Paleontology 29:129–144.

Stirton, R.A. 1935. A review of the Tertiary beavers. Univ. Ca. Pubs., Geol. Sci., Bull. 23:391–458.

———. 1965. Cranial morphology of *Castoroides.* Dr. D.N. Wadia Comm. Vol. Nim. & Metal. Inst. of India, pp. 273–285.

Wagner, H.M. 1981. Geochronology of the Mehrten Formation in Stanislaus County, California. Ph.D. dissertation, Dept. Earth Sci., Univ. of California, Riverside, 347 pp.

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CONTRIBUTIONS IN SCIENCE

STUDIES ON THE TAXONOMY AND DISTRIBUTION OF AMERICAN CENTRIDINE BEES (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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STUDIES ON THE TAXONOMY AND DISTRIBUTION OF AMERICAN CENTRIDINE BEES (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling[1]

ABSTRACT. This study focuses primarily on the Centridini of North America south of the United States and includes a key to the three genera of Centridini: *Centris, Ptilotopus,* and *Epicharis.* Within the genus *Centris* keys are provided for species in the subgenera *Paracentris, Centris, Xanthemisia, Acritocentris, Melanocentris, Trachina, Hemisiella,* and *Heterocentris*; one new monotypic subgenus is described: *Ptilocentris* (type-species: *Centris festiva* F. Smith, 1854).

The following new species are described: *C.* (*Xerocentris*) *griseola* (Mexico); *C.* (*C.*) *aethiocesta* (El Salvador to Panama); *C.* (*Acritocentris*) *satana* (Mexico, United States); *C.* (*Melanocentris*) *agiloides* (Mexico to Costa Rica); *C.* (*M.*) *gelida* (Mexico, Guatemala); *C.* (*Trachina*) *eurypatana* (Mexico); *C.* (*T.*) *xochipillii* (Mexico). *Centris* (*C.*) *meaculpa* is proposed as a new name for *C.* (*C.*) *erubescens* Snelling, 1974, not *C. costaricensis* var. *erubescens* Friese, 1925. *Centris atripes* var. *ferrisi* Cockerell is a valid species in *Paracentris*; the types are males, not females as stated by Cockerell.

The following new synonymy is proposed in *Centris*: *C. cockerelli resoluta* Cockerell = *C.* (*Paracentris*) *cockerelli* W. Fox; *C. clypeata* Friese, *C. anthracina* Snelling = *C.* (*P.*) *nigrocaerulea* F. Smith; *C. limbata* Friese = *C.* (*P.*) *atripes* Mocsáry; *C. strawi* Snelling = *C.* (*Acritocentris*) *albiceps* Friese; *C. robusta* Cockerell, *C. segregata* Crawford = *C.* (*C.*) *inermis* Friese; *C. citrotaeniata* Gribodo, *C. flavifrons* var. *rufescens* Friese, *C. flavifrons* var. *nigritula* Friese = *C.* (*C.*) *flavifrons* (Fabricius); *C. chlorura* Cockerell = *C.* (*Ptilocentris*) *festiva* F. Smith; *C. ignita* F. Smith, *C. bakerella* Friese, *Epicharis cisnerosi* Cockerell = *C.* (*Melanocentris*) *agilis* F. Smith; *C. fusciventris* var. *scutellata* Mocsáry = *C.* (*M.*) *fusciventris* Mocsáry; *C. melanochlaena* F. Smith, *Epicharis zamoranensis* Cockerell = *C.* (*M.*) *obsoleta* Lepeletier; *C. schwarzi* Cockerell = *C.* (*Trachina*) *labiata* Friese; *C. confinis* Pérez = *C.* (*Hemisiella*) *nitida* F. Smith; *C. ruae* Cockerell = *C.* (*H.*) *transversa* Pérez; *C. dentipes* F. Smith, *C. rufomaculata* Cockerell, *C. lanipes subtarsata* Cockerell = *C.* (*H.*) *trigonoides* Lepeletier; *C. costaricensis* var. *erubescens* Friese = *C.* (*H.*) *vittata* Lepeletier; *C. triangulifera* Cockerell = *C.* (*Heterocentris*) *labrosa* Friese.

Ptilotopus is elevated to generic rank from its previous status as a subgenus of *Centris*; *P. zonalis* Mocsáry of Panama is the only species in North America.

A key is given for all the subgenera of *Epicharis* and keys are given for the species of each subgenus known to occur in North America. Two new species are described in the subgenus *Epicharana*: *E. angulosa* (Costa Rica) and *E. bova* (Costa Rica, Panama). The following are new synonyms: *E. salazari* Cockerell = *E.* (*Epicharana*) *elegans* F. Smith; *E. rustica* var. *flava* Friese = *E.* (*Epicharana*) *rustica* (Olivier); *E. phenacura* Cockerell, *E. conura* Cockerell = *E.* (*Parepicharis*) *metatarsalis* Friese. North American distribution data are cited for all species.

Included is a synonymic list of the recognized North and Central American Centridini.

RESUMEN. Este estudio se refiere principalmente a los Centridini de Norte América al sur de los Estados Unidos e incluye una clave para los tres géneros de Centridini: *Centris, Ptilotopus* y *Epicharis.* Dentro del género *Centris* se incluyen claves para las especies de los subgéneros *Paracentris, Centris, Xanthemisia, Acritocentris, Melanocentris, Trachina, Hemisiella* y *Heterocentris*; un subgénero monotípico nuevo se describe, *Ptilocentris* (especie-tipo: *Centris festiva* F. Smith, 1854).

Ptilotopus se eleva al rango genérico desde su estatus previo de subgénero de *Centris*; *P. zonalis* Mocsáry de Panamá es la única especie en Norte América.

Se da una clave para todos los subgéneros de *Epicharis* y para las especies de cada subgéneros conocidos en Norte América.

Se describen ocho nuevas especies para el género *Centris* y dos para el género *Epicharis.* Estas al igual que los nuevos sinónimos se incluyen en el "Abstract."

Se citan datos de distribucion de Norte América para todas las especies. Se incluye una lista de los Centridini reconocidos de Norte América y de las sinonimias conocidas.

INTRODUCTION

The present paper is a continuation of my earlier work on the *Centris* of North and Central America (Snelling, 1956, 1966, 1974). New data on the distribution of previously treated species, as well as investigations into the systematics of previously unstudied groups are presented below. Although my previous investigations involved only the genus *Centris,*

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[1] Section of Entomology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.

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the study has now expanded to include the genera *Epicharis* and *Ptilotopus,* the latter newly elevated to generic status from its previous position as a subgenus of *Centris.*

SPECIMENS EXAMINED

Material utilized in this study is from the following institutional and private collections: American Museum of Natural History (AMNH), Robert W. Brooks, personal collection (RWB), California Academy of Sciences (CAS), Cornell University (CORN), Florida State Department of Plant Industry (DPIF), Museum of Comparative Zoology (MCZ), Museum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum of Los Angeles County (LACM), John L. Neff, personal collection (NEFF), Oregon State University (ORSU), D. Roubik, personal collection (ROUB), United States National Museum of Natural History (USNM), University of California, Berkeley (UCB), University of California, Davis (UCD), University of Kansas (UKAN), and Thomas J. Zavortink, personal collection (TJZ).

SPECIMEN DATA

New data on distribution, capture dates, and plant association are fully cited for many species since there are few published records. Localities are organized by country and by state, province or department within that country. The designation "state," "department," or "province" is omitted to conserve space. Thus, a locality cited under "COSTA RICA, SAN JOSÉ" is from San José Province in Costa Rica.

Specimen data are cited for most species, but some species are common, widely distributed and abundant. For such species, only general range is given.

TERMINOLOGY

In general, the morphological terminology employed below is that which is traditional is apoid systematics, following Michener (1944, 1954, 1965). A few terms, however, should be explained, in order that they may be correctly employed (in the sense of this paper) by others.

Antennal socket diameter. Since the antennal socket is not circular it follows that two different measurements are possible. In this study, the antennal socket diameter is measured perpendicular to the long axis of the head (i.e., the transverse diameter); measurement is made from the summit of the rim on the opposite side. Associated measurements include the *interantennal distance* and the *antennocular distance.*

Interantennal distance is measured as the least distance between the summits of the two antennal socket rims.

Antennocular distance is the least distance from the inner eye margin to the summit of the rim of the adjacent antennal socket.

Several features of the clypeus should be defined for consistent usage. The *clypeal disc* is the central portion of the clypeus, from base to apical margin and roughly bounded on either side by an imaginary line extended distad from the junction of the subantennal sutures with the base of the clypeus. *Clypeal length,* when compared to clypeal width, is measured along the midline, from the base to the apical margin. *Clypeal width* is measured as the greatest distance between the apicolateral extremities of the clypeus (i.e., that portion nearest the inner eye margin). The distance between the clypeus and the eye is measured as the least distance between the apicolateral extremity and the nearest point on the inner eye margin.

Elaiospathe is a new term: It is a combination of the Greek words *elaion* (oil) and *spathe* (a paddle for stirring or mixing; a broad blade). This term refers to the modified oil-gathering structures present in female centridine and exomalopsine bees. The elaiospathe most commonly consists of a row of long, erect, apically spatulate and curved setae, usually on the pro- and mesobasitarsi; in Centridini they are situated anteriorly on the "inner" surface of the segment, in some Exomalopsini they are external and may be present in males as well as females, and are limited to the probasitarsi. However, oil-collecting structures may also be present on the abdominal venter, at least in some species of *Tapinotaspis* (*Tapinotaspoides*). For an excellent survey of the morphology and function of the elaiospathe, see Neff and Simpson (1981).

The *lower frontal width* is measured as the distance between the inner eye margins at the level of the apicolateral angle of the clypeus. It is compared with the upper frontal width to determine the degree of convergence of the inner eye margins. The *upper frontal width* is the minimum distance between the inner eye margins at about the level of the ocelli.

The *diameter of the anterior ocellus* is the greatest transverse (perpendicular to long axis of head) diameter of the anterior ocellus. *Interocellar distance* is the minimum distance between the posterior, or lateral, ocelli. *Ocellocular distance* is the minimum distance between one of the posterior ocelli and the nearest point on the eye margin. *Ocelloccipital distance* is measured in dorsal view and is the minimum distance from the posterior margin of one of the posterior ocelli to the occipital declivity. *Transocellar distance* is measured as the maximum distance between the *outer* margins to the two posterior ocelli. In all cases, the ocellus is, for purposes of measurement, considered to be only the transparent amber-colored lens.

Pilosity. In general, centridines, like most other anthophorids, are densely hairy bees, with much of the head, thorax, and first abdominal tergum clothed with long, plumose, decumbent to fully erect hairs. Similarly, the legs are hairy, but hairs tend to be decumbent to subappressed on the outer faces of the tibiae and basitarsi and are often stout and simple. Long, plumose hairs are usually present, but sparse, on the femora. On the abdomen, the hairs on the discs of the segments generally become longer and more erect on succeeding segments, plumose hairs as a rule being absent from the discs of the second and third terga.

The abdominal sterna normally have long, plumose hairs which tend to be longest and most abundant along the midline. As a rule, males are more densely pubescent on the sterna than are the females.

Punctation. The description of characteristics related to the punctation of the integument of bees and other Hymenoptera have long been the bane of taxonomists since the terminology has always been undefined and subject to considerable variation in interpretation. Punctures which one author considers to be fine, another might describe as moderate in size. The distances between punctures, whether dense, close, or sparse, have likewise been troublesome. A few years ago I (Snelling, 1980) introduced a system of terminology to solve this difficulty in the genus *Hylaeus.* After considering the objections by Harris (1979), I can find no valid reason not to apply the same terminology of absolute measurements to the Centridini. I do not agree that punctation need be described relative to the size of the entity. Admittedly, I was initially uncomfortable at describing as "coarse" those punctures on a centridine bee that I was accustomed to considering to be moderate-sized. This is, however, strictly a perceptual problem, one which has ceased to disturb my sense of "rightness."

Therefore, I propose to expand the usage of my system to include the Centridini. Such a system must be considered, at this point, to be experimental; some adjustment or modification may prove to be necessary as this method is tried on other groups. A micrometer disk in one ocular of a microscope is, obviously, necessary and I use a minimum magnification of 64×; several punctures of about the same apparent size are measured and averaged. The appropriate terminology is as follows:

minute—puncture diameter 0.010–0.019 mm
fine—puncture diameter 0.020–0.035 mm
moderate—puncture diameter 0.036–0.055 mm
coarse—puncture diameter 0.056–0.070 mm
very coarse—puncture diameter over 0.070 mm

Since punctures are often not uniform in size on a given segment or area, it may be necessary to combine terms into phrases such as "fine to moderate" (puncture diameter varying between 0.020 and 0.055 mm), though usually a more limited size range, such as moderate, may prevail.

The relative density of punctures may also be standardized and I use the following terminology below:

Contiguous—punctures so close that they are often deformed; interspaces are compressed and sharp-edged.

Subcontiguous—punctures separated by more or less flat interspaces up to about 0.30 times a puncture diameter; some punctures may be deformed.

Dense—punctures separated by more or less flat interspaces between 0.30 and 0.70 times a puncture diameter; punctures usually round but may be elongate.

Close—punctures separated by more or less flat interspaces 0.70 to 1.50 times a puncture diameter.

Sparse—punctures separated by more or less flat interspaces 1.50 to 3.00 times a puncture diameter.

Scattered—puncture interspaces are very irregular and range from about 3.00 to 6.00 or more times a puncture diameter.

Variations in puncture density may be expressed by combining terms: "sparse to scattered."

Clypeal punctation is usually described from the middle one-third of the disc.

Mesoscutal punctation is described from the area between the parapsidal line and the median line at the level of the tegula; punctures are commonly less close posteromesally on the segment and are closer laterad of the parapsidal line. Scutellar and metanotal sculpture is described from the mesal one-third of the segment. The middle of the mesopleural disc is the standard for that segment.

The first abdominal segment has a nearly vertical anterior and a horizontal posterior face; the latter is referred to as the disc of the segment. Tergal punctation is described from the mesal one-third of the postgradular area of the segments beyond the first, and anterior to the apical zone.

The distal portion of the abdominal terga, especially of the second and following segments, except the last, is commonly depressed in bees; this area is usually called the apical depression and it is often sculptured differently from the disc. In centridines this area is usually not obviously depressed, especially across the middle two-thirds of the segment, but is usually more sparsely and less coarsely sculptured than the disc; herein I refer to this as the *apical zone.*

In the description of new taxa, measurements and proportions are based on the primary type specimens. The corresponding range of measurements and proportions of paratypes only (if any) are indicated parenthetically after those of the primary type.

NESTING BIOLOGY

The little that is known of centridine nesting biology was reviewed by Coville, Frankie, and Vinson (1983). They concluded that the choice of nesting substrate by the female bees is roughly correlated with taxonomic groupings. Thus, those species in the subgenera *Wagenknechtia, Paracentris, Xerocentris, Centris* s. str., *Exallocentris,* and *Melanocentris* normally excavate original tunnels in soil. About one-half of the species cited utilize flat soil and about one-half excavate in more or less vertical banks or mud walls; two species evidently are capable of choosing either flat or vertical surfaces.

Species belonging to the subgenera *Hemisiella* and *Heterocentris* generally utilize preexisting cavities in a variety of substrates. Some species, at least, seem to be highly opportunistic in choice of substrate and may choose old bee cells and burrows in soil, abandoned *Sceliphron* nests, or holes in wood. Of two species of *Trachina* cited, one nested in the walls of a living arboreal termitarium and the other chose flat soil.

Species of *Ptilotopus,* herein treated as a separate genus, were uniform in excavating their nests in the walls of living arboreal termitaria. There is some suggestion that the arrangement of cells within the nest may similarly substantiate the present groupings of subgenera, but the data are very fragmentary.

SYSTEMATICS

The general interpretation of the Centridini has been that there are two genera, *Centris* and *Epicharis* (e.g., Michener, 1954). One result of my recent work in this tribe is that I now believe that *Ptilotopus,* formerly treated as a subgenus of *Centris*, must be elevated to generic status; justification for this decision will be provided below. The three genera of Centridini which I recognize may be separated as follows.

KEY TO GENERA OF CENTRIDINI

1a. Marginal cell of forewing shorter than distance from its apex to tip of wing; occipital flagelliform setae usually absent, but if present, not reaching as far back as anterior margin of tegula 2

b. Marginal cell of forewing longer than distance from its apex to tip of wing; occipital flagelliform setae present and usually extending to, or beyond, level of anterior margin of tegula . . . . *Epicharis*

2a. Occipital flagelliform setae absent; mesosternum of female without tubercles; hypoepimeron flat or slightly convex; pronotal lobe low and moderately convex, never conspicuously tuberculate . . . . *Centris*

b. Occipital flagelliform setae present and extending to anterior margin of mesoscutum, or slightly beyond; mesosternum of female with a pair of stout tubercles hidden in dense cluster of hairs; hypoepimeron usually prominently coniform, but if not, its lower margin is sharply elevated above adjacent portions of mesepisternum; pronotal lobe often tuberculate . . . . *Ptilotopus*

Genus *Centris* Fabricius

Centris is a primarily tropical genus, with 11 subgenera; these subgenera are separated in keys by Michener (1951) and Snelling (1974). The separation of *Ptilotopus* from *Centris* (see below) removes the only group with flagelliform occipital setae. The North American species of the subgenera *Xerocentris* and *Paracentris* were treated by Snelling (1974). The North American species of the remaining subgenera are treated below.

Subgenus *Xerocentris* Snelling

Centris subg. *Xerocentris* Snelling, 1974:3–4. Type-species: *Centris californica* Timberlake, 1940; original designation.

This subgenus was proposed for a number of species found in arid regions of North and South America. Although *Xerocentris* is related to *Paracentris*, females lack an elaiospathe on the pro- and mesobasitarsi, present in *Paracentris* and *Centris* s.s., and the pygidial plate is convex along the median line. Males are much like those of *Paracentris*, but the ocellocular distance is less than the diameter of a lateral ocellus, and the abdominal terga are covered with abundant fully erect, often pale, hairs.

One new species of *Xerocentris* is described below.

Centris (Xerocentris) griseola, new species

DIAGNOSIS

Female runs to *C. vanduzeei* Cockerell in my key (1974), but mandible tridentate (quadridentate in *C. vanduzeei*), mesoscutum and scutellum with mixed black and pale erect hairs (wholly pale in *C. vanduzeei*), prepygidial brush blackish brown (bright fulvous in *C. vanduzeei*) and distal portion of median ridge of pygidium low and rounded (cariniform in *C. vanduzeei*). Male unknown.

DESCRIPTION

HOLOTYPE FEMALE. Measurements (mm). Head width 5.18 (5.03–5.28); head length 3.79 (3.23–3.33) wing length 10.1 (10.2–10.3); total length 13.0 (13.0–15.5).

Head. 1.58 (1.51–1.62) times broader than long; occipital margin nearly flat in frontal view; inner orbits strongly convergent above, upper frontal width 0.84 (0.82–0.84) times lower frontal width. Maxillary palp five-segmented. Mandible slender, tridentate, second preapical tooth absent; inner tooth prominent, triangular, and nearly perpendicular to long axis of mandible. Labrum unmodified; shiny between subcontiguous, moderate punctures. Clypeus flattened, weakly protuberant; disc slightly shiny, surface roughened, irregularly, obliquely to transversely rugose. Frons and vertex moderately shiny to shiny between fine subcontiguous to dense punctures, but with extensive smooth areas in front of, and laterad to, ocelli; gena less than half as wide as eye, moderately shiny between fine, dense punctures. Interantennal distance 2.92 (2.32–3.67) times antennal socket diameter; antennocular distance 1.62 (1.65–2.00) times antennal socket diameter; scape short, robust, scape length 0.73 (0.67–0.70) times length of first flagellar segment; first flagellar segment 4.83 (5.06–5.50) times length of second. Ocelli, in frontal view, well below occipital margin; interocellar distance 2.23 (2.20–2.24) times ocellar diameter; ocellocular distance 1.50 (1.52–1.58) times ocellar diameter; ocelloccipital distance 2.50 (2.52–2.65) times ocellar diameter.

Thorax. Mesoscutum shiny between subcontiguous to dense moderate punctures; scutellum narrowly shiny and impunctate across anterior margin but mostly weakly shiny, interspaces conspicuously roughened between dense, moderate punctures; metanotum vertical, shiny between sparse, fine punctures; mesopleuron moderately shiny, moderately tessellate between subcontiguous to dense, fine punctures; metapleuron similar but a little shinier. Propodeal disc smooth and shiny between scattered minute to fine punctures; side of propodeum less shiny, punctures dense to sparse, minute. Metabasitibial plate about twice longer than broad, strongly narrowed apicad, secondary plate poorly defined and merging into primary plate, anterior depression small (all specimens worn, details uncertain); scopal hairs largely plumose along margins, mostly simple elsewhere.

Abdomen. Discs of all terga moderately shiny and weakly tessellate between dense to sparse, fine punctures; pygidium elongate-triangular, apex narrowly rounded; median elevation rounded and not attaining apex.

Color. Generally blackish brown, abdominal terga with weak blue-green reflections; mandibles dark ferruginous; flagellum and legs brown; tergal margins yellowish; tegula piceous; wings slightly brownish, veins and stigma brown.

Pilosity. Of head, thorax and abdomen fully erect, whitish, with that of vertex largely brownish; pale and blackish hairs about equally abundant on mesoscutum, scutellum and pronotal lobes; tergal hairs shorter and sparser, plumose; fourth tergite with a few, and fifth with many, long, curled blackish bristles; prepygidial fimbria dark; sixth tergite with dark bristles and hairs; sternites with dark discal hairs and pale distal hair bands, those of fourth and fifth segments broadly interrupted; sixth segment dark pubescent; scopal hairs white; some brownish bristles on protibia; bristles of protarsus and thoracic venter brown; bristles on inner side of meso- and metabasitarsi brownish ferruginous.

TYPE MATERIAL

Holotype female and three paratypes. MEXICO, *GUERRERO:* Iguala, 2000 ft. elev., 4 Feb. 1954 (R.R. Dreisbach). Holotype and two paratypes in UKAN; one paratype in LACM.

ETYMOLOGY

Modern Latin *griseolus* (gray) because of the grayish appearance of the thoracic dorsum.

DISCUSSION

Although *C. griseola* superficially resembles *C. vanduzeei* Cockerell of Lower California, it is easily separated from that species by the characters given above in the Diagnosis. Especially distinctive is the tridentate mandible. The only other species of *Xerocentris* with tridentate mandible is *C. pallida* W. Fox, of the arid western deserts. In that species, the maxillary palp is four-segmented, the pygidial apex is truncate and with a broad median ridge which extends to the apex, the thoracic integument is dull, and the scopal hairs are all plumose.

The unknown male of *C. griseola* probably resembles the female in that the clypeus will be black and the thoracic hairs will be a mixture of dark and light hairs.

Pollen samples from two specimens were examined by J.L. Neff. His conclusion (personal communication) was that in both cases, the samples were "... a mixture of *Cercidium* and *Hoffmanseggia* (or possibly *Caesalpinia*) with the former predominating."

Subgenus *Paracentris* Cameron

Paracentris Cameron, 1903:235–236. Type-species: *Paracentris fulvohirta* Cameron, 1903; original designation.

Penthemisia Moure, 1950:390. Type-species: *Centris chilensis* Spinola, 1851; original designation.

Hemisia, subg. *Penthemisia:* Michener, 1951:3–4.

Centris, subg. *Trichocentris* Snelling, 1956:3. Type-species: *Centris rhodoleuca* Cockerell, 1923; original designation.

Centris, subg. *Paracentris:* Snelling, 1974:5–7.

The North American species of *Paracentris* were treated in 1974; 14 species were recognized, four of which were known from only one sex. Since then, I have seen opposite sexes for three of these species. One previously described form, *C. atripes ferrisi* Cockerell, was not considered in 1974 because it was known only from the deficient original description. I have now seen the type specimens. It seems appropriate, therefore, to present a new key to the North American species of *Paracentris* to accommodate these new data.

KEY TO NORTH AMERICAN *PARACENTRIS*

1a. Female, antenna 12-segmented and basitibial plate present on metatibia 2

b. Male, antenna 13-segmented and basitibial plate absent from metatibia 15

2a. Pubescence of head, thorax, and legs entirely or predominantly black, that of mesepisternum wholly black 3

b. Pubescence of head, thorax, and legs entirely or predominantly pale, that of mesepisternum pale, at least in part 7

3a. Pubescence of thoracic dorsum entirely black 4

b. Pubescence of thoracic dorsum largely pale 6

4a. Integument of abdominal tergites black; punctures of second tergite uniformly distributed across disc, not notably sparser along midline, their hairs simple or plumose, interspaces polished or roughened 5

b. Integument of abdominal tergites dark blue; punctures of second tergite dense at sides, distinctly more separated (sometimes sparse) in middle, their hairs decumbent and simple, interspaces polished .... *laevibullata* Snelling

5a. Punctures of disc of second tergite fine, little greater in diameter than hairs arising from them, hairs fine, plumose, suberect; interspaces of second tergite roughened and dull .... *nigrocaerulea* F. Smith

b. Punctures of second tergite conspicuously greater in diameter than coarse, simple, decumbent hairs arising from them; interspaces of second tergite polished and shiny .... *aterrima* F. Smith

6a. Large species, 14.5–18.5 mm long; pubescence of vertex and pronotal lobes black; clypeal punctures sparse, obscure apicad, median impunctate line evanescent .... *mexicana* F. Smith

b. Smaller species, 12.5–14.5 mm long; pubescence of vertex and pronotal lobe whitish; clypeus with sharply defined median impunctate line, punctures sharply defined .... *zacateca* Snelling

7a. Clypeal integument entirely blackish 8

b. Clypeal integument at least partially yellowish, orange or red 11

8a. Discs of second and third terga with evenly spaced, distinct punctures throughout 9

b. Discs of second and third terga polished and shiny, with scattered fine punctures which become coarse and distinct laterad, most of disc virtually impunctate .... *fisheri* Snelling

9a. First flagellar segment a little longer than following three segments combined; abdominal terga black; punctures of scutellum separated by much less than a puncture diameter 10

b. First flagellar segment a little shorter than following three segments combined; abdominal terga with definite metallic bluish reflections; punctures of scutellum mostly more separated, with many interspaces of more than a puncture diameter .... *lanosa* Cresson

10a. Median line of clypeus broad, smooth, shiny, and impunctate; punctures of disc mostly well separated; hairs at side of dorsal face of first tergum short, light brown anteriorly, becoming short and fuscous toward distal margin .... *angustifrons* Snelling

b. Median line of clypeus narrow, roughened and dull; punctures of disc mostly subcontiguous; some hairs of dorsal face of first tergum conspicuously long, erect, plumose, and pale whitish .... *harbisoni* Snelling

11a. Small species, 8.5–13.5 mm long; clypeus with distinct impunctate median line, punctures elsewhere separated by less than twice a puncture diameter (if clypeal punctures somewhat sparse, scape, femora, and tibiae ferruginous) 12

b. Larger species, 15.5–18.5 mm long; clypeus polished between scattered punctures, usually separated by more than twice a puncture diameter, and median impunctate line undefined (scape, femora, and tibiae dark brownish) .... *caesalpiniae* Cockerell

12a. Color of mandible, labrum, and clypeus usually not as below; clypeus polished and shiny, median impunctate line present and usually well defined; tergal discs moderately to strongly shiny, with or without bluish reflections; scape, femora, and tibiae brown or red 13

b. Mandible (except apex), labrum, and clypeus dull orange-ferruginous; clypeus usually contiguously punctate, dull and without median impunctate line, but may be moderately shiny and with narrow impunctate line; tergal discs dull and closely tessellate, with dull bluish reflections; scape, femora, and tibiae brown .... *ferrisi* Cockerell

13a. Basal face of first tergum with abundant long, plumose, white hairs, some of which extend onto dorsal face in middle; terga with definite bluish reflections 14

b. Basal face of first tergum with sparse plumose, white hairs, those in middle shorter and not extending to dorsal face in middle; terga black, without bluish reflections .... *cockerelli* W. Fox

14a. Mandible, labrum, clypeus, scape, femora, and tibiae mostly or entirely bright ferruginous; apical margins of second and third terga with short bands of appressed pale hairs; first flagellar segment shorter than following three combined .... *rhodopus* Cockerell

b. Mandible, scape, and legs brown, labrum and most of clypeus yellowish; second and third terga with all hairs blackish; first flagellar segment longer than following three combined .... *atripes* Mocsáry

15a. Clypeus wholly black; pubescence of mesepisternum wholly blackish 16

b. Clypeus largely or entirely whitish, yellowish or reddish; pubescence of mesepisternum pale or dark . . 18

16a. Pubescence of thoracic dorsum pale 17

b. Pubescence of thoracic dorsum blackish .... *aterrima* F. Smith

17a. Pubescence of pronotal lobe, and usually of entire lateral pronotal area, pale; first flagellar segment 2.6–3.1 times longer than second .... *zacateca* Snelling

b. Pubescence of entire lateral pronotal area, including lobe, blackish; first flagellar segment 3.8–3.9 times longer than second .... *mexicana* F. Smith

18a. Pubescence of head and thorax at least partially pale 19

b. Pubescence of head and thorax blackish .... *nigrocaerulea* F. Smith

19a. Metabasitarsus much broadened toward apex, about twice longer than greatest width; metafemur swollen and about twice longer than wide 20

b. Metabasitarsus slender and parallel-sided, at least 3.5 times longer than wide; metafemur usually about three times longer than wide, but may be swollen 22

20a. Punctures equally dense on mesoscutum and scutellum; mesepisternum finely, closely punctate; clypeus pale yellow 21

b. Punctures of mesoscutum much sparser than those of scutellum; mesepisternum with scattered, obscure, fine punctures; clypeus orange-ferruginous .... *ectypha* Snelling

21a. First flagellar segment longer than following three combined; punctures of clypeal disc mostly separated by a puncture diameter or more .... *angustifrons* Snelling

b. First flagellar segment a little shorter than following three combined; punctures of clypeal disc mostly separated by less than 0.75 times a puncture diameter .... *harbisoni* Snelling

22a. Discs of second to fourth tergites closely and sharply punctate, punctures separated by no more than twice a puncture diameter and clearly greater in diameter than hairs arising from them 23

b. Discs of second to fourth tergites polished and shiny between scattered, obscure punctures little greater in diameter than hairs arising from them .... *fisheri* Snelling

23a. Clypeus polished or not, punctures mostly separated by two puncture diameters or less; ocellocular distance no more than 1.25 times diameter of anterior ocellus; smaller species, head width 3.8–5.3 mm, almost always less than 5.0 mm 24

b. Clypeus polished, nearly impunctate; ocellocular distance at least 1.65 times diameter of anterior ocellus; larger species, head width 5.0–6.5 mm, almost always more than 5.3 mm .... *caesalpiniae* Cockerell

24a. Clypeus slightly shiny to shiny, punctures of disc mostly subcontiguous, usually with distinct impunctate median line, sometimes with median line roughened and dull; abdominal terga without pale hairs beyond first segment; legs medium to dark brown and metatibia mostly dark pubescent 25

b. Clypeus polished between sparse punctures and median impunctate line very broad and poorly defined; discs (or at least apical margins) of second to sixth terga with subappressed (suberect in metander), mostly simple, pale hairs; legs almost always ferruginous and metatibia at least largely whitish pubescent. . *rhodopus* Cockerell

25a. Face narrow, eye length at least 1.56 (and usually more than 1.60) times interocular distance at level of antennal sockets; ocellocular distance no more than, and usually less than, diameter of anterior ocellus 26
  b. Face broad, eye length no more than 1.51 (and usually less than 1.45) times interocular distance at level of antennal sockets; ocellocular distance a little greater than diameter of anterior ocellus 27
26a. Paraocular area, mandible (mostly) and underside of scape (usually) yellow; clypeus closely punctate and median impunctate line narrow; abdominal terga with bluish reflections .... *lanosa* Cresson
  b. Paraocular area and underside of scape dark, mandible ferruginous; clypeus with median impunctate line broad and punctures mostly separated by about a puncture diameter; abdominal terga black, without bluish reflections .... *cockerelli* W. Fox
27a. Median area of clypeus sharply roughened and dull, contrasting to shiny, closely punctate areas on either side; discs of abdominal terga two to five sharply tessellate and slightly shiny .... *ferrisi* Cockerell
  b. Clypeal disc shiny, with distinct smooth, impunctate median line; discs of abdominal terga two to five shiny, not obviously tessellate .... *atripes* Mocsáry

Centris (*Paracentris*) *angustifrons* Snelling

Centris (*Paracentris*) *angustifrons* Snelling, 1966:13–14. ♀.

The type locality for *C. angustifrons* is Huachuca Mountains, Arizona and this species was based on a single female collected nearly 80 years ago. A few additional specimens are now available, including the previously unknown males. The males are very similar to those of *C. harbisoni*, especially in the shape of the metabasitarsus, but are easily separated by the characteristics cited in the key above.

The females of *C. angustifrons* and *C. harbisoni* are even more similar, a fact I had not fully appreciated when I prepared my 1974 key. The present key brings the two species to the same couplet; the differences between them are noted there and should present few difficulties.

NEW RECORDS

MEXICO, *SONORA:* 1♂, Aduana, 15 Mar. 1962 (L.A. Stange, UCD); 6♀♀, 2♂♂, Rio Cuchuhaqui, 8 mi. S Alamos, 1–13 Apr. 1975 (A. Brewster; LACM), on *Parkinsonia* sp. (2♀♀, 1♂), *Fourquieria* sp. (1♂), *Cercidium* sp. (2♀♀), and *Prosopis* sp. (2♀♀).

Centris (*Paracentris*) *aterrima* F. Smith

Centris aterrima F. Smith, 1854:378. ♂.
Centris (*Paracentris*) *aterrima:* Snelling, 1974:7, 8 (key).

NEW RECORDS

UNITED STATES, *ARIZONA, Cochise Co.:* 1♀, Rustler Park, Chiricahua Mountains, 4 Aug. 1971 (LACM); 6♀♀, 1 mi. E Douglas, 14 Aug. 1969 (J.G. and K.C. Rozen; AMNH); 1♀, Yaqui Canyon area, 5370–5700 ft. elev., Huachuca Mountains, 29 Aug. 1972 (R.R. Snelling; LACM), on *Acacia angustissima. Pima Co.:* 2♀♀, Arivaca, 18 July and 24 Aug. 1974 (J.L. Neff; LACM). *Santa Cruz Co.:* 1♀, 1♂, Sycamore Canyon, near Ruby, 16–17 Aug. 1961 (J.C. Bequaert; LACM); 1♂, Nogales, 24 Aug. 1939 (R.H. Crandall; LACM); 1♂, Patagonia, 24 Aug. 1955 (F.G. Werner and G.D. Butler; LACM); 1♀, White Rock Campground, 0.5 mi. S Peña Blanca, 9 Aug. 1972 (D.C. Frack; LACM); 1♀, Peña Blanca, 27 July 1972 (D.C. Frack; LACM). MEXICO, *CHIAPAS:* 1♀, 3♂♂, 12 mi. W Ocozocoautla, 26 July 1953 (E.E. Gilbert and C.D. MacNeill; UCB). *OAXACA:* 1♂, 4 mi. N Pochutla, 150 m elev., 11 Oct. 1975 (J.L. Neff; LACM), on "Mint 7115"; 3♀♀, 4 mi. W Zanatepec, 200 m elev., 16 Sept. 1975 (J.L. Neff; LACM, NEFF), on *Krameria revoluta. SINALOA:* 1♀, 30 mi. E Villa Union, 570 m elev., 20 Mar. 1980 (J.L. Neff; NEFF).

Centris (*Paracentris*) *atripes* Mocsáry

Centris atripes Mocsáry, 1899:254: ♂.
Centris limbata Friese, 1899:44. ♀. NEW SYNONYMY.
Centris atriventris W. Fox, 1899:68. ♀ ♂. Preoccupied.
Centris Foxi Friese, 1900b:350. New name for *C. atriventris* W. Fox.
Centris (*Paracentris*) *atripes:* Snelling, 1974:8, 9–10 (key, distr., var.).

Friese described *C. limbata* from a single female collected by G. Birkmann at Fedor, Lee County, Texas. The most distinctive feature of this species was the presence of distinct bands of pale hairs on the metasomal terga. Since no specimens resembling the description have been subsequently collected, *C. limbata* remained an enigma.

At my request, R.W. Brooks examined the type of *C. limbata* in the Berlin Museum and he provided several photographs and sketches. A photograph of the lateral view of the type specimen clearly shows that the abdomen is glued to the thorax. The abdomen is distinctly fasciate in dorsal view and a prominent, apically truncate pygidial plate, without a secondary plate, is present. In fact, both the abdominal bands and the pygidial plate are typical, not of *Centris*, but of a *Melissodes* male! The head and thorax of the type are just as clearly those of a *C. atripes* female. Since the species was described as a *Centris*, I consider these parts to be the true type; the abdomen is extraneous. This restriction negates any possible nomenclatural confusion within *Melissodes*.

NEW RECORDS

COSTA RICA, *GUANACASTE:* 1♀, 8 km NW Liberia, 9 Feb. 1975 (G.R. Frankie; TAMU), on *Cassia biflora*, 0900. GUATEMALA: 1♀, 8 mi. NE El Progreso, 8 July 1965 (A. Raske and C. Slobodchikoff; UCB); 1♂, Jieara, 8 May 1931 (J. Bequaert; AMNH). UNITED STATES, *OKLAHOMA:* 1♀, Norman, Cleveland Co., "8/4 1949" (W.T. Nailon; UKAN).

Centris (*Paracentris*) *cockerelli* W. Fox

Centris lanosa: W. Fox, 1899:69; Cockerell, 1906:97; Lutz and Cockerell, 1920:556; Timberlake, 1940:138; Snelling, 1956:7 (in part, misidentifications).

Centris cockerelli W. Fox, 1899:68. ♀.
Centris cockerelli resoluta Cockerell, 1923:76–77. ♀ ♂. NEW SYNONYMY.
Centris lanosa lanosa: Snelling, 1966:6 (misidentification).
Centris lanosa resoluta: Snelling, 1966:6.
Centris (*Paracentris*) *cockerelli cockerelli:* Snelling, 1974:10–11.
Centris (*Paracentris*) *cockerelli resoluta:* Snelling, 1974:11.

For complete literature citations of this common species, see Snelling (1974) under *C. cockerelli* and *C. c. resoluta.* This is the species long improperly called *C. lanosa.* Although I have attempted to maintain recognition of *C. c. resoluta,* I no longer believe this to be correct. In the females there are two principal phenotypes: an eastern form with whitish to yellowish clypeus and a western form with a reddish yellow clypeus. There are no apparent differences to be seen in the males associated with these females. The two female forms intergrade continuously from western Texas and Tamaulipas through New Mexico and Chihuahua. In my opinion these variants are the end-points of a cline of variation and are not worthy of formal separation.

Centris (*Paracentris*) *ferrisi* Cockerell

Centris atripes subsp. *ferrisi* Cockerell, 1924:49. "♀" = ♂!

This was described from two specimens from La Paz, Baja California Sur, Mexico; although Cockerell stated the specimens to be females, both are males. The types are in the CAS. In my key (1974), the males will run to *C. atripes.* Males differ from those of *C. atripes,* and other species of similar appearance, in that the integument of the abdominal tergites is dull and sharply roughened between minute, obscure punctures; the clypeus, especially basad, is distinctly roughened between well-separated punctures. The females, too, will key to *C. atripes* and, as in the male, have the tergal sculpture distinct, dulling the surface; the facial marks are dull ferruginous rather than yellow as in *C. atripes*; in *C. ferrisi* the first flagellar segment is as long as the following three combined, shorter in *C. atripes.* The male clypeus is usually ferruginous, but is yellow in some specimens.

In addition to the types of *C. ferrisi* I have seen the following, all from MEXICO, *BAJA CALIFORNIA SUR:* 1 ♂, Cabo San Lucas, 8–14 Sept. 1978 (J.P. and K.E. Donahue; LACM); 1♀, 1♂, Cañon de la Zorra, 260 m elev., 11 km W Santiago, 4–5 Sept. 1977 (R.R. Snelling; LACM), on *Parkinsonia aculeata*; 2♀♀, 4 km N Los Barriles, 10 m elev., 4 Sept. 1977 (R.R. Snelling; LACM); 1♀, 3.7 mi. W La Burrera, 1400 ft. elev., 7–8 Oct. 1975 (R.R. Snelling; LACM), on *Antigonon leptopus*; 1♂, 2.5 mi. SE La Huerta, 2200 ft. elev., 8–9 Oct. 1968 (E.L. Sleeper and F.J. Moore; LACM); 1♀, 2 mi. S La Paz, 6 Aug. 1966 (J.A. Chemsak; UCB), on *P. aculeata*; 1♂, 7 mi. SW La Paz (J.A. Chemsak; UCB), on *Wislizenia refracta* var. *mamillata*; 1♀, 23 km W La Paz, 24–27 Apr. 1975 (E.M. and J.L. Fisher; LACM); 1♀, 68 km S Loreto, Km 76 on Hwy 1, 29 July 1977 (D. Weismann and C. Mullinex; CAS); 1♂, La Paz, 15 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 1♀, 25 mi. W La Paz, 30 Aug. 1959 (E.W. Radford and F.G. Werner; CAS); 1♀, 3 mi. E San Pedro, 15 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 1♂, 52 mi. NW La Paz, 15 Mar. 1980 (J.L. Neff; NEFF), on *Cercidium peninsulare*; 1♀, La Laguna (Sierra de la Laguna), 1829 m elev., 23 Oct. 1977 (D.E. and W.R. Breedlove; CAS); 1♂, 11 mi. NE Todos Santos, 16 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 1♀, 25 km E Todos Santos, near La Burrera, 1829 m elev., 21 Oct. 1977 (D.E. and W.R. Breedlove; CAS); 1♂, Miraflores, 17 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 1♀, 1 mi. S Agua Caliente, 17 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 2♀♀, 5 mi. W San Ignacio, 13 Sept. 1983 (R.R. Snelling; LACM), on *Tephrosia tenella*; 2♀♀, same, except 19 Sept. 1983.

Centris (*Paracentris*) *fisheri* Snelling

Centris (*Paracentris*) *fisheri* Snelling, 1974:12. ♂.

This was described from two males collected near San Ignacio, Baja California Sur, Mexico. The female will go to, and closely resembles, *C. harbisoni* Snelling in my key (1974) to species of *Paracentris,* but differs immediately in that the abdominal terga are polished and very sparsely punctate; in *C. fisheri* the first flagellar segment is shorter than the scape and shorter than the combined lengths of the second to fourth flagellar segments; the first flagellar segment is longer in *C. harbisoni.*

NEW RECORDS

MEXICO, *BAJA CALIFORNIA SUR:* 11♀♀, 5♂♂, 5 mi. W San Ignacio, 13 Sept. 1983 (R.R. Snelling; LACM), on *Tephrosia tenella*; 5♀♀, 10♂♂, same, except 19 Sept. 1983; 1♀, 19 km NW Mulegé, 8 Sept. 1977 (R.R. Snelling; LACM), on *Hoffmanseggia* sp.; 1♂, 35 mi. N Loreto, 5 Oct. 1975 (R.R. Snelling; LACM), on *Wislizenia refracta*; 5♂♂, 9.6 mi. N Loreto, 14 Sept. 1983 (R.R.Snelling; LACM), on *Antigonon leptopus*; 1♀, Estación Microondas "Ligui," 48 km S Loreto, 425 m elev., 14 Sept. 1983 (R.R. Snelling; LACM), on *A. leptopus*; 2♂♂, 68 km S Loreto, Km 76 on Hwy 1, 29 July 1977 (D. Weismann and C. Mullinex; CAS).

Centris (*Paracentris*) *harbisoni* Snelling

Centris (*Paracentris*) *harbisoni* Snelling, 1974:14–16. ♀ ♂.

NEW RECORDS

MEXICO, *BAJA CALIFORNIA SUR:* 1♀, San José del Cabo, 11–16 Sept. 1967 (J. Chemsak, A. and M. Michelbacher; UCB); 1♂, 52 mi. NW La Paz, 15 Mar. 1980 (J.L. Neff; NEFF) on *Cercidium peninsulare*; 4♀♀, 106 km N La Paz, 18 Mar. 1980 (J.L. Neff; NEFF), on *Krameria parvifolia.*

Centris (*Paracentris*) *laevibullata* Snelling

Centris (*Paracentris*) *laevibullata* Snelling, 1966:17–18. ♀; Snelling, 1974:7 (key).

This species was described from a female from Orizaba, Vera

Cruz, Mexico (type locality) and another collected 14 mi. NW Zitacuaro, Michoacán, Mexico. The male is unknown.

NEW RECORDS

MEXICO, *DURANGO:* 1♀, Durango, 13 Aug. 1962 (A.E. Michelbacher; UCB). *JALISCO:* 1♀, 3.5 mi. E [Río] Magdalena, 5 Sept. 1965 (A.R. Gillogly; LACM); 1♀, 25 mi. W Guadalajara, 4700 ft. elev., 29 Sept. 1957 (H.A. Scullen; ORSU); 1♀, 13 mi. NW Lagos de Moreno, 3 Sept. 1975 (J.L. Neff; LACM). *MICHOACÁN:* 1♀, 7.7 km NE Pátzcuaro, 2088 m elev., 23 Sept. 1976 (C.D. George and R.R. Snelling; LACM). *NUEVO LEÓN:* 1♀, 18 mi. W Linares, 2700 ft. elev., 26 Sept. 1975 (J.A. Powell, J. Chemsak, and T. Friedlander; UCB). *SAN LUIS POTOSÍ:* 1♀, 52 mi. S. Tamazunchali, 5700 ft. elev., 7 Oct. 1957 (H.A. Scullen; ORSU).

Centris (*Paracentris*) *lanosa* Cresson

Centris lanosa Cresson, 1872:284. ♂.
Centris subhyalina W. Fox, 1899:69. ♀.
Centris birkmanii Friese, 1899:44. ♂ ♀.
Centris (*Paracentris*) *lanosa:* Snelling, 1974:8, 16–17 (key, syn.).

NEW RECORDS

UNITED STATES, *FLORIDA:* 1♀, Austin Carey, Alachua Co., 22–24 May 1975 (G.B. Fairchild; DPIF); 1♀, Gainesville, Alachua Co. (DPIF); 1♀, Trenton, Gilchrist Co., 14 Apr. 1925 (D.M. Bates; DPIF). *KANSAS:* 1♀, 3 mi. S Sawyer, Pratt Co., 16 June 1962 (C.D. Michener and party; UKAN), on *Amorpha canescens*. *OKLAHOMA:* 1♀, near Ardmore, Carter Co., 3 June 1961 (Univ. Kans. Mex. Exped.; UKAN); 1♀, Cleveland Co., 31 May 1951 (H.L. Parker; UKAN); 1♀, Ft. Sill, Comanche Co., 24 June 1974 (T.E. Rogers; LACM). *TEXAS:* 5♀♀, Bastrop, Bastrop Co., 2 May 1969 (Brothers, Krueger, Michener; UKAN).

Centris (*Paracentris*) *mexicana* F. Smith

Centris mexicana F. Smith, 1854:378. "♀" = ♂!
Centris (*Paracentris*) *mexicana:* Snelling, 1974:7, 8, 17–18 (key, tax., distr.).

NEW RECORDS

MEXICO, *OAXACA:* 4♀♀, 2♂♂, Tamazulapam, 6200 ft. elev., 2 Sept. 1965 (S.J. Arnold; UCB), on *Salvia* sp.; 1♂, Monte Alban ruins, 3 Aug. 1964 (H.V. Daly; UCB). *VERA CRUZ:* 1♀, 2♂♂, Cotaxtla Exp. Sta., Cotaxtla, 9 Aug. 1962 (D.H. Janzen; UCB).

Centris (*Paracentris*) *nigrocaerulea* F. Smith

Centris nigro-caerulea F. Smith, 1874:369. ♀ ♂.
Centris clypeata Friese, 1899:41. ♀ ♂. Preoccupied. NEW SYNONYMY.
Centris (*Paracentris*) *anthracina* Snelling, 1966:14–17. ♀ ♂. NEW SYNONYMY.

DISCUSSION

I have examined the female and male type specimens of *C. nigro-caerulea* and they are conspecific with *C. clypeata* and *C. anthracina*. Smith's types are from an unspecified locality in Mexico; the female is herewith designated lectotype and the male as paralectotype. Both are in the collections of the British Museum (Natural History).

NEW RECORDS

MEXICO, *CHIAPAS:* 3♂♂, 7♂♂, 3 mi. W Navenchuac, 1–2 Apr. 1953 (R.C. Bechtel and E. I. Schlinger; UCB); 1♀, between Tuxtla [Gutierrez] and Chilapa, 23 Jan. 1974 (S. Buchmann; LACM), on *Cassia* sp. *JALISCO:* 3♂♂, "env. de Guadalajara," 1903 and May 1913 (L. Diguet; MNHN). *MORELOS:* 1♀, Cuernavaca, 6000 ft. elev., 7 Feb. 1954 (R.R. Dreisbach; UKAN). *OAXACA:* 1♂, Oaxaca, 12 Oct. 1963 (A.E. and M.M. Michelbacher; UCB); 4♀♀, 20 mi. S Taxco, 6 Feb. 1954 (R.R. Dreisbach; UKAN). *SONORA:* 1♂, Aduana (near Alamos), 15 Mar. 1962 (F.D. Parker; UCD); 1♂, Rio Cuchuhaqui, 8 mi. S Alamos, 1–13 Apr. 1975 (A. Brewster; LACM), on *Parkinsonia* sp. GUATEMALA: 3♀♀, San Miguel Duenas, 5200 ft. elev., 1–7 Dec. 1975 (S.W.T. Batra; LACM); 1♀, Ciudad de Guatemala, Dec. 1911 (W.M. Wheeler; MCZ); 1♀, Universidad del Valle, Ciudad de Guatemala, 25 Nov. 1975 (S.W.T. Batra; LACM). PANAMA, *CHIRIQUÍ:* 2♂♂, Potrero Grande, 28 Jan. 1981 (D.W. Inouye; ROUB).

Subgenus *Acritocentris* Snelling, 1974

Centris subg. *Acritocentris* Snelling, 1974:36. Type-species: *Centris* (*Melanocentris*) *ruthannae* Snelling, 1966; original designation.

In the years subsequent to the description of this subgenus and my treatment of its component species, I have been able to examine many more specimens than were then available. As a result, I can now provide a more adequate account of these species. The key given then (Snelling, 1974) will not always work for the females and should be replaced by the new one given below.

KEY TO SPECIES OF *ACRITOCENTRIS*

1a. Female, antenna 12-segmented and basitibial plate present 2
b. Male, antenna 13-segmented and basitibial plate absent 4
2a. Pubescence of thoracic dorsum whitish 3
b. All pubescence blackish .... *ruthannae* Snelling
3a. First abdominal tergite nearly impunctate toward apical margin, especially in middle; median area of clypeus dull and roughened but not rugose, laterad with rounded, separated punctures; basal shiny area of clypeus broadened in middle .... *albiceps* Friese

b. First abdominal tergite closely, though minutely, punctate to apical margin; median area of clypeus rugose and dull, laterad with coarse, close, elongate punctures; basal shiny area narrow across entire clypeal base . . . . *agameta* Snelling

4a. Thoracic dorsum dark pubescent 5

b. Thoracic dorsum pale pubescent 6

5a. Labrum, clypeus, paraocular area, and supraclypeal area all yellow-maculate . . . . *ruthannae* Snelling

b. Entire face black . . . . *satana*, new species

6a. Face marks whitish, absent from paraocular and supraclypeal areas, clypeus broadly blackish along lateral and basal margin, disc smooth and shiny . . . *albiceps* Friese

b. Face marks yellowish, usually present on paraocular and supraclypeal areas, lateral and basal margins of clypeus narrowly, or not at all, blackish, disc dull and roughened . . . . *agameta* Snelling

Centris (*Acritocentris*) *albiceps* Friese

Centris mexicana var. *albiceps* Friese, 1899:289. ♂.

Centris (*Melanocentris*) *strawi* Snelling, 1966:27–28. ♂. NEW SYNONYMY.

Centris (*Acritocentris*) *strawi* Snelling, 1974:37, 38 (in part) (key, distr.).

I suggested (1974) that *C. mexicana* var. *albiceps* might be an older name for *C. strawi.* Friese based this name on a specimen from an unknown locality in Mexico. The type is in the Berlin Museum and was examined at my request by R.W. Brooks who confirmed the above synonymy. The type is not so marked, and bears two labels: "11 6 59/Mexico" and "*Centris*/*mexicana*/v. *albiceps*/Friese 1898."

The females which in 1974 I believed to belong to *C. albiceps* (as *C. strawi*) are now known to be those of *C. agameta.* The true females of this species are very similar to those of *C. agameta,* but the disc of the clypeus, although dull and roughened, lacks the characteristic irregular rugulae present in *C. agameta.* The first two abdominal terga are much more weakly punctate toward the margins in *C. albiceps,* and in *C. albiceps* females the labrum and posterior pronotal lobes are without pale hairs.

NEW RECORDS

MEXICO, *CHIAPAS:* 3♀♀, 9♂♂, Municípío Chiapo de Corzo, El Chorreadero, 753 m elev., 1 Nov. 1976 (D.E. and J.A. Breedlove; CAS); 1♀, Municípío Motozintla, betw. Motozintla and Mazapa, 1219 m elev., 5 Oct. 1976 (D.E. and J.A. Breedlove; CAS). *HIDALGO:* 2♀♀, Zimapán, 6400 ft. elev., 8 Oct. 1957 (H.A. Scullen; ORSU). *MICHOACÁN:* 2♀♀, Lake Pátzcuaro, 6800 ft. elev., 21 Sept. 1957 (H.A. Scullen; ORSU); 1♂, 10 mi. N Morelia, 5900 ft. elev., 28 July 1962 (Univ. Kans. Mex. Exped.; UKAN), on Leguminoseae; 1♀, 2♂♂, Carapan, 1 Sept. 1962 (D.H. Janzen; UCB). *NUEVO LEÓN:* 1♀, 30 mi. N Linares, 1500 ft. elev., 11 Oct. 1957 (H.A. Scullen; ORSU). *OAXACA:* 1♂, 22 mi. SE Oaxaca, 5700 ft. elev., 2 Sept. 1957 (H.A. Scullen; ORSU); 1♀, 5 mi. NW Totolapán, 3800 ft. elev., 6 July 1953 (Univ. Kans. Mex. Exped.; UKAN) on *Lonchocarpus*; 5♀♀, 4 mi. N Totolapán, 1849 m elev., 15 Sept. 1975 (J.L. Neff; LACM, NEFF), on "*Cassia* 7064"; 1♀, 2 mi. S Totolapán, 15 Sept. 1975 (J.L. Neff; LACM), on "*Cassia* 7064"; 1♂, near Las Margaritas, 1400 m elev., 15 Sept. 1975 (J.L. Neff; LACM). *PUEBLA:* 1♂, 3 mi. NW Petlalcingo, 4600 ft. elev., 5 Sept. 1972 (Byers and Thornhill; UKAN); 1♀, 22 km NW Izúcar de Matamoros, 1158 m elev., 21 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Cassia laevigata. QUERÉTARO:* 1♀, 10 mi. S Jct. Hwy 55 and 45, 30 Aug. 1963 (Scullen and Bollinger; ORSU). *SAN LUIS POTOSÍ:* 1♀, 9 mi. E Ciudad [del] Maiz, 3975 ft. elev., 23 July 1962 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 5 mi. E Ciudad [del] Maiz, 4700 ft. elev., 22 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 11♂♂, 6 mi. W Guadalcazar, 2 Sept. 1975 (J.L. Neff; LACM, NEFF), on "mint 7031." *TAMAULIPAS:* 36♀♀, 38 mi. N El Mante, 1050 ft. elev., 11 Oct. 1957 (H.A. Scullen; ORSU); 16♀♀, 9, 12, and 24 mi. S [Ciudad] Victoria, 11 Oct. 1957 (H.A. Scullen; ORSU); 4♀♀, 15 mi. SW Ciudad Victoria, 5000 ft. elev., 19 Sept. 1976 (J.A. Chemsak et al.; UCB); 20♀♀, 35 mi. S Villagran, 15 Sept. 1977 (Chemsak and Michelbachers; UCB), on *Solanum*; 1♀, 7 mi. S Villagran, 26 Sept. 1975 (J. Powell et al.; UCB); 1♀, 15 mi. NE Juamava, 2500 ft. elev., 19 Sept. 1976 (J. Chemsak et al.; UCB). *VERA CRUZ:* 1♂, 3 mi. E Acultzingo, 1600 m elev., 21 Aug. 1977 (E.I. Schlinger; UCB); 1♀, 2♂♂, E Citlaltepetl, 6000 ft. elev., 25 June 1964 (L.W. Swan; CAS).

Centris (*Acritocentris*) *agameta* Snelling

Centris (*Acritocentris*) *agameta* Snelling, 1974:37–38. ♂.

NEW RECORDS

MEXICO, *GUERRERO:* 1♀, Acapulco, 6 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN). *JALISCO:* 3♀♀, 1♂, Hwy 15, 0.2 mi. from Nayarit State line, 11 Aug. 1963 (D. Byers; UKAN); 3♀♀, 6 mi. NE El Rincón, 3 Aug. 1971 (E.M. Fisher; LACM); 1♀, Puente Grande, 5000 ft. elev., 20 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN); 1♀, Barra de Navidad, 6 Sept. 1966 (E.M. Fisher; UKAN); 1♂, 3 mi. NW Tequila, 4000 ft. elev., 15 July 1953 (Univ. Kans. Mex. Exped.; LACM), on *Vitex pyramidata*; 1♂, 8 km W Tequila, 18 July 1951 (P.D. Hurd; UCB); 1♂, 7 km N Tequila, 6 Sept. 1975 (J.L. Neff; LACM); 1♂, 14 mi. NW [Río] Magdalena, 3500 ft. elev., 19 July 1953 (Univ. Kans. Mex. Exped.; UKAN), on *Vitex pyramidata. MORELOS:* 1♀, 14 mi. S Cuernavaca, 3 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 12 mi. E Cuernavaca, 4300 ft. elev., 14 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 8.7 mi. NE Yautepec, 4400 ft. elev., 15 Aug. 1963 (Ordway and Roberts; UKAN); on *Cuphea* sp.; 1♂, 6.7 mi. S Yautepec, 29 July 1963 (Naumann and Willis; UKAN). *NAYARIT:* 3♀♀, Ixtlán del Río, 5 Aug. 1963 (P. Fonda-Bonardi; LACM). *OAXACA:* 3♀♀, 1♂, Salina Cruz, 7 Sept. 1965 (D.H. Janzen; UKAN); 4♂♂, 20 mi. E El Camarón, 7 Aug. 1956 (J.W. MacSwain; UCB). *PUEBLA:* 1♀, 1♂, 7 mi. N Izúcar de Matamoros, 4450 ft. elev., 19 Aug. 1962 (Univ. Kans. Mex. Exped.; UKAN), on *Cuphea* sp. *SAN LUIS POTOSÍ:* 1♂, 9 mi. E Ciudad [del] Maiz, 3975 ft. elev., 23 July 1962 (Univ. Kans. Mex. Exped.; UKAN). *TAMAULIPAS:* 4♂♂, 40 km N Soto la Marina, 5 Sept. 1975 (E.M. and J.L. Fisher; LACM). *SINALOA:* 1♀, 7♂♂, 31 km N Mazatlán, 76 m elev., 29 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Antigonon leptopus.*

Centris (*Acritocentris*) *ruthannae* Snelling

Centris (*Melanocentris*) *ruthannae* Snelling, 1966:28–30. ♂ ♀.
Centris (*Acritocentris*) *ruthannae:* Snelling, 1974:37, 40 (distr.).

This species has been previously known only from southern Arizona.

NEW RECORDS

MEXICO, *CHIHUAHUA:* 1♀, Temoris, 13 Sept. 1970 (T.A. Sears et al.; UCD). *SINALOA:* 1♀, 2.5 mi. W Concordia, 25 Sept. 1977 (J.A. Chemsak, A. and M. Michelbacher; UCB). *SONORA:* 1♀, Bahia San Carlos, 20 July 1965 (D.S. Verity; LACM); 1♀, 20 km N Guaymas (Km 141), 16 Aug. 1979 (E.M. Fisher; LACM); 1♀, 1♂, Navajoa, 12 Sept. 1964 (A.E. and M.M. Michelbacher; UCB), on morning glory, 0750–0800; 2♀♀, 2♂♂, Cerro Masiaco, ca. 11 road mi. SSE Bacabachi, ca. 750 ft. elev., 29 Aug. 1976 (J.P. and K.E. Donahue; LACM); 1♂, 37 km SE Bacabachi (Km 90), 14 Aug. 1976 (E.M. Fisher; LACM), on *Caesalpinia* sp.

***Centris* (*Acritocentris*) *satana*, new species**

Figures 1–4

DIAGNOSIS

Male unique within *Acritocentris* by the entirely blackish integument and pubescence; female unknown.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 6.15 (5.33–5.74); head length 4.56 (4.00–4.10); wing length 13.5 (13.0–13.5); total length 18.0 (15.0–17.0).

Head. 1.35 (1.33–1.40) times broader than long; occipital margin, in frontal view, very weakly convex and barely raised above level of tops of eyes; ocelli well below occipital margin in frontal view; inner orbits weakly convergent above, upper frontal width 0.91 (0.85–0.87) times lower frontal width. Mandible slender, tridentate. Labrum about two-thirds as long as broad, apical margin narrowly rounded; disc shiny, moderately rugosopunctate to contiguously punctate. Disc of clypeus obtusely raised along midline over basal one-half, integument weakly to moderately shiny, surface with dense, moderate punctures or with very irregular, fine, anastomosing rugules; punctures on side of clypeus subcontiguous, elongate. Remainder of head shiny between fine to moderate, dense to subcontiguous punctures (sparse mesad in ocellocular area), but sparse, minute and obscure over most of gena. Interantennal distance 2.35 (2.13–2.33) times antennal socket diameter; antennocular distance 1.00 (0.87–0.97) times antennal socket diameter; scape moderately stout, 2.36 (2.29–2.42) times longer than wide, scape length 1.06 (1.08–1.14) times length of first flagellar segment; first flagellar segment shorter than length of following three segments combined, 4.00 (3.22–4.06) times length of second; interocellar distance 1.79 (1.61–1.90) times diameter of anterior ocellus; ocellocular distance 1.29 (0.94–1.16) times diameter of anterior ocellus; ocelloccipital distance 2.21 (1.97–2.09) times diameter of anterior ocellus.

Thorax. Mesoscutum shiny between subcontiguous to dense, moderate punctures; scutellum similar, but punctures contiguous to subcontiguous and slightly elongate. Mesepisternum moderately shiny, punctures dense, fine and oblique. Metepisternum shiny, punctures fine and sparse anteriorly, becoming dense to subcontiguous along posterior margin. Metafemur stout, more than twice longer than thick; metabasitarsus about three times longer than broad.

Abdomen. Tergal discs shiny between dense to sparse, fine to moderate punctures which become sparser mesad and on succeeding segments; punctures in apical zone minute. Pygidial plate narrowly truncate to shallowly notched at apex.

Terminalia. Seventh sternite (Fig. 1) with lateral margins of distal process convex, apical margin concave, with definite mesoapical row of short hairs. Eighth sternite (Fig. 2) with distal process slender, compressed; hairs numerous, long, coarsely plumose. Dorsal process of gonocoxite (Fig. 4) long, slender, nearly straight, slightly hooked at apex; gonostylus slender, setae long and coarse along basal margin, shorter and finer distad.

Pilosity. Hairs uniformly dark brown to blackish.

Color. Blackish brown, abdominal terga with strong bluish reflections. Mandible, antenna and legs reddish brown, femora more conspicuously reddish. Wings dark brown, veins and stigma black.

TYPE MATERIAL

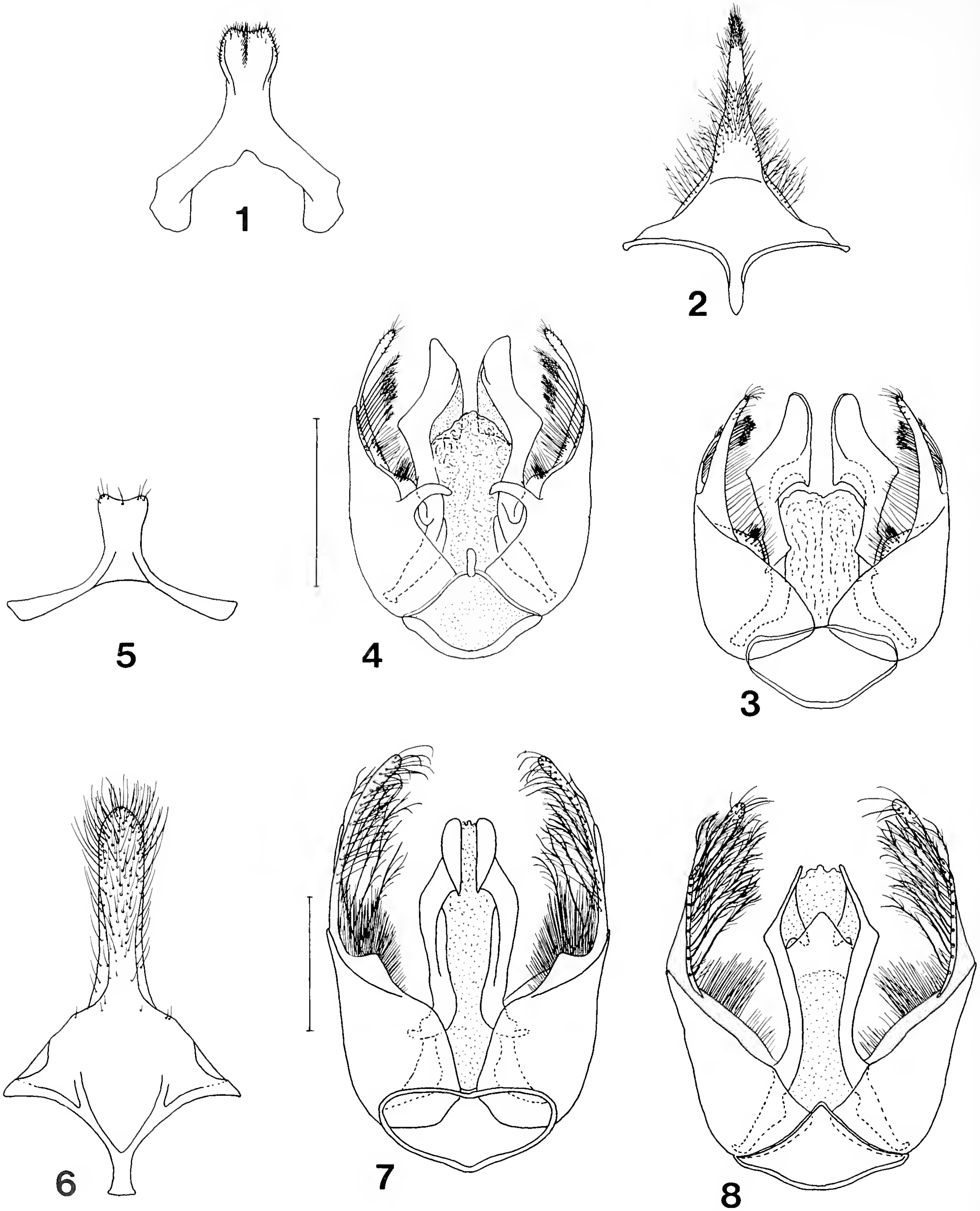
Holotype male: Tepoxtlan, Morelos, MEXICO, 28 Aug. 1964 (E. Fisher and D. Verity), in Natural History Museum of Los Angeles County. Paratypes, MEXICO: 1♂, Carapan, Michoacán, 1 Sept. 1962 (D.H. Janzen; UCB); 1♂, 3.4 km NW Tequila, 1295 m elev., Jalisco, 6 Sept. 1976 (C.D. George and R.R. Snelling; LACM); 1♂, 5 mi. W Durango, Durango, 21 July 1964 (J. Powell; UCB); 2♂♂, 25 mi. W Hidalgo del Parral, 6800 ft. elev., Chihuahua, 15 July 1964 (J.A. Chemsak, J. Powell; UCB); 1♂, "Guanajuato, Mexique" (Duges; MNHN). UNITED STATES: 1♂, Atascosa Mts, 4800 ft. elev., 5.6 mi. W Peña Blanca Lake, Santa Cruz Co., Arizona, 15 Aug. 1974 (T.J. Zavortink; TJZ), on *Acacia angustissima,* 1145–1200.

ETYMOLOGY

From Hebrew, literally an enemy or an evil spirit; in modern zoological nomenclature an epithet for a species of black or dark color or threatening appearance.

DISCUSSION

The wholly black pubescence will immediately separate *C. satana* from *C. agameta* and *C. albiceps,* since both have



Figures 1–8. Male seventh and eighth sternites and genitalia (ventral and dorsal views), respectively, of: **1–4,** *Centris* (*Acritocentris*) *satana,* scale line = 1.00 mm; **5–8,** *C.* (*C.*) *aethiocesta,* scale line = 0.50 mm.

pale dorsal thoracic pubescence. The black, rather than yellow, clypeus will distinguish *C. satana* from *C. ruthannae.* Additionally, males of *C. ruthannae* have metallic blue reflections on the abdominal terga and the hairs of the second and third segments are conspicuously plumose.

The female of *C. satana* is unknown, but very likely will be black-haired like the male and will have a similarly black abdomen, without metallic blue reflections.

Subgenus *Exallocentris* Snelling

Centris subg. *Exallocentris* Snelling, 1974:35. Type-species: *Centris* (*Melanocentris*) *anomala* Snelling, 1966; monobasic and original designation.

Although I had originally placed this monotypic subgenus near *Melanocentris,* Neff and Simpson (1981) have rightly pointed out its affinities to *Paracentris.* In *Exallocentris* the elaiospathe of the female pro- and mesobasitarsi is replaced by dense pads of fine-branched setae and the secondary basitibial plate is sharply marginate and projects over the primary plate. Males differ from those of *Paracentris* in lacking branched setae on the gonocoxite at the base of the gonostylus; a conspicuous pygidial plate is present, the innermost mandibular tooth is truncate, and the lateral ocellus is separated from the inner eye margin by about its own diameter. Males resemble those of *Melanocentris,* but the scutellum is not bilobed on its dorsal surface and the upper inner mandibular carina ends near the base of the innermost tooth.

Centris (*Exallocentris*) *anomala* Snelling

Centris (*Melanocentris*) *anomala* Snelling, 1966:31–32. ♂ ♀.
Centris (*Exallocentris*) *anomala:* Snelling, 1974:35–36 (tax.).

This species has previously been known only from the vicinity of Guadalajara, Jalisco, Mexico. I have recently seen a few specimens of the cleptoparasitic bee, *Mesoplia dugesi* (Cockerell), which were collected with the type series of *C. anomala.* One of the specimens bears the following note: "Ericrocis??/Very evasive. flying low/Parasite ?? of the/big Hemisia? not numerous."

NEW RECORDS

MEXICO, *HIDALGO:* 1♂, 22 mi. SW Actopan, 6800 ft. elev., 27 Aug. 1962 (Ordway and Marston; UKAN). *JALISCO:* 1♀, 103 mi. NE Guadalajara, 6200 ft. elev., 1 Oct. 1957 (H.A. Scullen; ORSU); 10♂♂, 8 mi. NE Chapala, 5150 ft. elev., 30 Sept. 1957 (H.A. Scullen; ORSU); 1♀, "env. de Guadalajara" (L. Diguet; MNHN). *MICHOACÁN:* 2♀♀, 33 km NE Arteaga (Hwy 37, km 242), 980 m elev., 10 Nov. 1976 (E. Fisher and P. Sullivan; LACM). *OAXACA:* 1♀, 9 mi. SE Nochixtlan, 7 Nov. 1963 (R.F. Smith; UCB); 3♂♂, Monte Alban, 12 Oct. 1963 (A.E. and M.M. Michelbacher; UCB). *PUEBLA:* 9♂♂, "env. de Tehuacan" (L. Diguet; MNHN). *ZACATECAS:* 1♀, 10 mi. S Jalpa, 18 Sept. 1970 (R.M. Bohart; UCD).

Subgenus *Xanthemisia* Moure

Xanthemisia Moure, 1945:401. Type-species: *Centris bicolor* Lepeletier, 1841; monobasic and original designation.
Hemisia subg. *Xanthemisia:* Michener, 1951:2, 3, 5–6.
Centris subg. *Xanthemisia:* Michener, 1954:140. Snelling, 1974:2, 3.

This subgenus was described for a small group of species characterized, in the females, by possessing a low, blunt tooth on the inner surface of the mandible, near the base of the apical tooth. In this sex, too, the pygidial plate is abruptly narrowed a short distance beyond the secondary plate so that the distal portion is narrow and parallel-sided. Males of *Xanthemisia* possess giant branched setae near the base of the gonostylus, which is much broadened on a vertical plane and the maxillary palp is four-segmented.

KEY TO NORTH AMERICAN *XANTHEMISIA*

1a. Male, antenna 13-segmented, basitibial plate absent 2
b. Female, antenna 12-segmented, basitibial plate present 4
2a. Labrum and clypeus wholly black; pubescence of dorsum of scutellum yellow; erect hairs of mesoscutum longer than interocellar distance 3
b. Labrum, entirely, and clypeus mostly, yellow; pubescence of dorsum of scutellum black; erect hairs of mesoscutum shorter than interocellar distance .... *rubella* F. Smith
3a. Pubescence of mesoscutum wholly yellow; abdomen black and wholly blackish pubescent; ocellocular distance less than diameter of anterior ocellus .... *lutea* Friese
b. Mesoscutum with interalar band of blackish pubescence; abdomen reddish, with golden brown pubescence; ocellocular distance greater than diameter of anterior ocellus .... *carolae* Snelling
4a. Clypeus immaculate and pubescence of dorsum of scutellum yellow; abdomen blackish or dark brown; scopal hairs dark 5
b. Clypeus usually with a pair of preapical spots; pubescence of dorsum of scutellum dark brown; abdomen dull ferruginous; scopal hairs pale .... *rubella* F. Smith
5a. Mesoscutum wholly yellow pubescent; abdomen blackish, with blackish pubescence; first flagellar segment longer than following three combined .... *lutea* Friese
b. Mesoscutum wholly blackish pubescent; abdomen dark brown with reddened apical zone and yellowish to yellowish red pubescence; first flagellar segment no longer than following three combined ...... *carolae* Snelling

Centris (*Xanthemisia*) *carolae* Snelling

Centris (*Xanthemisia*) *carolae* Snelling, 1966:24–25. ♂.

This species has been previously known only from the unique male type from Tuxtla Chico, Chiapas, Mexico. A few females are now available. They may be separated from our other species by the largely blackish pubescence on the thoracic dorsum, yellowish only on the scutellum and metanotum. The pubescence of the abdomen is dull reddish over the brownish integument.

NEW RECORDS

EL SALVADOR: 2♀♀, Cerro Verde, 6800 ft. elev., 29 June 1963 (M.E. Irwin and D.Q. Cavagnaro; UCB); 1♀, same data (CAS). COSTA RICA: 1♀, "El Fuente," 8 July 1937 (A. Alfaro No. 177; AMNH).

Centris (*Xanthemisia*) *lutea* Friese

Centris lutea Friese, 1899:43. ♂ ♀.
Centris (*Xanthemisia*) *lutea*: Michener, 1954:140 (distr.).

Among the North American *Centris*, this species is easily known by the wholly blackish pubescence, except that of the thoracic dorsum which is bright lemon-yellow. Michener (1954) recorded this primarily South American species from Panama.

NEW RECORDS

MEXICO, *CHIAPAS:* 2♂♂, 46 km N Chilpacingo, 580 m elev., 4–6 Aug. 1977 (E.M. Fisher and P. Sullivan; LACM). *JALISCO:* 1♂, 48 mi. N Guadalajara, 8 Sept. 1966 (R.J. Hamton; LACM). *OAXACA:* 1♂, 20 mi. E El Camarón, 21 July 1956 (J.W. MacSwain; UCB). COSTA RICA, *GUANACASTE:* 1♀, [Hacienda] Comelco, 8 km NW Bagaces, 21 Jan. 1972 (P.A. Opler; UCB), on *Byrsonima* sp.; 1♀, Hacienda Comelco, 24 km NW Cañas, 7 Feb. 1972 (E.R. Heithaus; LACM), on *Byrsonima crassifolia*, 0730–0830. *SAN JOSÉ:* 1♀, San José, no further data (USNM).

Centris (*Xanthemisia*) *rubella* F. Smith

Centris rubella F. Smith, 1854:372. ♀.
Hemisia (*Xanthemisia*) *rubella:* Michener, 1951:6 (tax.).

The ferruginous abdomen and maculate female clypeus will readily separate *C. rubella* from all other species of *Xanthemesia*. This species has previously been known only from South America.

NEW RECORDS

PANAMA, *CANAL ZONE:* 1♀, Barro Colorado Island, 19 Aug. 1968 (L.S. Kimsey; LACM), "wood nester"; 3♀♀, same locality, 27 Apr., 3 May, 5 May 1980 (K.E. Steiner; LACM, UCD), on *Byrsonima crassifolia*; 1♀, Gatun, 20 May 1980 (K.E. Steiner; UCD), on *B. crassifolia*; 3♀♀, same locality, 30 Oct. and 3 Nov. 1977 (K.E. Steiner; UCD), on *Stigmaphyllon hypargyreum*.

Subgenus *Centris* Fabricius

Centris Fabricius, 1804:354. Type-species: *Apis haemorrhoidalis* Fabricius, 1775; designated by Internatl. Comm. Zool. Nomencl., op. 567, 1959.
Hemisia Klug, 1807:227. Type-species: *Apis haemorrhoidalis* Fabricius, 1775; designated by Cockerell, 1906.
Centris subg. *Cyanocentris* Friese, 1900b:243. Type-species: *Apis versicolor* Fabricius, 1775; designated by Sandhouse, 1943.
Centris subg. *Poecilocentris* Friese, 1900b:244. Type-species: (*Centris* [*Poecilocentris*] *fasciatella* Friese, 1900) = *Centris fasciata* F. Smith, 1854; designated by Sandhouse, 1943.

Species in this subgenus normally have the abdomen metallic blue or blue-green in both sexes and with pale tergal maculae in the male and often in the female as well. In a few species, such as *C. inermis* Friese, the abdomen is largely ferruginous and in others, such as *C. eisenii* W. Fox, both sexes have much of the terga taken up by yellow bands. In both sexes, too, the mandibles, labrum, and clypeus are conspicuously maculate, the clypeal maculation of the female usually in an inverted T-shape or, more rarely, an inverted Y-shape. Both sexes have five-segmented maxillary palps, the female with slender, usually quadridentate, mandible, and a distinct secondary basitibial plate with an overhanging margin. Males possess giant branched setae along the inner margin of the styliform apical process of gonocoxite.

Some of the most exasperating taxonomic problems in *Centris* are encountered in the nominate subgenus. Many of the species are widely distributed and may be locally abundant. The more widely distributed species tend to exhibit a variety of phenotypes throughout their ranges, phenotypes that are often strikingly different from one another. Many of these variant populations have been given formal names. As a rule, these divergent populations represent selected points along a cline of variation and it is impossible to fix to any of these a discrete distribution and set of identifying characteristics.

The situation becomes more complex when a species is distributed through the islands of the Caribbean. Since the ranges are disjunct, the various insular populations tend to breed true. Even here, however, there usually are discrete clinal trends, proceeding from one end of the island distribution to the other. But, a great deal of collecting must be done in the Caribees before any understanding can be gained of these forms.

Further complicating the taxonomy of this subgenus is the fact that some species perhaps most, possess metanders, i.e., males which are unusually large and robust, with very stout legs, and much more extensively maculate than normal males. Metanders may be easily assumed to represent a different species. In general, all large, robust, richly marked males should be assumed to be probable metanders.

Yet another difficulty is that at least one species (*C. inermis*) is dichromatic in both sexes. There is a color phase with red abdomen and one with metallic blue-green abdomen. There is some evidence that one phase tends to fly earlier than the other, but there is a broad temporal overlap. Not surprisingly, the two color phases have been thought to be separate species. There are very likely more such cases in this subgenus.

The following key is for those species which occur in Central America; it does not include *C. errans* W. Fox, a species found only in Florida.

KEY TO CENTRAL AMERICAN *CENTRIS*, S. STR.

1a. Male, antenna 13-segmented and basitibial plate absent 2

b. Female, antenna 12-segmented and basitibial plate present 9

2a. Disc of fourth tergum with simple, usually blackish, hairs only (plumose hairs may be present on apical zone) 3

b. Disc of fourth tergum with abundant, usually whitish, suberect plumose hairs which extend onto apical zone (may be only a band across segment basad of apical zone, often extended cephalad in middle) 7

3a. Second to sixth abdominal terga with broad preapical yellow bands which cover most of each segment, narrow basal area bluish to rufescent, apical margin transparent; sterna largely rufescent 4

b. Second to sixth abdominal terga largely bluish or ferruginous, second usually with lateral spots only, following segments with lateral spots, narrow transverse bands (often interrupted and usually hidden under margin of preceding segment) or immaculate; if bands are present, they are dull reddish, usually interrupted in middle, and fourth tergum with broad area along distal margin with abundant plumose hairs 5

4a. Facial marks whitish; first flagellar segment at least 1.25 × scape length; hairs along apical band of fourth tergum dark, mostly simple .... *eisenii* W. Fox

b. Facial marks distinctly yellowish; first flagellar segment about as long as scape, rarely as much as 1.1 × scape length; apical band of fourth tergum with abundant plumose pale hairs .... *aethyctera* Snelling

5a. Ground color of abdominal segments ferruginous, second segment maculate at side, rarely with a complete or narrowly interrupted subbasal band; transverse bands of remaining segments, if present, hidden under margin of preceding segment 6

b. Ground color of first terga, and of sterna, bluish, sublateral spots or narrowly interrupted bands on one or more segments; rarely, second to sixth segments with broad, transverse, median yellowish or rufescent bands .... *inermis* Friese (part)

6a. Hairs of thoracic dorsum black-tipped .... *obscurior* Michener

b. Hairs of thoracic dorsum uniformly ochreous .... *inermis* Friese (part)

7a. Pubescence of thoracic dorsum uniformly ochreous to ferruginous, no blackish hairs present; smaller species, head width less than 6.1 mm and usually less than 6.0 mm; (metander unknown) 8

b. Pubescence of thoracic dorsum pale anteriorly and posteriorly, a broad interalar brown to black band present, often replacing much pale pubescence, especially on scutellum; larger species, head width at least 5.5 mm and usually over 6.3 mm (*metander* larger, robust, legs and abdomen abundantly yellow maculate or both areas largely ferruginous with limited yellow maculae) .... *flavifrons* group (see Text)

8a. Apical two or three abdominal terga reddish; mandible mostly yellowish on outer face; pubescence of thoracic dorsum usually ochreous .... *adani* Cockerell

b. Fourth and fifth, usually sixth, abdominal tergites blue, except colorless margins; mandible with small pale spot near base; pubescence of thoracic dorsum usually dark ferruginous .... *decolorata* Lepeletier

9a. Terga 2–5 each with entire transverse yellow fascia 10

b. Terga 2–5 without yellow fasciae 11

10a. Hairs of thoracic dorsum black-tipped; scape yellow beneath; fourth tergum with erect, plumose, white hairs; HW less than 6.0 mm .... *aethyctera* Snelling

b. Hairs of thoracic dorsum not black-tipped; scape immaculate beneath; fourth tergum with simple hairs only; HW at least 6.3 mm .... *eisenii* Fox

11a. Thoracic dorsum with conspicuous interalar band of black pubescence which may cover much of mesoscutum (sometimes reduced to median patch), sharply contrasting with pale scutellar hairs 12

b. Thoracic dorsum without interalar band of black pubescence; scutellar hairs not contrastingly colored 14

12a. Larger species, head width greater than 6.5 mm, but if as little as 6.25 mm, scopa is principally black; disc of clypeus, in profile, distinctly convex basad and flattened distad (Fig. 16) 13

b. Smaller species, head width 5.95–6.25 mm; scopa pale, with golden brown hairs apicad on metabitarsus; disc of clypeus, in profile, very weakly convex basad (Fig. 15) .... *aethiocesta*, new species

13a. Larger species, head width 7.17–7.7 mm; scopa with pale hairs at least anterobasally on metatibia, often largely pale; pygidial plate and basitibial plate as in Figs. 38 and 29 .... *flavifrons* (Fabricius)

b. Smaller species, head width 6.27–7.2 mm; scopa black, a few posteroapical hairs on metabasitarsus pale at tips; pygidial and basitibial plates as in Figs. 39 and 30 .... *flavofasciata* Friese

14a. Abdomen mostly ferruginous, one or more terga often partially bluish or greenish toward apical margin .. 15

b. At least first three terga wholly dark blue or blue-green 17

15a. Hairs of thoracic dorsum not dark-tipped; if slightly tipped, terga 2–4 with conspicuous apical hair bands; erect plumose hairs of tergum 4 pale 16

b. Hairs of thoracic dorsum conspicuously dark-tipped *and* terga 2–4 without apical hair bands; erect plumose hairs of tergum 4 dark .... *obscurior* Michener

16a. Terga 2–4 with conspicuous apical hair bands; basal margin of labrum convex across entire width, convex ridge with fine, widely spaced longitudinal ridges; external stripe of protibia not reaching apical three-fourths of segment .... *meaculpa*, new name

b. Terga 2–4 without apical hair bands; basal margin of labrum smooth and flat between punctures; external stripe of protibia reaching three-fourths, or more, of tibial length .... *inermis* Friese (part)

17a. Apical margin of tergum 4 and all of tergum 5 ferruginous; scopa entirely pale or entirely dark; terga 2–3 with or without apical hair bands 18

b. Terga 4 and 5 blue-green; scopa pale, with brownish setae posteriorly and apically on basitarsus; terga 2–3 without apical hair bands ..... *decolorata* Lepeletier

18a. Scopa black; terga 2–3 without apical hair bands; external stripe of protibia extending half, or more, length of segment .... *inermis* Friese (part)

b. Scopa pale; terga 2–3 with apical hair bands, that of 2 interrupted in middle; external stripe of protibia less than half length of segment, often absent .... *adani* Cockerell

Centris (*Centris*) *aethyctera* Snelling

Centris (*Centris*) *aethyctera* Snelling, 1974:23–26. ♂ ♀.

Centris aethyctera is a common species ranging from Mexico to Panama. It can only be confused with *C. eisenii* in this region, a larger species with the hairs of the thoracic dorsum without black tips. In previous literature it has been confused with the Antillean species, *C. fasciata* F. Smith (see Snelling, 1974), and all records of *C. fasciata* (or its synonym *C. fasciatella* Friese) in Central America seem to be based on *C. aethyctera.*

In Panamanian populations of *C. aethyctera* the bands of the abdominal terga are conspicuously shorter. The abdomen thus appears to be principally ferruginous, with short, transverse yellow fasciae across the disc of each segment.

Centris (*Centris*) *decolorata* Lepeletier

Centris decolorata Lepeletier, 1841:160. ♂.

Centris (*Cyanocentris*) *decolorata:* Friese, 1900b:243, 325. ♂ (not ♀?).

Centris versicolor: Cheesman, 1929:142. Misidentification.

Centris (*Centris*) *obscuriventris:* Michener, 1954:138. Misidentification.

Centris (*Centris*) *decolorata:* Snelling, 1966:23 (distr.).

Friese (1900b) associated females with *C. decolorata,* but noted that the association might be incorrect. In the event that this should prove to be true, he proposed that the females be called *C. obscuriventris.* Whether or not his female specimens actually are those of *C. decolorata* can only be determined after his specimens are examined. In the meantime, *C. obscuriventris* must be considered a name of dubious validity and identity.

There is no doubt, however, that Central American specimens, previously identified as *C. obscuriventris,* are conspecific with *C. decolorata,* a common species throughout the Caribbean islands, coastal northern South America, and eastern Central America. The range extends north to southern Texas, but *C. decolorata* appears to be absent from Florida, even though present on Cuba. The record from Cristóbal, Canal Zone, Panama, of *C. versicolor* by Cheesman (1929) is based on misidentified specimens of *C. decolorata.*

Centris (*Centris*) *errans* W. Fox

Centris errans W. Fox, 1899:65. ♀.

Centris versicolor: Lutz and Cockerell, 1920:561 (in part); Mitchell, 1962:335–336 (misidentification).

Centris (*Centris*) *versicolor:* Hurd, 1979:2175 (in part, misidentification).

This species occurs in Florida and has often been cited as *C. versicolor* (Fabricius, 1775). However, Moure (1960b) examined the type of *C. versicolor* and redescribed the type specimen; the true *C. versicolor* is "probably confined to lesser Antilles," according to Moure. Until all the representatives of this very difficult complex can be reexamined, it seems best to follow Moure's restricted interpretation of *C. versicolor* and to regard *C. errans* as a distinct species.

Centris (*Centris*) *inermis* Friese

Centris inermis Friese, 1899:46. ♂ ♀.

Centris poecila var. *segregata* Crawford, 1906:159. ♀. NEW SYNONYMY.

Centris inermis var. *gualanensis* Cockerell, 1912:568. ♂. ♀.

Centris (*Rhodocentris*) *robusta* Cockerell, 1949:478–479. ♂. NEW SYNONYMY.

Centris inermis subsp. *pallidifrons* Cockerell, 1949:479. ♂.

Centris (*Centris*) *inermis:* Snelling, 1974:30 (syn., var.).

Centris (*Centris*) *segregata:* Snelling, 1974:34–35 (tax., distr.).

This is a common Central American species, ranging from Mexico to Panama and into northern South America. It is also a very unusual species, one which suggests that the taxonomy of the nominate subgenus may be fraught with more complexities than was previously supposed. Males of *C. inermis* are morphologically bimodal; there is a metandric form, very different in appearance from the normal males. Additionally, however, there are two very different color phenotypes in both sexes.

The nominate phenotype, in both sexes, has the legs and abdomen ferruginous; in females there is usually a conspicuous patch of metallic blue across the base of the fourth tergite. The second phenotype was described as *C. poecila* var. *segregata* and later considered to be a separate species. In this form the legs are blackish brown and the first four abdominal segments are dark metallic blue.

The recognition of *C. segregata* as a synonym of *C. inermis* is possible thanks to the observations of R. Coville and G. Frankie. They have found that emergent bees from nests provisioned by *C. inermis* females were, sometimes, the blue-abdomen form, *C. segregata.* This fact, coupled with the lack of morphological differences between the two forms, is the basis for the current synonymy. Additional support lies in the complete allopatry of the two forms. Frankie and Coville will publish their observations separately.

Centris (Centris) meaculpa, new name

Figure 33

Centris (*Cyanocentris*) *nitens:* Friese, 1900b:330. ♀ (in part; misidentification).

Centris (*Centris*) *erubescens* Snelling, 1974:27–28. ♀. Preoccupied.

My *C. erubescens* is a junior homonym of *C. costaricensis* var. *erubescens* Friese, 1925, a synonym of *C. vittata* Lepeletier. The new specific epithet is, of course, the Latin phrase for "my fault" and seems apropos in this case.

In some of the specimens recorded below, the abdominal tergites, especially the second to fourth segments, are extensively bluish, rather than wholly ferruginous. They thus somewhat resemble females of *C. adani*. However, *in C. adani* the erect hairs of the the fourth tergite are longer and are plumose at their tips, as noted in the key. In most specimens of *C. meaculpa* the clypeus is more or less distinctly obliquely rugulose, the rugulae directed toward the apical middle portion of the segment. The clypeus of *C. adani* tends to be smooth between well spaced punctures.

The female which Friese (1900b) recorded from Mexico as *C. nitens* Lepeletier, a Brazilian species, is misidentified. The specimen is in the Paris Museum and has been made available to me; it is a female of *C. meaculpa* with the first three abdominal terga primarily metallic bluish and the specimen agrees well with the characteristics of this species, especially in the structure of the labrum and of the basitibial plate.

When I originally described this species, I was not fully aware of its apparent affinities with a small group of primarily Brazilian species. Included in this group are *C. aenea* Lepeletier, 1841, *C. caixensis* Ducke, 1907, and *C. nitens* Lepeletier, 1841. Females of this group are similiar in that the pubescence of the thorax is ochreous (paler on the sides), the abdominal terga, except the fifth and sixth, are metallic greenish to bluish, the discs of the second and third segments possess abundant appressed simple hairs, and the margins of the second and third segments have a definite fascia of appressed pale hairs which may be plumose. In these Brazilian species the basal margin of the labrum is flat and is smooth and shiny between sparse punctures. The labrum of *C. meaculpa* has a definite convexity across the basal margin and the convex area is crossed by widely spaced longitudinal ridges.

Of the Brazilian species, *C. caixensis* appears to be the most distinct. I have seen a single female, marked as "Type," from the collections of the Paris Museum: Maranhão, Caixas, 30 June 1907, collected by A. Ducke. The second to fifth terga each bear a small, lateral, pale yellow mark; the basitibial plate (Fig. 32) is short, and the secondary plate is short, broad, and convexly transverse. In all of the other species, including *C. meaculpa* (Fig. 33), the secondary plate is elongate, with its anterior margin approximately parallel with, and well removed from, the anterior margin of the primary plate. The fascial hairs of the second and third terga of *C. caixensis* are yellow and simple.

Of the two remaining species, *C. aenea* may be recognized by the golden or somewhat coppery color of the discal and fascial hairs of the second and third terga. In *C. nitens* the discal hairs are fuscous, sharply contrasting with the golden to coppery color of the fascial hairs. The secondary pygidial plate is more abruptly narrowed in *C. nitens,* which is the smaller of the two species.

This species was described from two females 67 km E Escarcega, Campeche, Mexico. A few additional specimens are now available.

NEW RECORDS

MEXICO, *TAMAULIPAS:* 1♀, 8 mi. NW Nuevo Morelos, 22 July 1962 (Univ. Kans. Mex. Exped.; UKAN), on *Kallstroemia* sp. *SAN LUIS POTOSÍ*: 1♀, El Salto, 1800 ft. elev., 8 June 1961 (Univ. Kans. Mex. Exped.; UKAN); 1♀, El Salto (above falls), 21 July 1962 (Ordway and Roberts; UKAN), on Leguminoseae. *VERA CRUZ:* 1♀, 22 mi. SE Jalapa, 1100 ft. elev., 29 June 1953 (Univ. Kans. Mex. Exped.; UKAN); 2♀♀, 3 mi. SW Paso del Toro, 50 ft. elev., 23 June 1961 (Univ. Kans. Mex. Exped.; UKAN). *YUCATÁN:* 1♀, Piste, 12 June 1967 (E.C. Welling; LACM). *STATE UNKNOWN:* 1♀, "Mexique, Cote Occid.," no date except 1864 (L. Biart; MNHN).

Centris (*Centris*) *obscurior* Michener

Centris (*Centris*) *obscurior* Michener, 1954:138–140. ♀ ♂.

This species has previously been reported only from Panama.

NEW RECORDS

COSTA RICA, *HEREDIA:* 1♀, Puerto Viejo, Sarapiqui, 30 July 1965 (D.H. Janzen; UKAN); 8♀♀, 37♂♂, Finca La Selva, near Puerto Viejo, 6 May to 27 July (D.R. Perry; LACM), on *Dipteryx panamensis, Dussia* sp., *Hymenolobium* sp., *Byrsonima* sp., and *Vochysia* sp. *PUNTARENAS:* 1♀, 6 km S San Vito, 19–21 Mar. 1967 (UKAN). *SAN JOSÉ:* 2♀♀, San José, 1160 m elev., 17 July 1964 (M. Naumann; UKAN), on *Solanum* sp.; 2♀♀, San José, 1160 m elev., 8 June 1963 (C.D. and D.R. Michener; UKAN), on *Solanum wendlandi*; 2♀♀, Ciudad Universitaria, San José, 28 July 1965 (S.J. Arnold; UCB), on *Duranta repens*; 16♀♀, 1 mi. ESE San Isidro de General, 21 July 1965 (S.J. Arnold; UCB), on *Rhynchanthera mexicana,* 0815–0950. MEXICO, *CHIAPAS:* 1♀, Simojovel, 1–16 Aug. 1958 (J.A. Chemsak; UCB); 1♀, Santo Domingo, 15 mi. S Simojovel, 8 July 1958 (J.A. Chemsak; UCB); 3♂♂, 3 mi. SE San Juan del Bosque, 16 Aug. 1958 (J.A. Chemsak; UCB); 1♀, Yaxoquintela, 560 m elev., 30 Aug. 1978 (J.E. Rawlons; CORN).

Centris (*Centris*) *flavifrons* Group

To this group are assigned a number of medium-sized to large species in which the integument of the head, thorax, and legs is blackish with limited whitish or yellowish marks on the face and legs. The abdomen is mainly metallic blue to blue green, in the males with yellowish maculations, at least in the second tergite; the apical segments may be reddish. In both sexes the thorax is either largely cinereous pubescent and with a broad interalar band of blackish hairs, or principally dark pubescent but with the scutellum and metanotum pale pubescent. The wings are light brownish to blackish.

Morphologically, the species tend to be very similar and species limits are, at present, very poorly understood. The following key will serve to separate those species which I am presently able to recognize.

KEY TO SPECIES, *C. FLAVIFRONS* GROUP

1a. Male, antenna 13-segmented and basitibial plate absent 2

b. Female, antenna 12-segmented and basitibial plate present 6

2a. Ocellocular distance no more than 0.90 times diameter of anterior ocellus and usually less; lower inner mandibular carina ending in a small, obscure tooth-like process (Fig. 13); smaller species, head width less than 5.8 mm 3

b. Ocellocular distance at least 0.95 times diameter of anterior ocellus and often greater; lower inner mandibular carina often terminating in a prominent tooth-like process (Fig. 14); usually larger species, head width usually more than 6.0 mm, but may be a little as 4.8 mm . . 4

3a. Clypeus moderately shiny, punctures fine and close, interspaces very finely roughened; apical margin of third tergite with transverse band of pale yellowish hairs; pubescence of side of propodeum pale (Ecuador, Peru) . . . . *buchwaldi* Friese

b. Clypeus shiny and subpolished between fine, close punctures, except in broad, impunctate median line; third tergum blackish pubescent along apical margin; side of propodeum brown pubescent (El Salvador, Costa Rica, Panama) . . . . *aethiocesta,* new species

4a. Larger species, head width always over 5.2 mm and usually greater than 6.0 mm; clypeal disc, at least in large part, shiny and weakly, or not at all, tessellate; second tergum, at least, with transverse yellow fascia across base, sometimes narrowly interrupted in middle (widespread) 5

b. Smaller species, head width less than 5.0 mm; clypeal disc moderately shiny, conspicuously tessellate and roughened, more weakly so along midline; second tergum with a pair of widely separated spots (Eucador) . . . . *nigrofasciata* Friese

5a. Lower inner mandibular carina ending in a long, acute tooth-like process. *Normal male* with broad, basal, yellow fasciae across base of second to fourth terga which are complete or narrowly interrupted, that of second nearly as long as apical area beyond it; punctures of clypeal disc numerous and close, interspaces more or less distinctly tessellate, especially basad. *Metander* with clypeus slightly roughened, punctures close to sparse; clypeal disc entirely yellow (S Arizona to Panama) . . . . *flavofasciata* Friese

b. Lower inner mandibular carina ending in low, obtusely triangular process (Fig. 14). *Normal male* with narrow basal fasciae on second to fourth terga, that of second often broadly interrupted in middle, or, when complete, distinctly shorter in middle than apical area beyond it; clypeal disc smooth and polished, punctures at side sparse. *Metander* with clypeus smooth and polished, punctures sparse to scattered; laterobasal black mark of clypeus extending onto disc (widespread) . . *flavifrons* (Fabricius)

6a. Apical margin of third tergite with a narrow band of white or yellowish red hairs which sharply contrast with the black discal hairs, the pale hairs closer than those of disc and projecting well beyond margin 7

b. Apical margin of third tergite, across middle one-half with hairs short, black, no closer than short, black hairs of disc and hardly projecting beyond margin of segment 8

7a. Scopa pale; marginal hairs of third tergite whitish, straight; scape pale beneath; fifth tergite wholly ferruginous (Ecuador) . . . . *nigrofasciata* Friese

b. Scopa dark; marginal hairs of third tergite yellowish red, their tips curved laterad; scape dark; fifth tergite mostly metallic blue-green (Ecuador, Peru) . . *buchwaldi* Friese

8a. Head width usually exceeding 6.7 mm, rarely as little as 6.2 mm; scopa usually mostly dark; clypeal punctures moderate in size and on side of disc separated by a puncture diameter or more; hairs of side of propodeum pale, but if dark, pleural hairs also dark 9

b. Head width less than 6.3 mm; scopa pale; elypeal punctures fine and close; pleura with pale hairs and side of propodeum with brown hairs (El Salvador, Costa Rica, Panama) . . . . *aethiocesta,* new species

9a. Larger species, head width 7.0–7.7 mm; scopa with pale hairs, at least anterobasally on metatibia, often largely pale; pygidial and basitibial plates as in Figs. 38 and 29 (widespread) . . . . *flavifrons* (Fabricius)

b. Smaller species, head width 6.2–7.2 mm; scopa black, a few pale-tipped hairs posteroapically on metabasitarsus; pygidial and basitibial plates as in Figs. 39 and 30 (S Arizona to Panama) . . . . *flavofasciata* Friese

Centris (*Centris*) *aethiocesta,* new species

Figures 5–8, 13, 15, 31, 40

Centris (*Centris*) *nigrofasciata:* Michener, 1954:138. Misidentification.

DIAGNOSIS

Medium-sized species with thoracic pubescence whitish, but with black interalar band and brown pubescence on propodeal side; abdomen metallic blue-green. Female with pale scopa, broad basitibial plate, and clypeal disc flattened in profile. Male with clypeal disc flattened in profile; abdominal terga 4–7 metallic green, immaculate; punctures of clypeal disc numerous and mostly separated by about a puncture diameter.

DESCRIPTION

HOLOTYPE FEMALE. Measurements (mm). Head width 5.54 (5.95–6.26); head length 4.26 (3.95–4.21); wing length 11.0 (11.0–12.0); total length 15.5 (16.6–18.0).

Head. 1.43 (1.49–1.53) times broader than long; occipital margin nearly flat in frontal view and slightly below level of tops of eyes; ocelli anterior to occipital margin; inner orbits moderately convergent above, upper frontal width 0.90 (0.89–0.92) times lower frontal width. Mandible slender, tridentate, apical margin oblique. Labrum about twice broader than long, apical margin narrowly rounded. Disc of clypeus weakly depressed, nearly flat in profile (Fig. 15); broad median line impunctate, punctures fine on either side and mostly separated by about 1.5 times a puncture diameter, interspaces shiny, a little less so basad. Frons slightly to moderately shiny between fine, subcontiguous punctures; ocellocular area moderately shiny, impunctate adjacent to ocellus, densely to subcontiguously punctate near eye, with fine and minute punctures; preoccipital area slightly shiny between dense to subcontiguous fine punctures; gena shiny between irregularly close to subcontiguous punctures which are minute near eye, becoming fine to moderate ventrad. Interantennal distance 3.41 (3.13–3.48) times antennal socket diameter; antennocular distance 1.63 (1.57–1.63) times antennal socket diameter; scape slender, 2.29 (2.23–2.36) times longer than wide, scape length 0.72 (0.70–0.75) times length of first flagellar segment; first flagellar segment 5.28 (5.28–5.50) times length of second and distinctly longer than combined length of following three segments. Interocellar distance 2.09 (2.00–2.12) times diameter of anterior ocellus; ocellocular distance 1.31 (1.32–1.45) times diameter of anterior ocellus; ocelloccipital distance 1.88 (1.88–2.03) times diameter of anterior ocellus.

Thorax. Mesoscutum shiny between fine, dense punctures; scutellum similar, but punctures dense to subcontiguous and narrow median line impunctate; metanotum moderately shiny between scattered minute punctures; meso- and metepisterna shiny between dense, fine punctures. Basal area of propodeum moderately shiny, sharply tessellate and with sparse fine punctures except along anterior margin; propodeal side shiny between dense, fine punctures. Basitibial plate (Fig. 31) about twice longer than wide, lower margin broadly rounded; lower margin of secondary plate rounded.

Abdomen. First three terga shiny between dense, minute punctures; fourth and fifth terga shiny between dense, fine punctures which are a little more separated than on basal segments; pygidial plate (Fig. 40) narrow, apex narrowly truncate; secondary plate with margins slightly concave toward gradually narrowed apical ridge.

Color. Head, thorax, and legs blackish brown; scutellum dull reddish; first to fifth abdominal terga metallic blue-green, fourth and fifth more greenish; abdominal sterna brownish, with obscure metallic greenish tints, especially laterad. The following whitish: basal spot on mandible; labrum, except apex and along basal margin (sometimes reduced to lateral spots); inverted T-shaped clypeal mark (may be reduced to narrow median stripe and sublateral, preapical spots); narrow supraclypeal mark (present only in holotype); elongate spot on malar area; broad mark on paraocular area, ending narrowly on eye margin at, or slightly above, level of lower margin of antennal socket; basal spot on pro- and mesotibia (preapical protibial spot sometimes present). Tegula reddish. Wings dark brown; veins and stigma blackish.

Pilosity. Hairs whitish on head, but with broad preoccipital band of long, dark brown hairs; ocellar area pale-haired, but with brownish hairs on frons anterior to ocelli. Hairs of thorax whitish, but with broad interalar band of dark brown hairs and brown hairs on metepisternum and side of propodeum. Hairs on front face of first tergum pale; hairs on dorsal face of first, and on second and third terga appressed, simple, blackish, very short; hairs of fourth and fifth terga long, erect, mostly plumose, whitish; prepygidial fimbria golden reddish to brown. Hairs of legs mostly brownish black, but with glistening whitish hairs on coxae, trochanters, and posterior margins of profemora and protibia; scopal hairs whitish, becoming brownish distad on metabasitarsus.

MALE. Measurements (mm). Head width 5.79 (5.33–5.85); head length 3.79 (3.44–3.79); wing length 12.0; total length 14.0

Head. 1.53 (1.51–1.56) times broader than long; occipital margin nearly flat in frontal view and slightly below tops of eyes, ocelli anterior to occipital margin; inner orbits very strongly convergent above, upper frontal width 0.80 (0.72–0.82) times lower frontal width. Mandible slender, tridentate, inner tooth broad and with its apical margin concave. Labrum about 1.6 times broader than long, moderately shiny between sparse fine punctures and with interspersed minute punctures. Disc of clypeus nearly flat in profile, about as in female, moderately shiny, with broad median impunctate line, punctures on either side fine, mostly separated by about a puncture diameter. Punctation of remainder of head about as in female. Interantennal distance 2.72 (2.47–2.81) times diameter of antennal socket; antennocular distance 0.79 (0.77–0.93) times diameter of antennal socket; scape stout, 2.18 (2.07–2.18) times longer than wide, 0.71 (0.70–0.79) times length of first flagellar segment; first flagellar segment 5.60 (5.33–5.60) times length of second and longer than following three segments combined. Interocellar distance 1.82 (1.84–1.94) times diameter of anterior ocellus; ocellocular distance 0.88 (0.84–0.90) times diameter of anterior ocellus; ocelloccipital distance 1.76 (2.00–2.06) times diameter of anterior ocellus.

Thorax. As described for female, but mesoscutal punctures subcontiguous and scutellum slightly depressed along midline. Metafemur about twice longer than thick (dorsoventrally); metabasitarsus about three times longer than broad, posterior margin weakly curved.

Abdomen. As described for female; apex of last tergite broadly bilobate.

Terminalia. Sides of distal process of seventh sternite (Fig. 5) slightly divergent distad, apical margin weakly incised; setae short, sparse, simple. Distal process of eighth sternite (Fig. 6) weakly narrowed subbasally; setae long, numerous.

Gonostylus (Figs. 7, 8) a little broadened distad; ventral process broadly rounded.

Pilosity. As described for female, but hairs of apical abdominal sternite pale brown; hairs of metatibia and metabasitarsus mostly dark brownish, but with some along posteroapical margins of metatibia golden brown and some along posterior margin of metabasitarsus light brown, with pale tips.

Color. Body color as described for female, except whitish marks as follows: spot at base of mandible; entire labrum; clypeus, except along laterobasal margin; broad supraclypeal mark; spot on malar area; paraocular area, ending narrowly on inner eye margin slightly above level of lower margin of antennal socket; underside of scape; basal spot on all tibiae; outer stripe on protibia; sublateral mark at base of second tergite. Tarsi reddish brown to brown. Wings light brown.

TYPE MATERIAL

Holotype female and allotype: airstrip, Isla El Rey, Islas Perlas, PANAMA, 22 Feb. 1981 (D.W. Roubik), flying around *Dioclea megacarpa*, in Natural History Museum of Los Angeles County. Paratypes: 1♀, same data as holotype; 5♂♂, Coiba Island, Veraguas, PANAMA, 21–24 Oct. 1979 (D. Roubik); 1♀, Fort Kobbe, Canal Zone, PANAMA, 9 Sept. 1958 (W.J. Hanson); 1♂, Patilla Point, Canal Zone, PANAMA, 15 Jan. 1929 (C.H. Curran); 1♂, Bruja Point, Canal Zone, PANAMA, 25 Jan. 1929 (C.H. Curran); 1♀, La Chorrera, Panamá, PANAMA, 22 May 1912 (A. Busck); 1♂, 5 km E Comarca de San Blas, Puerto Obaldia, PANAMA, 11 Oct. 1979 (D. Roubik); 3♀♀, Tamarindo Beach, Guanacaste, COSTA RICA, 28 Feb. 1980 (G.W. Frankie); 2♀♀, same locality and collector, 30 Mar. 1980, on *Haematoxylon brasiletto*; 2♂♂, La Union, Playa El Icacal, EL SALVADOR, 8 July 1975 (E.M. and J.L. Fisher). Paratypes in AMNH, LACM, ROUB, UCB, UKAN, and USNM.

ETYMOLOGY

Combines the Greek words *aithiops* (swart or dark) and *kestos* (girdle or band).

DISCUSSION

Although this species superficially looks much like *C. flavifrons* and *C. flavofasciata*, it is smaller than either. The disc of the clypeus, in profile, is distinctly flatter in *C. aethiocesta* than in the other two species (compare Fig. 15 with Fig. 16) and, in both sexes, the disc is more closely and abundantly punctate. Small females of *C. flavofasciata* may be no larger than females of *C. aethiocesta* but have the tibial scopa black and the hairs of the side of the propodeum are whitish. The much larger size (head width greater than 7.0 mm) will separate *C. flavifrons* females from *C. aethiocesta*, as will the sparser clypeal punctation and the differently shaped basitibial plate. Males of *C. aethiocesta* have the apical abdominal segments dark and immaculate; in *C. flavifrons* and *C. flavofasciata* males the apical segments are usually reddish and commonly are yellowish maculate; in these two species, the hairs of the propodeum are usually whitish.

Two South American species also resemble *C. aethiocesta* and are of about the same size. Females of *C. buchwaldi* Friese, 1900, have a dark scopa, pale propodeal hairs, a band of prostrate, simple, golden brown hairs across the apical margin of the third tergite, and the erect hairs of the fourth tergite are simple. In females of *C. nigrofasciata* Friese, 1899, there is a band of pale hairs across the apical margin of the third tergite, the apical margin of the fourth tergite is ferruginous, the fifth tergite is ferruginous and with simple erect hairs, and the basitibial plate is more elongate, with a more acute apex.

In the males of both *C. buchwaldi* and *C. nigrofasciata* the clypeus is only slightly shiny, with the integument conspicuously roughened. Neither of these has brown hairs on the side of the propodeum and in both species the fifth and sixth tergites are ferruginous. Males of *C. nigrofasciata* also differ in that the ocellocular distance is greater than the diameter of the anterior ocellus.

Centris (*Centris*) *flavifrons* (Fabricius)

Figures 14, 29, 38

Apis flavifrons Fabricius, 1775:383. ♂.
Apis flavifrons brasiliana Christ, 1791:140.
Centris flavifrons: Lepeletier, 1841:152. F. Smith, 1874:361.
Centris citrotaeniata Gribodo, 1894:267. ♀. NEW SYNONYMY.
Centris flavifrons var. *nigritula* Friese, 1899:46. ♀. NEW SYNONYMY.
Centris flavifrons var. *rufescens* Friese, 1899:46. ♂. NEW SYNONYMY.
Centris (*Cyanocentris*) *flavifrons:* Friese, 1900b:317–318 (in part) (tax., distr.).
Centris (*Centris*) *flavifrons:* Michener, 1954:137 (distr.). Moure, 1960b:125–126 (tax.).
Centris (*Centris*) *rufescens:* Michener, 1954:137 (tax., status).
"*Centris fulvifrons*" Moure, 1960a:10 (lapsus for *C. flavifrons*).
Centris (*Centris*) *citrotaeniata:* Moure, 1960a:10–11 (tax.).
Centris (*Centris*) *nigritula:* Snelling, 1974:30–31 (tax. status).

Moure (1960b) examined and redescribed the type of *C. flavifrons*, from "Brasilia." He noted that, according to current concepts, *C. flavifrons* ranges from southern Brazil to Mexico. Throughout this range this is often a common bee and one subject to considerable variation. It is now apparent that my effort to separate *C. f. nigritula* as a distinct species (Snelling, 1974) was futile. Since that time I have examined several hundred specimens and seen so broad a range of variation that it is now apparent that *C. nigritula* is not worthy of recognition at any level.

Friese (1899) described *C. flavifrons* var. *rufescens* from a male from Chiriquí, Panama. It was said to differ from the nominate form in possessing wide, yellow abdominal bands and reddish pubescence on the legs. Although Michener (1954) thought that this seemed to represent a distinct species, I do not agree. Neither Michener nor I has seen the type of var. *rufescens* but I suspect that it is nothing more than a metander. Metanders of both *C. flavifrons* and *C. flavofasciata* are characterized by possessing broad abdominal fasciae and ferruginous pubescence on the legs. Since nothing in Friese's brief description would indicate to which of these species this form should be assigned, I have arbitrarily elected to follow Friese and include it under *C. flavifrons,* as a synonym. In Panama, *C. flavifrons* is more common than is *C. flavofasciata* and it seems more likely than the var. *rufescens* belongs with the former species.

Centris citrotaeniata was also described from Chiriquí, Panama, based on a single female specimen. The type is in the collections of the Museu Civico de Storia Naturale, Genoa, Italy, and was examined by Moure (1960a). Moure noted that this species was close to "*C. fulvifrons,*" evidently a lapsus for *C. flavifrons.* From the original description, as well as the supplemental notes provided by Moure, it is clear that *C. citrotaeniata* is equivalent to dark Panamanian individuals of *C. flavifrons,* and so Gribodo's species is here placed in synonymy.

Variation in females of *C. flavifrons* chiefly involves the extent of pale versus blackish pubescence on the thorax and on the scopa. In females from Brazil the thoracic hairs are mostly whitish, with a conspicuous broad interalar band of blackish pubeseence; a few dark brown hairs are present below the wing bases and the scopa is uniformly pale. In material from Guyana and French Guiana, there is considerable replacement of the pale pleural hairs by blackish hairs and the scopa is largely dark, but with conspicuous white hairs anteriorly on both the tibia and basitarsus. This dark variant also has many dark hairs on the fourth and fifth terga. A similar variant also appears sporadically in samples from Panama and Costa Rica. The darkest phenotype is from Trinidad, the var. *nigritula.* In these specimens, the thorax is entirely blackish pubescent, with only the axilla, scutellum, and thoracic venter whitish pubescent. Curiously, the scopa is predominantly pale, with only a few brownish hairs distally on the tibia and along the posterior margin of the basitarsus. Some of the Panamanian females have the thoracic hairs wholly pale, except for a small median patch of dark hairs on the mesoscutum; in these individuals the scopa is mainly dark.

The Central American populations vary on a smaller scale. Specimens from Mexico typically have a large inverted T-shaped clypeal mark, the labrum is mostly dark and the lateral face mark fills the paraocular area below the level of the tentorial pit. The transverse mesoscutal fascia of dark hair is preceded by a narrow band of white pubescence, the mesopleuron is largely dark pubescent, and the tibial scopa is only about one-half pale. Coloration becomes progressively darker toward the south and specimens from Costa Rica may be much darker: the labrum wholly black, the clypeal mark broken into two or three narrow segments, and the mesoscutum with only a small cluster of pale hairs on the anteromedian portion; the scopa is almost entirely dark, with pale hairs anteriorly on the metatibia and anterobasally on the metabasitarsus. Another characteristic of the Costa Rican specimens is that the hairs of the dorsal face of the first tergite are blackish. In the Mexican specimens the hairs are pale at the sides and across the basal portion of the dorsal face.

The tendency toward increasing melanism is partially reversed in Panama. A long series from Panamá Province, collected by R.W. Brooks, exhibits considerable variation. In some specimens the interalar fascia is nearly absent and in others it may cover up to two-thirds of the mesoscutum. In most specimens the mesepisternum has only a few dark hairs below the tegula and in others there may be a blackish hair patch over the upper one-half or more of the segment. The scopa varies from nearly wholly pale to about one-half black. Face marks may be greatly reduced: mandible and labrum entirely dark; clypeus with narrow median line and widely separated apicolateral spots and scape wholly dark. Reduction of face marks is not correlated with increased melanism in pubescence. Many of these specimens will match the color pattern of the type of *C. citrotaeniata.*

The darkest Costa Rican specimens superficially resemble the form from Guyana, French Guiana, and Trinidad described by Friese as the var. *nigritula.* They differ from that form, however, in that the plumose hairs of the fourth tergite are uniformly pale. In the var. *nigritula* there are many dark hairs on the fourth tergite and, in some specimens, pale hairs may be entirely lacking.

In general, then, this species becomes progressively more melanic, proceeding from central Brazil to northeastern South America. Westward across northern South America there is a reversal, toward decreased melanism, in Venezuela, Colombia, and Panama. The melanic trend is again evident in Costa Rica and Nicaragua, but decreases once more at the northern (Mexican) extremities of the range. There are numerous localized phenotypes which may depart, in one way or another, from the general cline.

The discussion thus far has focused primarily on the females, though the pubescent patterns of the males of *C. flavifrons* generally follow those of the females. There are, however, problems that are peculiar to the males. Both this species and the similar *C. flavofasciata* possess metanders, males which are unusually large and robust and much more extensively marked with bright yellow, especially on the legs and abdomen. While it is possible to separate normal males of the two species, the metanders are much less convincingly handled.

In part, this is due to a scarcity of fully developed metanders which can be assigned with surety to one or the other of these two species. And, in part, the metanders that are available tend not to exhibit the differences which separate the normal males. I do not believe that this in any way invalidates the distinctions between the two species, but it is merely another manifestation of a common problem within some subgenera: within a given complex males may be much less readily separated than their respective females. A final difficulty is that, unlike the situation in such subgenera as *Xerocentris* and *Paracentris,* the metandrous and normal males form a more or less continuous series, with many individuals of intermediate stature.

A series of about 30 males collected by J.A. Chemsak near Mazatlán, Sinaloa, Mexico, 12 Dec. 1980 (UCB) consists largely of metanders of *C. flavofasciata,* but with a few normal males and intermediates. While I have seen many males of *C. flavifrons* that seem to be intermediates, I have only three that are clearly fully developed metanders, two from Brazil and one from Mexico.

Normal males of *C. flavifrons* possess the following characteristics, each subject to moderate variation: the lower inner mandibular carina terminates in a low, obtusely triangular process (Fig. 14); the clypeal disc is smooth and polished throughout between fine, scattered punctures and is not wholly yellow; the laterobasal black mark of the clypeus extends onto the disc and sometimes the clypeus bears only an inverted (though broad) T-mark. The second to fourth abdominal terga are maculate; the maculation of the second segment often consists merely of two somewhat elongate sublateral spots, but may extend across the base of the segment as a continuous or narrowly interrupted band; when it is a band, it is almost always much shorter in the middle than the dark area distad to it.

In normal males of *C. flavofasciata* the lower inner mandibular carina ends in an elongate, acute, tooth-like process. The disc of the clypeus is wholly yellow and the areas on either side of the shiny, impunctate median line are less shiny and distinctly roughened between fine punctures that are mostly separated by 1.0 to 1.5 times a puncture diameter. The abdominal terga are almost always continuously fasciate and the yellow band of the second segment is as long as, or longer than, the dark area that follows it.

Most of these distinctions disappear in the metanders, or are at least less certain. Some metanders of *C. flavofasciata* have the clypeal disc nearly polished and the punctures about as sparsely distributed as in *C. flavifrons*. While very nearly all metanders of *C. flavofasciata* have the clypeal disc wholly yellow, there are a few in which the laterobasal black mark does extend slightly onto the disc. The abdominal banding breaks down completely, since metanders of both species have broad, continuous yellow fasciae on the second to sixth segments and an interrupted band across the dorsum of the first segment.

The only feature that seems to hold up is the shape of the termination of the lower inner mandibular carina. In metanders of *C. flavifrons* the terminus is low and obtuse, much as in the normal males. It is an acutely tooth-like process in *C. flavofasciata*. How consistent this difference is, I cannot now state, only that it does hold true for the specimens examined thus far.

There is obviously much to be done before the phenomenon of metandry can be adequately dealt with taxonomically. Presumably, the metanders of such species as *C. flavifrons* and *C. flavofasciata* are behaviorally different from their normal counterparts, perhaps in a manner similar to the situation in such species as *C.* (*Xerocentris*) *pallida* W. Fox, the only species studied thus far (Alcock et al., 1976, 1977). In that species metanders seek newly emerging females at nest sites of the previous year. The normal males establish territories at nectar/pollen sources and attempt to mate with females there.

A large nesting aggregation of *C. flavifrons* was observed in Panama. Normal males and the rufescent variety were present. Males were observed to ". . . purposely attack *Mesoplia* in the nest area—with a frequency far higher than the pursuit of other males or females" (D. Roubik and D. Yanega, in prep.).

Centris (*Centris*) *flavofasciata* Friese

Figures 16, 30, 39

Centris flavifrons var. *flavofasciata* Friese, 1899:46. ♂.
Centris (*Cyanocentris*) *flavifrons* var. *flavofasciata:* Friese, 1900b:318. ♂ (distr., tax.).
Centris (*Centris*) *flavofasciata:* Michener, 1954:137 (distr.). Snelling, 1966:23 (distr.).

Centris flavofasciata is a common Mexican species which ranges from southern Arizona to Panama. It is possible that the range extends into northern South America, but I have seen no specimens to substantiate that assumption. Most of the features by which this species may be separated from other members of the *C. flavifrons* groups are summarized in the keys.

Females of *C. flavofasciata* consistently have a dark scopa, with a few of the posteroapical hairs of the metabasitarsus with pale tips. Most females have a small patch of dark hairs below the base of the forewing; none has the side of the thorax extensively dark pubescent, as is usually true of Central American material of *C. flavifrons.* Those specimens of *C. flavifrons* with little dark pleural pubescence are from Panama.

Facial maculations of *C. flavofasciata* tend to be somewhat whitish in females, rather than definitely yellow as in *C. flavifrons* and, in both sexes, are more extensive; in the male the entire clypeal disc is yellow, not encroached upon by the black laterobasal mark. In females of *C. flavofasciata* the labrum is largely pale, rather than extensively dark and the vertical and lateral arms of the inverted T-mark of the clypeus are broad and never broken into segments.

***Ptilocentris*, new subgenus**

DIAGNOSIS

Differs from other subgenera of *Centris* by the following combination of characters. Maxillary palp five-segmented; tergal integument metallic blue-green, first four terga with pubescence long, dense, erect, plumose. Female: secondary basitibial plate with distinct overhanging margin, pro- and mesobasitarsi with elaiospathe; clypeal disc evenly rounded into lateral and basal faces, gently convex from side to side. Male: metabasitarsus without posterior carina; genitalia without branched setae; upper inner mandibular carina ending at base of inner tooth; eighth sternite expanded at apex.

DESCRIPTION

Mandible narrow, neither subapically broadened nor bent; tri- (male) or quadridentate (female); upper inner carina ending near base of innermost tooth; lower inner carina not subangularly produced, continuous to innermost tooth along upper margin. Labrum of female about 1.3 times broader than long, apex subacute; about as broad as long in male.

Clypeus broader than long and separated from inner eye margin by less than diameter of anterior ocellus; disc not at all flattened, low-convex from side to side and evenly rounded onto lateral faces and gently sloping toward base. First flagellar segment about as long as following three combined (female) or shorter (male). Ocellocular distance greater than anterior ocellus diameter. Pro- and mesobasitarsi with anterior elaiospathe on inner surface; basitibial plate of female with distinct secondary plate, its lower margin overhanging primary plate; metafemur of male robust, without ventral ridge or tubercle; metabasitarsus simple, without posterior ridge or carina. Female pygidial plate V-shaped, apex narrowly rounded; secondary plate distinct, apex acute. Male without distinct pygidial plate; seventh sternite (Fig. 9) subapically broadened and apical margin deeply emarginate; with abundant long, plumose hairs at apex, with short, simple hairs at base of apical lobe; eighth sternite (Fig. 10) with distal process long, its apex angularly spatulate, apical one-half of shaft and broadened distal portion with long, plumose hairs; genital capsule (Figs. 11, 12) robust, gonocoxite massive; gonostylus short, broad, with a few fine, simple setae. Abdominal terga metallic blue-green and four basal segments with abundant, erect, plumose hairs on discs.

TYPE-SPECIES

Centris festiva F. Smith, 1854, by present designation.

ETYMOLOGY

The subgeneric name combines Greek *ptilon* (feather) with the generic name *Centris* and refers to the presence of abundant long, erect, plumose hairs on the abdominal terga.

The subgeneric name proposed here was originally conceived by J.S. Moure and appears on specimens of *C. festiva* in various collections which he identified 20 years ago. It is an appropriate name and I am pleased to adopt it here.

DISCUSSION

The type-species is the only known representative of this subgenus.

Ptilocentris seems to be another segregate of the *Paracentris-Centris* s. str. complex of subgenera. In my key to the subgenera of *Centris* (Snelling, 1974) the female will go to *Centris* s. str.

Females differ from those of the nominate subgenus in lacking a stipital comb; in *Centris* s. str. the comb consists of a long row of stout, close-set, coarse, acute bristles. The labrum in *Centris* s. str. is much broader, with the apical margin broadly rounded. The broad, distinctly flattened, or slightly depressed, clypeal disc which abruptly slopes basad and toward the lateral margins is also distinctive of *Centris* s. str. In this regard, *Ptilocentris* is more like some species of *Paracentris* from which it immediately differs in possessing a sharply defined secondary basitibial plate with a distinct margin which extends slightly over the disc of the primary plate. Also, *Paracentris* is like *Centris* s. str. in the form of the comb of the stipes.

The male of *Ptilocentris* is unique among the *Paracentris-Centris* s. str. complex in the form of the genitalic structures. The shapes of the seventh and eighth sternites are distinctive and the lack of coarse, plumose setae on the genitalic capsule is also an unusual feature in this complex. So, too, is the short, broad gonostylus.

Centris (*Ptilocentris*) *festiva* F. Smith

Figures 9–12

Centris festiva F. Smith, 1854:375. ♀.

Centris chlorura Cockerell, 1919:188–189. ♀. NEW SYNONYMY.

This attractive and unusual species is easily recognized by the characteristic pattern of erect hairs on the discs of the abdominal terga. In most specimens the second and third terga have a basal zone of blackish hairs, but in some specimens the hairs may be wholly pale; one such pale haired specimen was the basis for *C. chlorura,* the type of which has been examined.

There are no previous records of this species from Central America. In South America, *C. festiva* is known to be present in Colombia, Ecuador, and Peru.

NEW RECORDS

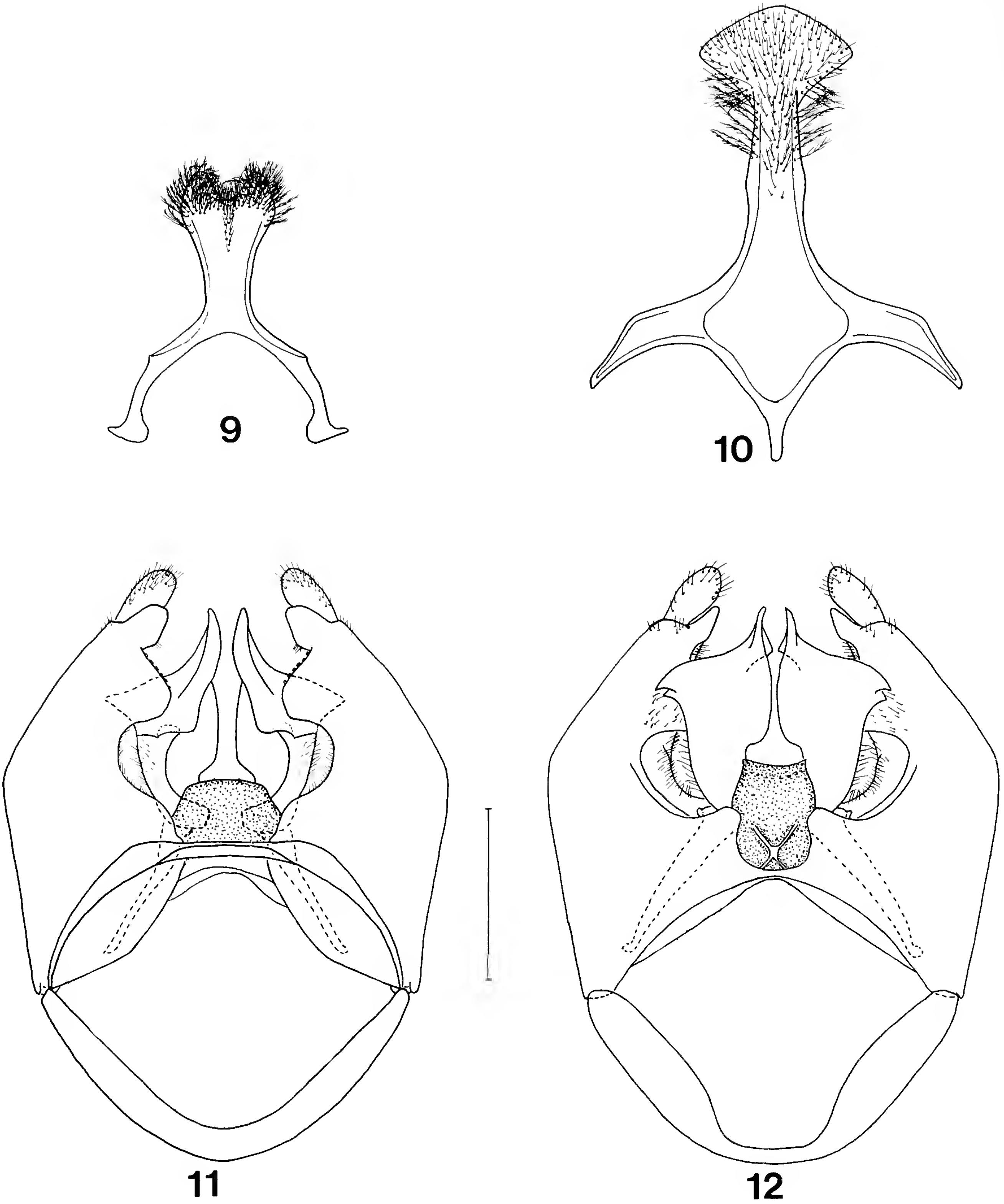
MEXICO, *DISTRITO FEDERAL:* 1♂, Los Venados, 6 Nov. 1938 (G. Vivas-Berthier; USNM). COSTA RICA, *ALAJUELA:* 1♂, 5 km S Vara Blanca, 11 Nov. 1973 (P.A. Opler; LACM). *SAN JOSÉ:* 1♀, San José, "1.6.19" (M. Valerio; USNM). PANAMA, *CHIRIQUÍ:* 1♂, Osra Clara, 26 Jan. 1981 (D.W. Inouye; ROUB). According to Roubik (pers. comm.): "Sandy Knapp also collected *C. festiva* in Chiriquí on 22 April 82 . . . at Cerro Colorado, about 1000 m elevation."

Subgenus *Melanocentris* Friese

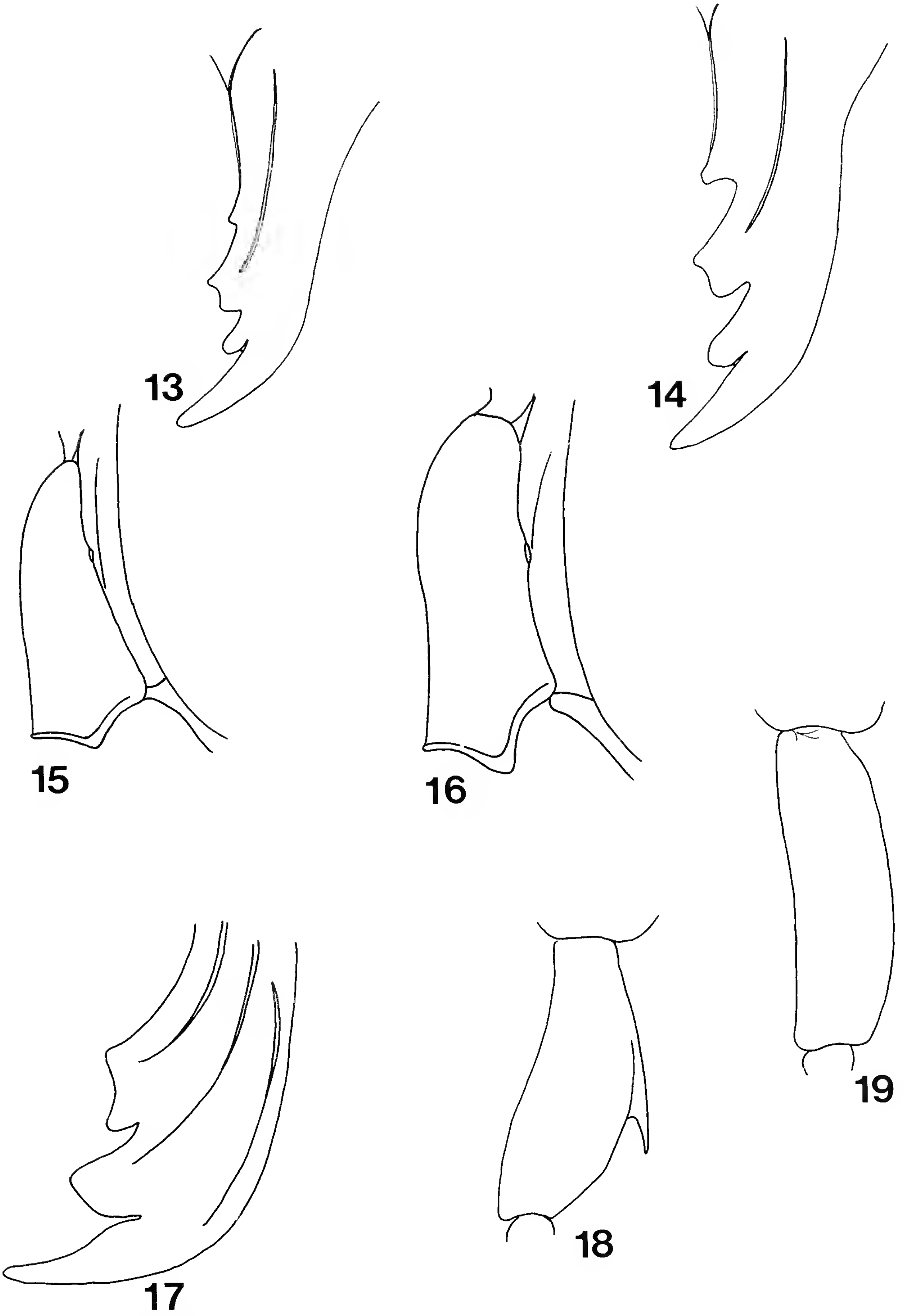
Centris subg. *Melanocentris* Friese, 1900b:241, 244. Type-species: *Centris atra* Friese, 1900b; designated by Sandhouse, 1943.

Species belonging to the subgenus *Melanocentris* are medium-sized to large bees, usually black (though with pale face marks in the males) or with the abdomen more or less dusky ferruginous. Less commonly the abdomen may have metallic blue or green reflections. The pubescence is mostly dark but there may be limited amounts of pale pubescence on the thorax, the hind legs, and on the abdomen. In both sexes the maxillary palp is five-segmented and the mandible is stout, quadridentate in the female and tridentate in the male; in the female the mandible is broadened and abruptly bent near the apex.

Additional characteristics of the female include the presence of an elaiospathe on the pro- and mesobasitarsi, the weakly bilobate scutellum, the upper inner carina of the mandible ends near the base of the subbasal tooth, and the margin of the secondary basitibial plate overhangs the primary plate. Males lack giant branched setae on the genitalia, the meta-



Figures 9–12. *Centris* (*Ptilocentris*) *festiva*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.



Figures 13–14, apex of left mandible of male; **13,** *Centris* (*C.*) *aethiocesta*; **14,** *C.* (*C.*) *flavifrons.* **Figs. 15–16,** clypeal profile of female: **15,** *C.* (*C.*) *aethiocesta*; **16,** *C.* (*C.*) *flavofasciata.* **Fig. 17,** apex of left mandible of male *C.* (*Melanocentris*) *fusciventris.* **Figs. 18–19,** metabasitarsus of male: **18,** *C.* (*Trachina*) *labiata*; **19,** *C.* (*T.*) *longimana.*

basitarsus is without an elevated carina on the posterior margin, the scutellum is weakly swollen on either side of the middle, and the upper inner mandibular carina ends near the base of the middle tooth.

This is primarily a South American group, and much in need of revisionary study. The few North American species may be separated by the following key.

KEY TO NORTH AMERICAN *MELANOCENTRIS*

1a. Male, antenna 13-segmented and basitibial plate absent 2

b. Female, antenna 12-segmented and basitibial plate present 8

2a. Integument of abdominal terga shiny, reddish or blackish, never strongly metallic; if dull, punctures subcontiguous to dense, sharply defined at least on second tergum; metafemur swollen, but without ventral ridge 3

b. Integument of abdominal terga dull to slightly shiny, dark blue, punctures on discs of second and third tergites very fine, obscured by dense tessellation and well separated; metafemur swollen, with low ventral ridge which terminates slightly beyond middle . . . . *plumipes* F. Smith

3a. Pilosity of thorax buff-colored to ferruginous (hairs of mesoscutum may be dark-tipped) 4

b. Pilosity of thorax dark brown to blackish (one species with light hairs on scutellum, metanotum, and propodeum) 5

4a. Inner mandibular tooth broad, cutting margin incised so that mandible approaches quadridentate condition (Fig. 17); pilosity of third and following tergites blackish . . . . *fusciventris* Mocsáry

b. Inner mandibular tooth narrow, triangular, mandible definitely tridentate; pilosity of third and following tergites ferruginous . . . . *flavilabris* Mocsáry

5a. Clypeus narrow, about 1.10 to 1.25 times broader than long; lower facial width no more than 1.5 times broader than interocular distance, latter always greater than transocellar distance 6

b. Clypeus broader, at least 1.40 times broader than long; lower facial width at least 1.6 (and usually more than 1.8) times minimum interocular distance, latter usually no more than transocellar distance, often less 7

6a. Abdomen dusky ferruginous; posterior part of thorax, metatibia and metabasitarsus pale pilose; disc of second tergum dull, punctures mostly separated by less than a puncture diameter . . . . *agiloides*, new species

b. Abdomen brownish to blackish; pilosity of thorax and leggs blackish; disc of second tergum moderately shiny between punctures mostly separated by a puncture diameter or more . . . . *sericea* Friese

7a. Dorsal face of scutellum depressed along midline and slightly raised on either side, apex of eminence impunctate or nearly so; basal area of propodeum slightly shiny and conspicuously tessellate; pubescence of legs dark . . . . *obsoleta* Lepeletier

b. Dorsal face of scutellum neither depressed along midline nor raised on either side, uniformly subcontiguously punctate; basal area of propodeum shiny, with very weak tessellation; hairs pale on metatibia and metabasitarsus . . . . *agilis* F. Smith

8a. Apex of pygidial plate broad, deeply and angularly incised (Fig. 42); scopa pale; yellowish marks often present on some part of lower face 9

b. Apex of pygidial plate narrowly truncate or acute, never incised (Figs. 41, 43); scopa often dark; face rarely maculate 10

9a. First four abdominal terga black, with strong metallic blue reflections . . . . species A

b. Entire abdomen dusky ferruginous . . . . *flavilabris* Mocsáry

10a. Lower half of clypeal disc slightly shiny to shiny, but conspicuously roughened or ridged between punctures; labrum and side of clypeus black; paraocular area usually black; integument of frons and mesopleuron black, without metallic bluish or greenish-bronze reflections 11

b. Lower half of clypeal disc smooth and polished between punctures; most of labrum, at least side of clypeus, and paraocular area yellowish maculate; frons and mesopleuron with metallic bluish or greenish-bronze reflections . . . . *plumipes* F. Smith

11a. Discs of second and third terga moderately to strongly shiny, punctures various but usually not subcontiguous and much coarser than hairs arising from them (if subcontiguous, scopa dark); scopa often dark; abdomen often black 12

b. Discs of second and third terga dull, contiguously punctate, punctures much coarser than hairs arising from them; scopa pale; abdomen ferruginous . . . . *agiloides*, new species

12a. Punctures of disc of second tergum, when visible, little larger than hairs arising from them and finer than those on disc of following segment; pubescence of thorax and/or scopa often partly pale; basitibial plate and pygidium various 13

b. Punctures of disc of second tergum subcontiguous, much coarser than hairs arising from them and conspicuously coarser than punctures of apical zone and of following segment; thoracic and scopal hairs black; secondary basitibial plate acute (Fig. 24); pygidial plate narrowly V-shaped, secondary plate short and broad . . . . *sericea* Friese

13a. Dorsal face of first tergum, across middle one-third, polished, without evident punctures and with only a few widely scattered, appressed simple hairs; pygidial plate broadly V-shaped and broadly truncate at apex, lateral margins somewhat convex at about midlength, secondary plate elongate and with median raised ridge extending from its apex to apical truncation (not always visible in worn specimens) (Fig. 43); scopa pale . . . . *agilis* F. Smith

b. Dorsal face of first tergum pubescent and/or punctate across middle half at least at summit of declivity; pygidium not as above (Fig. 41); scopa pale or dark . . 14

14a. Scopa entirely pale; abdomen largely reddish 15

b. Scopa entirely black or pale on tibia and brownish on basitarsus; abdomen dark 16

15a. Mesepisternal pubescence dark brownish; disc of second tergite with distinct, minute, close punctures; apex of pygidial plate narrowly truncate . . . . *gelida*, new species (part)

b. Mesepisternal pubescence pale, at least in part; disc of second tergite without obvious minute punctures, but with a few scattered, moderate, shallow punctures; apex of pygidial plate acute . . . . *fusciventris* Mocsáry

16a. Pubescence of first and second terga and of scopa blackish; clypeal punctures, except along impunctate midline, uniformly subcontiguous on disc . . . . *obsoleta* (Lepeletier)

b. Pubescence of adbominal terga pale (brownish golden on second segment); tibial scopa mostly pale; punctures of clypeal disc very irregularly spaced . . . . *gelida*, new species (part)

Centris (*Melanocentris*) *agilis* F. Smith

Figure 43

Centris agilis F. Smith, 1874:361. ♂.
Centris ignita F. Smith, 1874:362. ♀. NEW SYNONYMY.
Centris bakeri Friese, 1912:199. ♂. Preoccupied.
Centris bakerella Friese, 1913:89. New name for *C. bakeri* Friese, 1912, not *C. bakeri* Cockerell, 1912. NEW SYNONYMY.
Epicharis cisnerosi Cockerell, 1949:180. ♀. NEW SYNONYMY.

F. Smith (1874) described the two sexes as *C. agilis* and *C. ignita.* This is a common species in Mexico and one that is variable in the color of the abdominal integument. In both sexes, the abdominal terga, beyond the blackish first segment, may be wholly ferruginous. In these specimens the dense, short, simple discal hairs appear to be yellowish red. In other specimens, one or more of the following three segments may be blackish and when this is the case, the discal hairs appear to be yellowish or somewhat whitish, imparting a distinctly "frosted" appearance.

Friese's *C. bakeri* and Cockerell's *Epicharis cisnerosi* are based on specimens with dark tergites. Although I have seen no type material of *C. bakeri,* the description matches well the characteristics of dark males of *C. agilis.* I have examined the type of *Epicharis cisnerosi*; it is a normal, dark female of *C. agilis.*

NEW RECORDS

MEXICO, *CHIAPAS:* 1♀, 10 mi. NW Comitan, 9 Aug. 1963 (F.D. Parker and L.A. Stange; UCD); 1♀, Municipio Ocozocautla, El Aguacero de Derna, 762 m elev., 1 Sept. 1976 (D.E. and J.A. Breedlove; CAS); 1♀, 18♂♂, Municipio Angel Albino Corzo, Rio Custepec, below Finca Gadow, 853 m elev., 12 Sept. 1976 (D.E. and J.A. Breedlove; CAS); 1♂, Sumidero, Tuxtla Gutierrez, 17 Aug. 1964 (E. Fisher and D. Verity; LACM) 1♂, 82 mi. W Tuxtla Gutierrez, 2100 ft. elev., 30 Aug. 1957 (H.A. Scullen; ORSU); 2♀♀, NW slope Cerro Baul, 1768 m elev., W of Rizo de Oro, 12 Oct. 1979 (D.E. and J.A. Breedlove; CAS). *COLIMA:* 1♂, 10 mi. W Colima, 1 Aug. 1954 (M. Cazier, W. Gertsch, Bradts; AMNH). *GUERRERO:* 1♂, 4 mi. W Chilpancingo, 1530 m elev., 27 Aug. 1977 (E.I. Schlinger; UCB). *JALISCO:* 1♀, 25 mi W Guadalajara, 4700 ft. elev., 29 Sept. 1957 (H.A. Scullen; ORSU); 2♀♀, 5.6 km E Plan de Barranca, 914 m elev., 25 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Cassia* sp.; 1♀, 3.4 km E Plan de Barranca, 960 m elev., 25 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Cosmos sulphureus. MICHOACÁN:* 2♀♀, Tuxpan, 6550 ft. elev., 19 Sept. 1957 (H.A. Scullen; ORSU). *MORELOS:* 1♂, no locality or date (Crawford; LACM); 1♂, 7 mi. NE Yautepec, 4000 ft. elev., 18 Aug. 1962 (Univ. Kans. Mex. Exped.; UKAN) on Leguminosae; 1♀, 0.6 km S Teacalco, 1021 m elev., 16 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Crotalaria incana*; 1♂, Lake Tequesquitengo, 5000 ft. elev., 13 Sept. 1957 (H.A. Scullen; ORSU). *NAYARIT:* 2♀♀, 8 mi. N Tepic, 1 Sept. 1962 (D.H. Janzen; LACM). *OAXACA:* 2♂♂, El Camarón, 20 Aug. 1959 (L.A. Stange and A.S. Menke; UCB); 2♂♂, 48 mi. E La Ventosa, 21 July 1963 (J. Doyen; UCB); 1♀, near Pinotepa Nacional, 200 m elev., 12 Oct. 1975 (J.L. Neff; LACM), on Legume 7123; 2♀♀, 4 mi. W Zanatepec, 7 Oct. 1975 (J.L. Neff; LACM), on *Cassia* 7070; 1♀, Mixtla, 5600 ft. elev., 22 Aug. 1963 (Scullen and Bolinger; ORSU). *PUEBLA:* 1♀, 16.1 km NW Izúcar de Matamoros, 1250 m elev., 17 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Caesalpinia cacalaco;* 3♀♀, 22 km NW Izúcar de Matamoros, 1158 m elev., 21 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Cassia laevigata. SINALOA:* 6♀♀, 14 mi. SE Espinal, 14 Sept. 1964 (A.E. Michelbacher; UCB); 2♀♀, 33 km SE Esquinapa, 11 Sept. 1974 (E.M. Fisher; LACM). *VERA CRUZ:* 1♂, Catemaco, 6 Oct. 1976 (E. Barrera; LACM). HONDURAS: 1♀, Zamorano, 2 Nov. 1946 (G. Cisneros; USNM) (type of *Epicharis cisnerosi*). COSTA RICA, *SAN JOSÉ:* 1♀, San José, no date (M. Valerio, USNM).

***Centris* (*Melanocentris*) *agiloides,* new species**

Figures 20–23

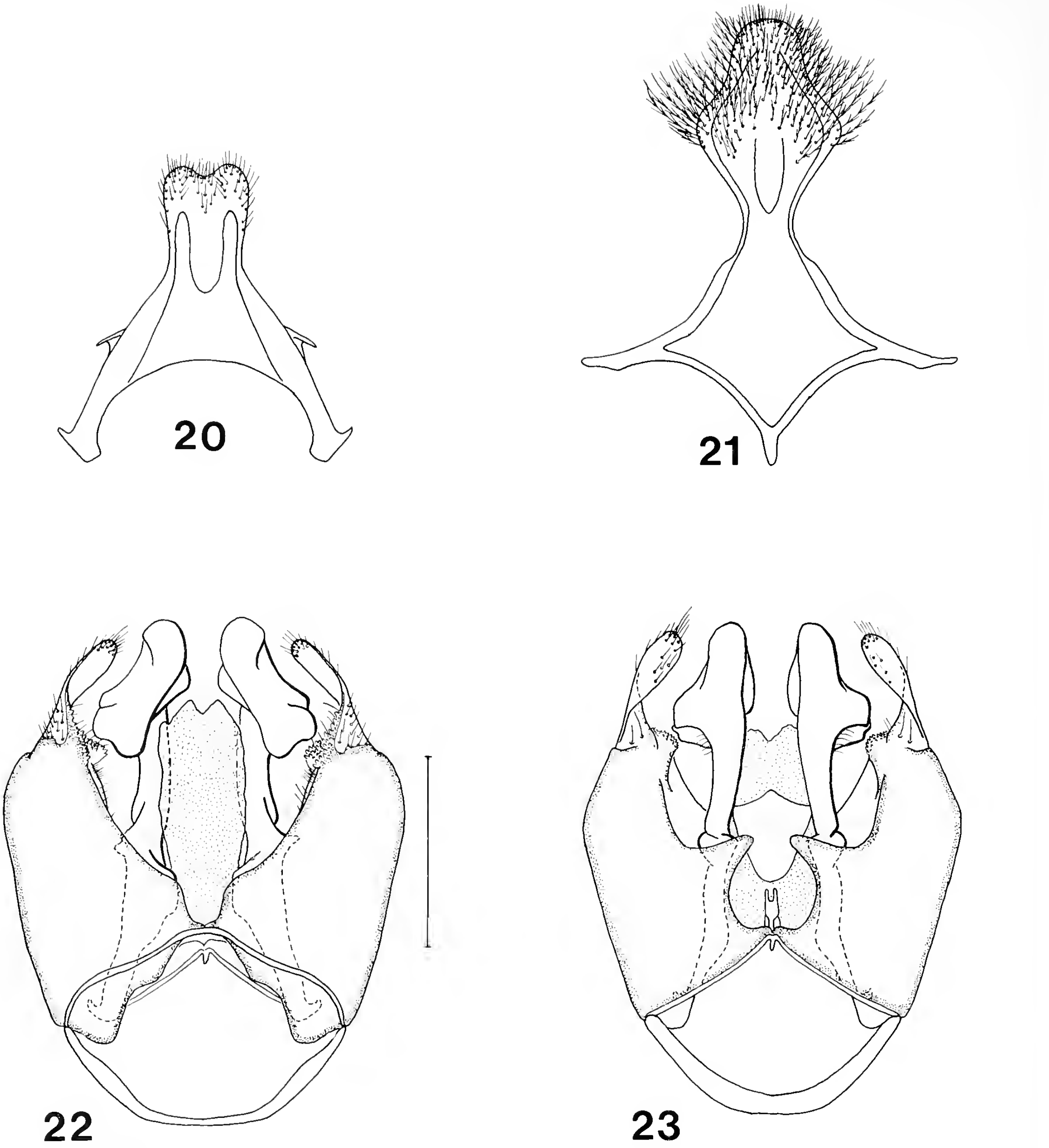
DIAGNOSIS

Abdomen ferruginous in both sexes, second tergite dull, subcontiguously punctate; male with clypeus narrow, pubescence of thoracic dorsum blackish except on metanotum and metafemur without ventral ridge; female with narrowly truncate pygidial plate and pale scopa.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 6.41 (6.00–6.62); head length 4.97 (4.56–5.03); wing length 15.0 (14.0–16.5); total length 19.0 (17.0–21.0).

Head. 1.29 (1.29–1.37) times broader than long; occipital margin slightly concave between tops of eyes; ocelli well anterior to occipital margin; inner orbits moderately convergent above, upper frontal width 0.65 (0.62–0.71) times



Figures 20–23. *Centris* (*Melanocentris*) *agiloides,* male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

lower frontal width. Mandible stout, tridentate, inner tooth acute and nearly as large as second tooth. Labrum about 1.5 times wider than long, apex subacute; disc shiny between dense to subcontiguous moderate punctures. Clypeus narrow, 1.1–1.2 times wider than long; median impunctate line narrow and poorly defined, basal area of disc moderately shiny, roughened and with sparse fine punctures, distal one-half, more or less, shiny and weakly or not roughened and with close to dense, fine punctures. Frons and preoccipital area moderately shiny between dense to subcontiguous fine punctures, except usual nearly impunctate areas adjacent to ocelli; gena shiny between sparse to close fine, punctures. Interantennal distance 1.62 (1.50–1.77) times antennal socket diameter; antennocular distance 0.46 (0.32–0.47) times antennal socket diameter; scape stout, 2.05 (1.90–2.21) times longer than wide; scape length 0.75 (0.69–0.76) times length of first flagellar segment; first flagellar segment longer than following three segments combined, 5.94 (5.00–5.53) times length of second. Interocellar distance 1.35 (1.26–1.47) times diameter of anterior ocellus; ocellocular distance 0.38 (0.30–0.50) times diameter of anterior ocellus; ocelloccipital distance 2.22 (2.16–2.50) times diameter of anterior ocellus.

Thorax. Mesoscutum moderately shiny between dense to subcontiguous, fine punctures which are a little more separated posteromedially; scutellum with a low, rounded eminence on either side, moderately shiny between dense to subcontiguous, fine punctures, shiny along midline; metanotum dull, conspicuously tessellate and with scattered fine punctures; mesepisternum and metepisternum moderately shiny, punctures subcontiguous to contiguous, fine, and shallow. Basal area of propodeum moderately shiny, tessellate between sparse, fine punctures; side and posterior face similar, but punctures dense to subcontiguous. Metafemur stout, about 1.9 times longer than thick; thickest at basal one-third; without ventral ridge; metabasitarsus weakly curved, about four times longer than wide.

Abdomen. Dorsum of first tergite moderately shiny, weakly tessellate between sparse, fine punctures; remaining tergites dull and sharply tessellate between subcontiguous, moderate punctures, sparser on fourth and following segments; seventh tergum weakly bilobate at apex.

Terminalia. Distal process of seventh sternite (Fig. 20) short, not well differentiated from disc; apical emargination broad and shallow; hairs sparse, mostly short and weakly plumose or simple. Median expansion of eighth sternite (Fig. 21) evenly rounded; apex slightly convex; hairs abundant, long, conspicuously plumose. Dorsal process of gonocoxite (Figs. 22, 23) nearly triangular; gonostylus nearly reaching level of apex of penis valve; ventral lobe of penis valve only slightly extended laterad of dorsal lobe.

Pilosity. Blackish brown on front and top of head, on thoracic dorsum, upper mesepisternum, anterior and middle legs, and first tergite; hairs on discs of second and third tergites very short, simple, decumbent, longer and more erect on following segments, with some very long, plumose, reddish brown hairs, especially laterad; hairs on underside of head, posterior margin of scutellum, metanotum, and remainder of thorax light brown. Metafemur and metabasitarsus with scopa-like yellowish hairs.

Color. Head and thorax blackish brown, legs and antenna more rufescent. Large labral mark, large discal spot on clypeus and narrow paraocular mark all very pale yellowish. Abdomen dull ferruginous. Wings dark brown, veins and stigma blackish.

FEMALE. Measurements (mm). Head width 6.56–7.08; head length 4.82–5.13; wing length 14.5–16.0; total length 20.0–24.5

Head. 1.26–1.38 times broader than long; ocelli well anterior to nearly flat occipital margin in frontal view; inner orbits moderately convergent above, upper frontal width 0.84–0.90 times lower frontal width. Mandible quadridentate, inner tooth acute and slightly larger than subbasal tooth. Labrum about twice broader than long, apex broadly rounded; disc shiny between subcontiguous to contiguous, moderate punctures. Clypeus mostly moderately shiny, but disc with variable area which is conspicuously shiny (up to distal two-thirds of median area); median impunctate line poorly defined; disc with sparse moderate punctures and a few low, irregular rugulae which are usually convergent distad or curved mesad at their lower ends. Punctation of frons and occipital area as described for male, but interspaces (including ocellar area) moderately shiny and conspicuously tessellate; gena as described for male. Interantennal distance 2.00–2.31 times antennal socket diameter; scape robust, 1.98–2.13 times longer than wide; scape length 0.71–0.77 times length of first flagellar segment; first flagellar segment slightly longer than following three segments combined, 4.52–5.40 times length of second. Interocellar distance 1.55–1.72 times diameter of anterior ocellus; ocellocular distance 1.08–1.21 times diameter of anterior ocellus; ocelloccipital distance 1.71–2.00 times diameter of anterior ocellus.

Thorax. As described for male, but scutellum tessellate and slightly shiny, except in basal middle where it is shiny. Basitibial plate slender, apex narrowly rounded.

Abdomen. Dorsal face of first tergite moderately shiny and weakly tessellate between close to dense, moderate punctures; second and following terga dull, contiguously and finely punctate to tergal margins; apex of pygidial plate narrowly truncate.

Pilosity. On head and thorax, as described for male, but hairs of metanotum and propodeum often very pale brownish; scopa yellowish white. Hairs on dorsal face of first tergite erect, dark, plumose; dark, very short, appressed, and simple on disc of second segment, becoming progressively longer and less appressed on following segments; fourth and fifth terga with a few suberect to erect dark bristles on either side; prepygidial fimbria dark reddish brown.

Color. As in male, but without pale face marks.

TYPE MATERIAL

Holotype male: Finca La Selva, 500 ft. elev., near Puerto Viejo, *Heredia Prov.*, COSTA RICA, 3 June 1975 (D.R. Perry), on *Dipteryx panamensis,* 0703–1100, in Natural History Museum of Los Angeles County. Allotype: same locality and collector, 6 May 1979, on *Dussia* sp., 1045–1115 (LACM). Paratypes (all COSTA RICA): 11♂♂, 6♀♀, same data as allotype (LACM); 1♂, same locality and collector, 4 June 1975, on *Dipteryx panamensis,* 1100–1400 (LACM); 1♂, same locality and collector, 14 June 1975, on *Dipteryx panamensis,* 0830–1030 (LACM); 1♂, same locality and collector, 24 July 1978 (LACM), on *Hymenolobium* sp.; 1♂, 8 km S Puerto Viejo, *Heredia Prov.,* 28–29 May 1971 (P.A. Opler; UCB), on *Ipomaea* sp., pink fl.; 1♂, Zapote de Upala (vic. Bijagua), *Alajuela Prov.,* 19 May 1972 (F. Cordero; UCB); 1♀, Dulce Nombre, *Cartago Prov.,* 25 Aug. 1967 (R.W. McDiarmid; LACM).

ADDITIONAL SPECIMENS (not paratypes)

MEXICO, *CHIAPAS:* 1♂, Mahosik', Tenejapa, 4800 ft. elev., 9–12 July 1966 (D.E. Breedlove and J. Emmel; CAS). *SAN*

LUIS POTOSÍ: 1♂, 26 mi. SW Tamazunchale, 4–5 July 1964 (E. Fisher and D. Verity; LACM); 1♀, 15 mi. Xilitla, 1350 m elev., 15 Aug 1977 (E.I. Schlinger; UCB). *VERA CRUZ:* 1♀, Peñuela, 13 Sept. 1974 (M. Sousa; LACM); 4♀♀, same locality, 2 Aug. 1974 (A. Delgado S.; LACM), on "*C. Doylei,*" 0800–1002; 1♀, "Rig. de Cordoba (A. Genin; MNHN). COSTA RICA, *SAN JOSÉ:* 2♂♂, San José, no date (M. Valerio; USNM). PANAMA, *PANAMÁ:* 1♂, Cerro Azul, N of Tocumen, 28 Apr. 1958 (W.J. Hanson; UKAN); 1♂, Curundu, 19 May 1981 (R.W. Brooks; RWB), on *Genipa americana.*

ETYMOLOGY

Combines the Latin suffix *-oides* (resembling) to *agilis,* because of the superficial resemblance to *C. agilis.*

DISCUSSION

Variation in non-meristic characters is negligible. In some specimens, particularly those of Mexico, the pubescence of the metanotum and propodeum is not conspicuously paler than that of the thoracic dorsum. In some males, the posterior femur, tibia, and basitarsus may be extensively reddish, but mostly dark in other specimens. The supraclypeal mark may be present or absent, and when it is present, it is transverse and very narrow. Although the scape is usually black in the males available, there is a distinct ventral maculation in the males from Mexico and Panama. One of the Mexican males has the clypeus largely pale.

In the females there is considerable variation in the extent of the shiny area on the clypeal disc. In most specimens the shiny portion of the disc occupies about one-half the length of the disc; in a few this is exceeded (up to nearly the entire length) and in others reduced to the apicomedian one-fourth of the segment. Similarly, the development of the oblique rugulae of the clypeal disc is variable, and the rugulae, while never becoming a dominant feature, are always present.

The uniformly subcontiguously punctate, dull, red abdomen is diagnostic for *C. agiloides.* The only species with a similarly dull abdomen is *C. sericea* but in both sexes of that species the abdomen is black, the posterior legs are black-haired, the abdominal punctures become much finer toward the margins of the segments, and the punctures of the third segment are much finer than those of the second.

Centris (*Melanocentris*) *flavilabris* Mocsáry

Centris flavilabris Mocsáry, 1899:253. ♀.
Centris flavilabris var. *boliviensis* Mocsáry, 1899: 253. ♀.

This is a primarily South American species, not previously recorded from Central America.

NEW RECORDS

COSTA RICA, *GUANACASTE:* 1♂, Volcán Miravalles, 2 km W Rio Navinjo, 15 Mar. 1973 (P.A. Opler; UCB). *PUNTARENAS:* 1♀, Rincon, 25 Apr. 1975 (C.L. Hogue; LACM).

Centris (*Melanocentris*) *fusciventris* Mocsáry

Figure 15

Centris fusciventris Mocsáry, 1899:252. ♀.
Centris fusciventris var. *scutellata* Friese, 1900b:273. ♂♀. NEW SYNONYMY.
Centris (*Melanocentris*) *fusciventris:* Moure, 1950:388 (tax.).
Centris (*Melanocentris*) *fusciventris scutellata:* Michener, 1954:144 (distr.).

The var. *C. f. scutellata* was described from both sexes from Chiriquí, Panama. The nominate form occurs widely in South America (Brazil, Colombia, Bolivia, Venezuela). Differences between the two forms are slight and fall within the range of variation seen in South American material.

NEW RECORDS

COSTA RICA, *HEREDIA:* 3♀♀, 1♂, Finca La Selva, near Puerto Viejo, 6 May 1979 (D.R. Perry; LACM), on *Dussia* sp. PANAMA, *COLÓN:* 2♂♂, Puerto Pilón, 22 km NE Santa Rita, 23 May 1982 (D. Roubik; ROUB). *DARIÉN:* 3♂♂, Bayano Bridge, 184 km SE Canglon, 16 May 1980 (D. Roubik; ROUB). *PANAMÁ:* 2♂♂, Panamá, Curundu, 17 May 1981 (R.W. Brooks, RWB), on *Genipa americana.*

***Centris* (*Melanocentris*) *gelida,* new species**

DIAGNOSIS

Female only: scopa yellowish on metatibia, brown on metabasitarsus; abdomen mostly ferruginous, dorsum shiny (obscured by pubescence) between minute punctures; dorsal face of first tergite pubescent and minutely punctate in middle; pubescence of first and second tergites pale. Male unknown.

DESCRIPTION

HOLOTYPE FEMALE. Measurements (mm). Head width 7.49 (7.38–7.64); head length 5.13 (5.03–5.13); wing length 18.0 (17.5–19.0); total length 22.0 (22.0–25.0).

Head. 1.46 (1.46–1.49) times broader than long; occipital margin nearly flat in frontal view and slightly below tops of eyes; ocelli anterior to occipital margin; inner orbits strongly convergent above, upper frontal width 0.85 (0.81–0.84) times lower frontal width. Mandible stout, quadridentate. Labrum about twice broader than long. Disc of clypeus slightly depressed, moderately shiny (duller, obviously tessellate laterobasad), with broad, poorly defined median impunctate line, punctures fine and irregularly spaced a puncture diameter or more apart. Frons roughened and slightly shiny between fine, dense punctures; vertex slightly shiny and with punctures minute and subcontiguous in ocellocular area, shiny between dense to sparse fine punctures in preoccipital area; gena shiny between dense to close, minute punctures. Interantennal distance 2.04 (2.00–2.24) times antennal socket diameter; antennocular distance subequal to antennal socket diameter; scape stout, about twice longer than wide, scape length 0.72 (0.63–0.72) times length of first flagellar segment; first flagellar segment slightly longer than following three combined, 4.33 (4.35–4.65) times longer than second. Interocellar distance 1.60 (1.42–1.59) times diameter of anterior ocellus; ocellocular distance 1.07 (1.00–1.07) times diameter of anterior ocellus; ocelloccipital distance 1.72 (1.68–1.82) times diameter of anterior ocellus.

Thorax. Mesoscutum and dorsum of scutellum shiny between fine, dense to close punctures, posterior face of scutellum with subcontiguous, fine punctures; scutellum weakly depressed along midline; metanotum slightly shiny, sharply tessellate between sparse, minute punctures; mesepisternum moderately shiny between subcontiguous to dense, fine punctures; basal area of propodeum slightly depressed on either side, moderately shiny and tessellate between sparse, fine punctures; disc shinier, closely and more finely punctate; side shiny between fine, close punctures. Basitibial plate about twice longer than wide, secondary plate narrowly rounded at apex, primary plate more broadly rounded. Scopal hairs plumose nearly to tips.

Abdomen. Summit of first tergite shiny between sparse micropunctures in middle and close to sparse, minute punctures laterad; discs of second and third tergites shiny between dense to close, minute punctures; fourth tergite less shiny, densely, finely punctate; fifth tergite slightly shiny, subcontiguously, finely punctate. Pygidium narrowly truncate at apex, sides straight, secondary plate acute at apex.

Color. Color generally blackish brown, distal half of second, all of following tergites and all sternites ferruginous; tarsi and underside of flagellum dark ferruginous. Wings strongly brownish, veins and stigma blackish brown.

Pilosity. Dark brown to blackish on head, thorax, and legs, except most of metatibial scopa yellowish and metabasitarsal scopa light brown; hairs of mesoscutum very dense, concealing surface; hairs of first tergite moderately long, erect, plumose, dirty white; hairs of second to fifth tergites short, simple, subappressed, whitish to yellowish brown, especially on discs of second and third segments; prepygidial and pygidial fimbriae ferruginous; sternites with sparse erect whitish hairs, longer along midline and forming weak distal fimbriae, that of fifth segment ferruginous.

TYPE MATERIAL

Holotype female: Santa Rita, 10 mi. E Nahuala, 7100 ft. elev., Dept. Solola, GUATEMALA, 3 Sept. 1965 (S.J. Arnold), on *Canavalia villosa,* in California Academy of Sciences. Paratypes: 2♀♀, same data as holotype (UCB); 1♀, 25 mi. S El Bosque, 5500 ft. elev., Chiapas, MEXICO, 5 Sept. 1965 (S.J. Arnold; UCB); one paratype in LACM, two in UCB.

ETYMOLOGY

The specific name is a Latin word for "frosted" and refers to the characteristic appearance of the abdominal dorsum.

DISCUSSION

An additional female, not a paratype, is from Município Motozintla, ridge between Cerro Boqueron and Niguivil, 2438–2743 m elev., Chiapas, MEXICO, 15 Dec. 1976 (D.E. and J.A. Breedlove; CAS). This specimen is assumed to be conspecific with the type series, agreeing closely in most features. It does differ, however, in having the abdomen uniformly blackish, rather than mostly dull reddish. Abdominal color is somewhat variable in some members of this subgenus.

The only other species in Central America with a similarly "frosted" abdomen is *C. agilis.* In *C. agilis* the disc of the first tergite is polished and nearly devoid of punctures and pubescence across most of its breadth and the secondary plate of the pygidium is extended distad as a cariniform ridge.

Centris (*Melanocentris*) *obsoleta* Lepeletier

Figure 39

Centris obsoleta Lepeletier, 1841:153. ♀.

Centris melanochlaena F. Smith, 1874:360. ♂. NEW SYNONYMY.

Epicharis zamoranensis Cockerell, 1949:480. ♀. NEW SYNONYMY.

DISCUSSION

I have examined the type of *C. melanochlaena,* from Orizaba, Mexico. It corresponds to the concept of *C. obsoleta,* in the sense of Friese (1900b) and subsequent workers, and it is typical of Central American males since the clypeus is almost wholly yellowish.

I have also seen the type and one cotype of *Epicharis zamoranensis.* Cockerell described the thoracic dorsum as being devoid of hairs; this is true of the type, but not of the cotype. The hairs are worn off in the type specimen. There is no doubt that *E. zamoranensis* is conspecific with *C. obsoleta,* a common species in Central America and northern South America.

NEW RECORDS

MEXICO, *NAYARIT:* 1♀, 16 mi. S Acaponeta, 12 Aug. 1963 (M.G. Naumann; UKAN). *OAXACA:* 1♂, 5♀♀, Salina Cruz, 7 Sept. 1965 (D.H. Janzen; UKAN); 1♀, 12 mi. S Chivela, 18 Aug. 1959 (A.S. Menke and L.A. Stange; UCD); 1♂, 8 km W Tehuantepec, 9–10 Aug. 1974 (E.M. and J.L. Fisher; LACM). *PUEBLA:* 1♀, 16.1 km S Izúcar de Matamoros, 1280 m elev., 17 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Caesalpinia cacalaco. SINALOA:* 1♀, 35 km SE Esquinapa, 11 Sept. 1974 (E.M. Fisher; LACM). HONDURAS: 2♀♀, Zamorano, 2600 ft. elev., 5 Nov. 1946 (G. Cisneros; USNM, LACM) (type and cotype *E. zamoranensis*). COSTA RICA, *GUANACASTE:* 1♂, Hacienda Comelco, 8 km NW Bagaces, 19 Nov. 1971 (P.A. Opler; UCB), on *Stachytarpheta frantzii.*

Centris (*Melanocentris*) *sericea* Friese

Figures 24–28

Centris sericea Friese, 1899:41. ♀.

Dr. R.W. Brooks has examined the type of *C. sericea,* a female from an unspecified Mexican locality, and found it to be conspecific with those recorded below. I have redescribed *C. sericea* to facilitate its comparison with similar species.

DIAGNOSIS

Abdomen black and hind legs black pubescent in both sexes. Male metafemur swollen, without ventral ridge; inner mandibular tooth acute; clypeus about 1.2 times broader than long; punctures of second tergum separated by a puncture diameter or more. Female with punctures of disc of second tergum coarser than those of apical zone; pygidial plate with margins strongly convergent apicad, apex subacute; thoracic pubescence wholly dark.

DESCRIPTION

MALE. Measurements (mm). Head width 5.90–6.31; head length 4.46–4.72; wing length 15.0–16.0; total length 18.5–20.0.

Head. 1.32–1.34 times broader than long, occipital margin, in frontal view, slightly concave between tops of eyes, ocelli well anterior to occipital margin; inner orbits moderately convergent above, upper frontal width 0.68–0.70 times lower frontal width. Mandible robust, tridentate, inner tooth acute and subequal to middle tooth. Labrum about twice broader than long; apical margin narrowly rounded; disc shiny between subcontiguous, moderate punctures. Clypeus narrow, about 1.2 times broader than long; disc moderately shiny to shiny (apical area), minutely roughened between close to sparse, moderate punctures, without distinct median impunctate area. Frons slightly shiny between dense, fine punctures, area in front of anterior ocellus and laterad of posterior ocelli impunctate, tessellate and moderately shiny; vertex moderately shiny between dense, fine punctures; preocciput similar but punctures sparse; gena moderately shiny, punctures sparse to close, minute near eye grading to fine toward gular margin. Interantennal distance 1.75–1.89 times antennal socket diameter; antennocular distance 0.48–0.61 times antennal socket diameter; scape stout, 1.97–2.08 times longer than broad; scape length 0.69–0.77 times length of first flagellar segment; first flagellar segment longer than following three combined, 4.41–5.44 times length of second. Interocellar distance 1.54–1.67 times diameter of anterior ocellus; ocellocular distance 0.51–0.69 times diameter of anterior ocellus ocelloccipital distance 2.03–2.15 times diameter of anterior ocellus.

Thorax. Mesoscutum shiny between dense to subcontiguous, moderate punctures, interspaces tessellate and moderately shiny in posterior middle; scutellum slightly shiny, tessellate between dense to subcontiguous, moderate punctures, a very low convexity on either side of middle; metanotum moderately shiny and sharply tessellate between sparse, weak, fine punctures; mes- and metepisterna moderately shiny between dense to subcontiguous, moderate punctures. Basal area of propodeum moderately shiny and sharply tessellate between sparse, fine punctures; side moderately shiny and roughened between close to dense, fine punctures. Metafemur robust, about 1.8 times longer than thick, without ventral ridge; metabasitarsus slender, about 3.6 times longer than broad.

Abdomen. Elevated basal area of dorsal face of first tergite much shorter, in middle, than apical zone, slightly shiny and tessellate between sparse, fine punctures; apical zone of first tergite long, shiny between scattered fine punctures; disc of second tergum moderately shiny between dense, moderate punctures which are conspicuously coarser and closer than those of apical zone; disc of third tergite moderately shiny and tessellate between close, fine punctures which are replaced with fine setigerous papillae on apical zone; fourth to sixth tergites moderately shiny and tessellate between close, slightly coarser setigerous papillae.

Terminalia. Seventh sternite (Fig. 25) with apical incision deeper and more angular than in *C. agiloides* (Fig. 18) and hairs more numerous and more conspicuously plumose. Eighth sternite (Fig. 26) more angularly expanded in middle than in *C. agiloides* (Fig. 19). Gonostylus (Figs. 27, 28) ending well short of level of end of penis valve; ventral lobe of penis valve extended well beyond margin of dorsal lobe.

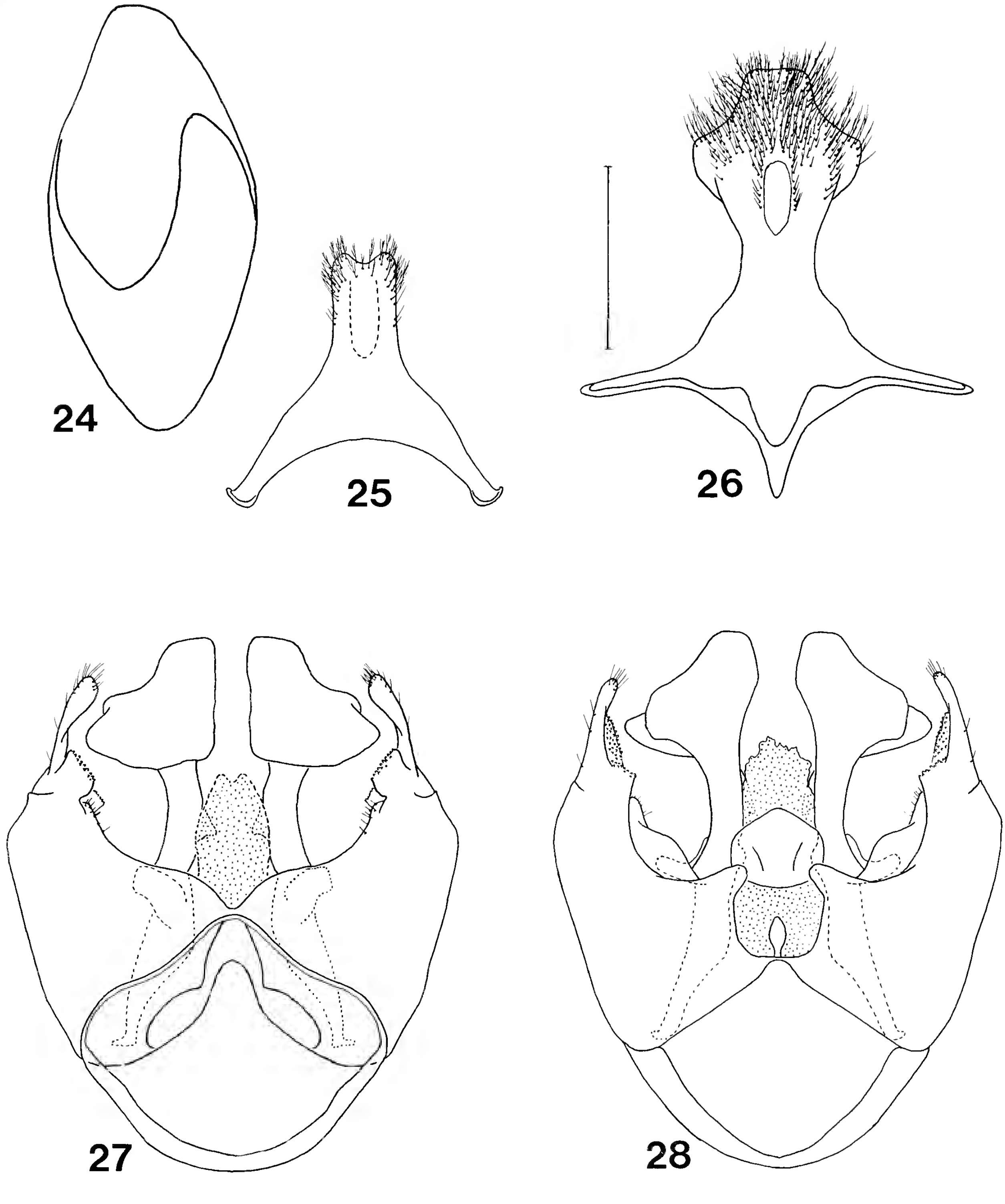
Pilosity. Blackish brown on head, thorax, legs, and first tergite; second and following tergites with whitish hairs, very short and appressed on second segment, becoming progressively longer and more erect on succeeding segments; golden-brown hairs laterad on fourth and following terga, on pygidial plate and on sternites.

Color. Integument blackish brown on most areas; antenna, tegula, and legs dark reddish brown; apical abdominal segments light brown. The following pale yellow: large spot on labrum; clypeus, except small sublateral brown spots near base; transverse supraclypeal mark; paraocular area, not extending above lower margin of antennal socket; preapical spot on underside of scape. Wings dark brown, veins and stigma blackish.

FEMALE. Measurements (mm). Head width 6.67–7.08; head length 4.92–5.33; wing length 16.0–17.0; total length 20.5–23.0.

Head. 1.31–1.37 times broader than long; occipital margin, in frontal view, nearly flat and, in center, slightly above level of tops of eyes; ocelli well below occipital margin; inner orbits weakly convergent above, upper frontal width 0.85–0.93 times lower frontal width. Mandible stout, quadridentate, inner tooth acute and subequal to adjacent tooth. Labrum about twice broader than long, apex narrowly rounded, shiny between subcontiguous, moderate punctures. Clypeus as described for male, but about 1.3 times broader than long and median impunctate line a little more evident, but still poorly defined. Punctation of frons, occipital area, and gena as in male. Interantennal distance 2.37–2.53 times antennal socket diameter; scape stout, 2.00–2.27 times longer than broad, scape length 0.61–0.73 times length of first flagellar segment; first flagellar segment longer than following three segments combined, 4.64–5.41 times longer than second. Interocellar distance 1.66–1.95 times diameter of anterior ocellus; ocellocular distance 1.24–1.45 times diameter of anterior ocellus; ocelloccipital distance 1.87–1.97 times diameter of anterior ocellus.

Thorax. Punctation and form as described for male. Basi-



Figures 24–28. *Centris* (*Melanocentris*) *sericea*, female basitibial plate, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line (25–28) = 1.00 mm.

tibial plate (Fig. 24) elongate, apices of primary and secondary plates narrowly rounded.

Abdomen. First tergum as described for male, but tessellate area limited to lateral areas of dorsal face; disc of second tergum slightly shiny and tessellate between fine, subcontiguous punctures which are conspicuously coarser than punctures of apical zone; disc of third tergite slightly shiny between dense, minute and scattered, fine punctures; fourth tergite slightly shiny, more sharply tessellate between dense, fine punctures; fifth tergite duller between subcontiguous, fine punctures and scattered setigerous papillae. Margins of pygidial plate strongly convergent apicad, apex narrowly truncate or subacute; secondary plate short and broad.

Pilosity. As described for male; prepygidial fimbria golden brown.

Color. As described for male, but pale facial marks absent and fifth tergite dull reddish.

SPECIMENS EXAMINED

MEXICO, *MÉXICO:* 1♀, Cañon de Lobos, 1200 m elev., 12–13 July 1969 (M. Sousa; LACM). *MORELOS:* 2♀♀, Yautepec, 31 July 1963 (F.D. Parker and L.A. Stange; UCD); 1♀, 4 mi. SW Yautepec, 3800 ft. elev., 2 July 1961 (C.D. Michener; UKAN), on *Cassia* sp.; 1♂, 4.3 mi. W Yautepec, 4000 ft. elev., 17 Aug. 1962 (Ordway and Marston; UKAN). *NAYARIT:* 2♂♂, Km 190, 1200 m elev., NW of Guadalajara, 6 Sept. 1975 (J.L. Neff; LACM), on "legume 7046"; 9♀♀, 8 mi. N Tepic, 1 Sept. 1962 (D.H. Janzen; UCB), on *Crotalaria* sp.

DISCUSSION

Although the male of *C. sericea* closely resembles that of *C. obsoleta*, the clypeus is broader in the latter species, at least 1.4 times broader than long. The inner margins of the eyes are more strongly convergent above in *C. obsoleta*, so that the distance between the eyes at their upper ends is less than the distance between the lateral margins of the two posterior ocelli. In *C. sericea* males the transocellar distance is less than the distance between the eyes at their upper ends. These same features will readily distinguish *C. sericea* from *C. agilis*, as will the less shiny, uniformly dark abdomen and the lack of the pale hairs on the hind legs. From males of *C. agiloides*, this species may be separated by the blackish abdomen, lack of pale pubescence on the hind legs, the mostly pale clypeus, and the generally more uniformly dark thoracic pubescence, as well as differences in abdominal punctation.

Females of *C. sericea*, by virtue of their uniformly dark color and narrowly truncate pygidial plate can only be confused with those of *C. obsoleta*. They differ from that species, however, in that the disc of the second tergite is densely punctate, the punctures conspicuously coarser than those of the apical zone and those on the disc of the following segment. Additionally, the clypeus is less closely punctate and the pygidial plate is more strongly narrowed distad and less broadly truncate.

Centris (*Melanocentris*) *plumipes* F. Smith

Centris plumipes F. Smith, 1854:373. ♀ ♂.

This species, originally described from Santarem, Brazil, is easily recognized by the features cited in the key.

NEW RECORDS

COSTA RICA, *HEREDIA:* 3♂♂, Finca La Selva, near Puerto Viejo, 6 May 1979 (D.R. Perry; LACM), on *Dussia* sp.; 5♂♂, same locality and collector, 24 July 1979 (LACM), on *Hymenolobium* sp.

Centris (*Melanocentris*) species A

Figure 42

This is known only from four females. In this species, pubescence is dark, except light brownish on the posterior part of the scutellum and yellowish on the scopa, the apex of the pygidial plate is angularly emarginate, and the clypeus is conspicuously maculate. Although the integument is generally blackish, the abdominal terga have weak metallic bluish reflections.

SPECIMENS EXAMINED

COSTA RICA, *HEREDIA:* 1♀, Finca La Selva, near Puerto Viejo, 6 May 1979 (D.R. Perry; LACM), on *Dussia* sp. PANAMA, *CANAL ZONE:* 1♀, Barro Colorado Island, 9 July 1979 (H. Wolda; ROUB); 1♀, Frijoles, 19 May 1980 (K.E. Steiner; UCD), on *Byrsonima crassifolia*; 1♀, Pipeline Road, 3.7 mi. NW Gamboa, 9 May 1980 (K.E. Steiner; LACM), on *B. crassifolia*.

Subgenus *Trachina* Klug

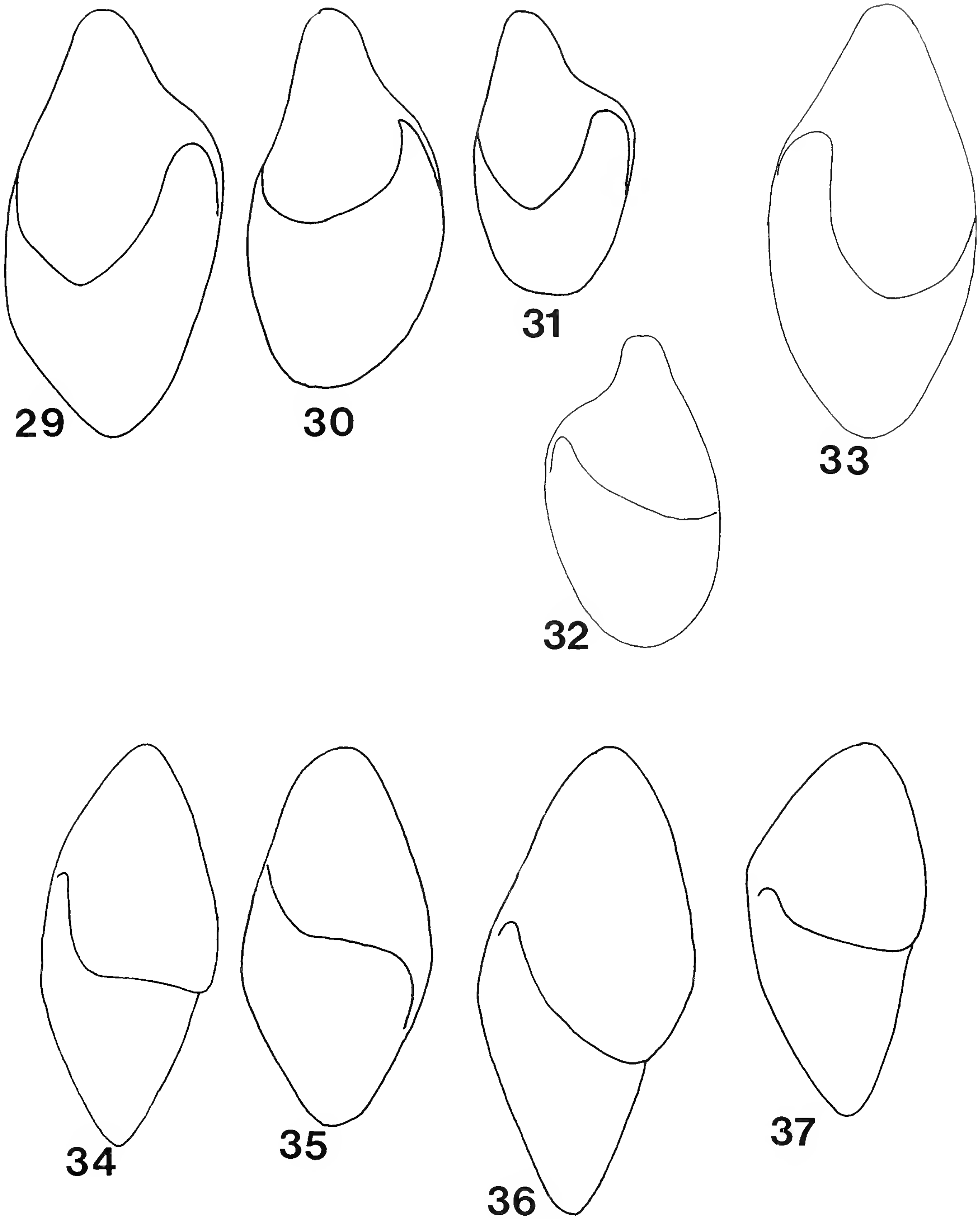
Trachina Klug, 1807:226. Type-species: *Centris longimana* Fabricius, 1804; monobasic.

Paremisia Moure, 1945b:406. Type-species: "*Paremisia lineolata* (Lepeletier, 1841)" = *Bombus similis* Fabricius, 1804.

Trachina is a member of a small group of subgenera, the other two being *Heterocentris* and *Hemisiella*, characterized by the three-segmented maxillary palp in both sexes, the swollen hind legs of the male and the metabasitarsus of the male with a sharp posterior carina or ridge which terminates in a raised tooth (Fig. 18).

Michener (1951) suggested that these three subgenera might well be united into a single genus. While there are some similarities, it seems to me that *Trachina*, at least, is distinct from both *Heterocentris* and *Hemisiella*. The latter two subgenera share a procoxal modification which appears to be unique in *Centris*. There is a sharply depressed groove along the inner, ventral margin of the procoxa; such a groove is not present in *Trachina* or the other subgenera. Females of *Heterocentris* and *Hemisiella* have some scopal hairs, especially basad on the metatibia, simple; in *Trachina* and other subgenera, the scopal hairs are conspicuously plumose. *Trachina* females possess a distinct secondary basitibial plate; in *Heterocentris* and *Hemisiella*, the basitibial plate has a basal convexity, but no secondary plate.

Both sexes of *Trachina* differ from species of *Hemisiella* and *Heterocentris* in possessing a longitudinal, median yellow line on the clypeus. Sometimes, this line may not be evident when the black of the clypeus is reduced to a pair of subbasal, sublateral spots. Clypeal maculae in *Heterocentris* and *Hemisiella* are usually present as a pair of subapical spots or a subapical band (females, some males) or else the clypeus is yellow except across the base (some males). Males of *Tra-*

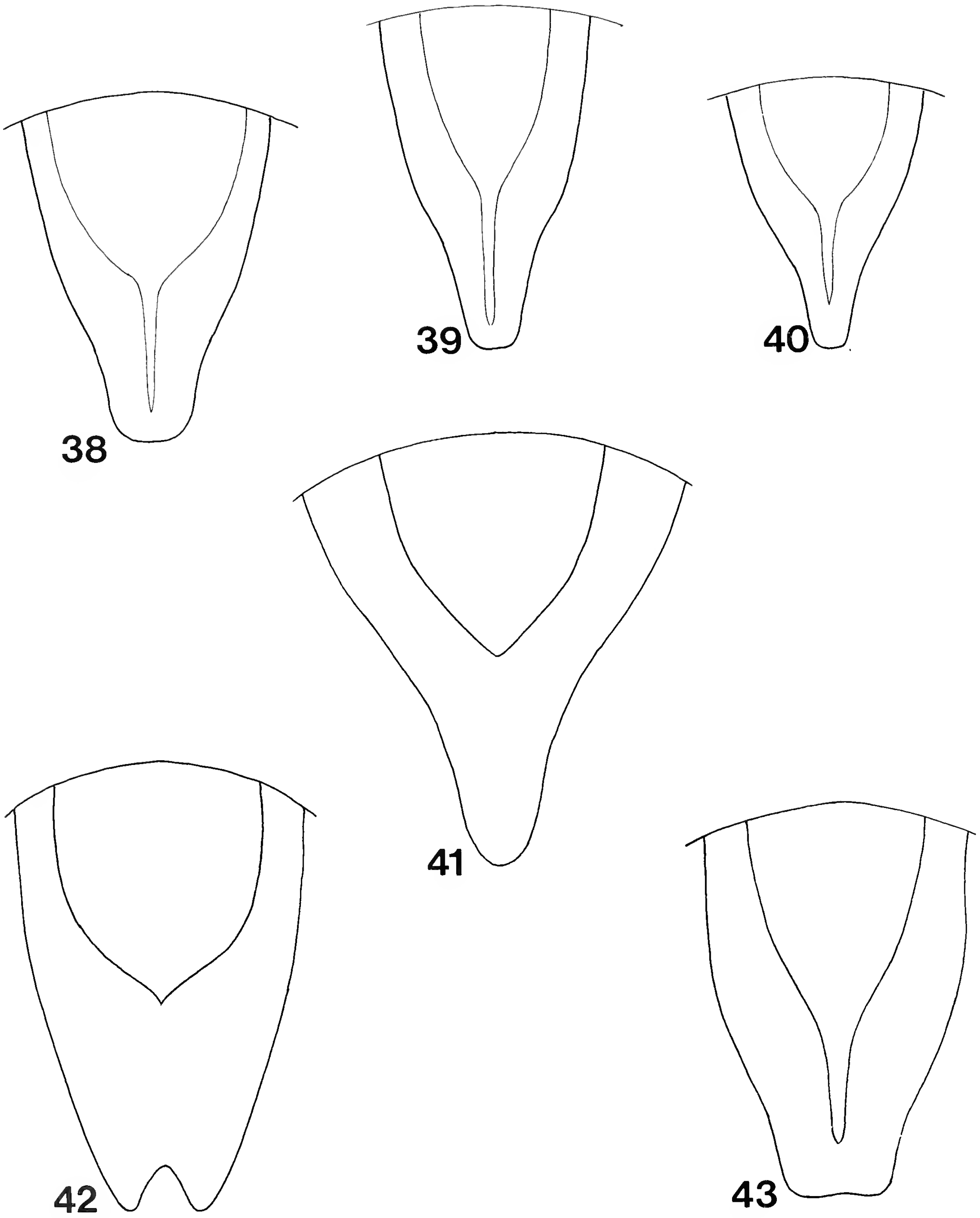


Figures 29–37, left basitibial plate of female: **29**, *Centris* (*C.*) *flavifrons*; **30**, *C.* (*C.*) *flavofasciata*; **31**, *C.* (*C.*) *aethiocesta*; **32**, *C.* (*C.*) *caixensis*; **33**, *C.* (*C.*) *meaculpa*; **34**, *C.* (*Trachina*) *eurypatana*; **35**, *C.* (*T.*) *fuscata*; **36**, *C.* (*T.*) *dentata*; **37**, *C.* (*T.*) *xochipillii*.

china further differ in that the apical lobe of the seventh sternite is greatly reduced, so that the segment is essentially a transverse band.

KEY TO NORTH AMERICAN *TRACHINA*

1a. Male, antenna 13-segmented, basitibial plate absent 2



Figures 38–43, pygidial plate of female: **38**, *Centris* (*C.*) *flavifrons*; **39**, *C.* (*C.*) *flavofasciata*; **40**, *C.* (*C.*) *aethiocesta*; **41**, *C.* (*Melanocentris*) *obsoleta*; **42**, *C.* (*M.*) species A; **43**, *C.* (*M.*) *agilis*.

b. Female, antenna 12-segmented, basitibial plate present 10

2a. Ocellocular distance greater than diameter of anterior ocellus; in full frontal view, distance from anterior ocellus to clypeal base a little shorter than distance from anterior ocellus to occipital margin 3

b. Ocellocular distance less than diameter of anterior ocellus; in full frontal view, distance from anterior ocellus to clypeal base much greater than distance from anterior ocellus to occipital margin 4

3a. Thoracic pubescence uniformly blackish, except white on scutellum and metanotum; metabasitarsus with sharp ridge along posterior margin, terminating in sharp spiniform process beyond midlength (Fig. 18) ..... *labiata* Friese

b. Hairs of mesoscutum dark brownish distally, base and branches pale, so that pubescence appears "clouded"; metabasitarsus without posterior ridge (Fig. 19) ..... *longimana* (Fabricius)

4a. Abdomen largely or wholly ferruginous; if brownish or blackish, hairs of mesoscutum red or pale ochreous 5

b. First three, and most of fourth, terga blackish, apical band of fourth and all of fifth to seventh terga pale reddish; hairs of mesoscutum black except for band of whitish hairs across anterior one-fourth ..... *vidua* Mocsáry

5a. At least first four terga dark brown to blackish (fourth may be ferruginous on apical margin 6

b. Abdomen largely or entirely ferruginous 7

6a. Terga 5–7 dark, with glistening whitish hairs; mesoscutal hairs pale to dark ferruginous; in frontal view, occiput arcuately raised above tops of eyes ..... *similis* (Fabricius)

b. Terga 5–7 ferruginous, with yellowish to ferruginous hairs; mesoscutal hairs pale ochreous; in frontal view, occiput flat or slightly concave between tops of eyes ..... *xochipillii,* new species

7a. Procoxa without distal spine; wings uniformly light yellowish brown 8

b. Procoxa with slender distal spine (hidden in dense pubescence); forewing, basad of basal vein, clear and colorless and distinctly brownish beyond basal vein ..... *eurypatana,* new species

8a. Hairs of mesoscutum pale ochreous or ferruginous; metafemur usually stout, subbasal ventral process usually tooth-like (Fig. 57, 58); second and third terga moderately shiny, disc finely tessellate; middle and hind legs with conspicuous brownish to blackish pubescence 9

b. Hairs of mesoscutum (and of most of thorax) whitish, though often slightly dusky anteriorly; metafemur less stout, subbasal ventral process low and not tooth-like (Fig. 56); second and third terga shiny, discs weakly or not at all tessellate; pubescence of legs whitish to pale ferruginous, ferruginous on inner surface of metabasitarsus ..... *heithausi* Snelling

9a. Disc of seventh sternite triangular, apex acute (Fig. 46); apical swelling of eighth sternite short and broad (Fig. 47); basal lobes of penis valve short and broad ..... *dentata* F. Smith

b. Disc of seventh sternite quadrate, apical margin straight or concave (Fig. 44); apical swelling of eighth sternite long and narrow (Fig. 45); basal lobes of penis valve relatively slender ..... *fuscata* Lepeletier

10a. Hairs of mesoscutum dark brownish to blackish and either (a) with a transverse band of white hairs across front of mesoscutum or (b) hairs of scutellum whitish 11

b. Hairs of mesoscutum whitish, yellowish, red or with dark apices, but without sharply contrasting pale hairs anteriorly or on scutellum 12

11a. Mesoscutum with a band of whitish hairs across anterior margin and hairs of scutellum and metanotum dark; first four terga blackish (fourth pale reddish apically), last two segments pale reddish ..... *vidua* Mocsáry

b. Mesoscutum without pale hairs anteriorly, but whitish hairs on posterior margin of scutellum and all of metanotum; terga wholly ferruginous ..... *labiata* Friese

12a. First three terga dark brownish to blackish 13

b. First three terga ferruginous 14

13a. Terga 4 and 5 dark, margins colorless, with long, glistening whitish hairs; scopa black; mesoscutal hairs usually dark reddish; tergum 4, across middle, with fine dense piligerous punctures ..... *similis* (Fabricius)

b. Terga 4 and 5 ferruginous, with yellowish hairs, scopa pale yellowish; mesoscutal hairs ochreous; tergum 4, across middle, with sparse fine piligerous punctures ..... *xochipillii,* new species

14a. Head width less than 5.75 mm; in frontal view, occiput weakly convex between tops of eyes; ocellocullar distance less than 1.5 × diameter of anterior ocellus; hairs of thoracic dorsum whitish to ferruginous 15

b. Head width more than 7.0 mm; in frontal view, occiput arcuately raised above tops of eyes; ocellocular distance about twice diameter of anterior ocellus; hairs of thoracic dorsum with blackish shafts and pale branches near base ..... *longimana* (Fabricius)

15a. Thoracic pubescence ochreous to light brownish ferruginous; scape distinctly maculate beneath; second and third terga finely and closely punctate, surface moderately shiny 16

b. Thoracic pubescence whitish, tinged with pale brownish on mesoscutum; scape obscurely, if at all, maculate; second and third terga shiny between fine punctures mostly separated by twice a puncture diameter or more ..... *heithausi* Snelling

16a. Wings light to medium yellowish brown; lower margin of secondary basitibial plate strongly oblique (Fig. 36) *or,* if somewhat transverse, posterior margin is continuous with that of primary plate (Fig. 35) 17

b. Wings blackish brown; lower margin of secondary basitibial plate transverse, anterior margin curved basad well before anterior margin of primary plate (Fig. 34) . . . . *eurypatana,* new species

17a. Basitibial plate broad, lower margin of secondary plate usually transverse across middle portion, posterior margin continuous with that of primary plate (Fig. 35) . . . . *fuscata* Lepeletier

b. Basitibial plate narrow, lower margin of secondary plate strongly oblique throughout, posterior margin extended over that of primary plate (Fig. 36) . *dentata* F. Smith

Centris (*Trachina*) *dentata* F. Smith

Figures 36, 46, 47, 58

Centris dentata F. Smith, 1854:374. ♂.
Centris proxima Friese, 1899:45. ♂ ♀.

Michener (1954) recorded *C. dentata* from Panama. In addition to material from Panama, I have seen several females from Mixtepec, Oaxaca, Mexico, 28 Feb. 1974 (M. Sousa; LACM). This appears to be an uncommon species in Central America, although widely distributed in South America; the types of both *C. dentata* and *C. proxima* were from Brazil.

Centris (*Trachina*) *eurypatana,* new species

Figures 34, 48–51, 57

DIAGNOSIS

Male distinguished from all other *Trachina* by the presence of a slender spine at the apex of the procoxa. Female separable from other *Trachina* by the following combination: pubescence pale ochreous, abdomen ferruginous, wings dark brown, posterior margin of secondary basitibial plate extended beyond that of primary plate.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 5.90; head length 4.10; wing length 13.0; total length 15.0.

Head. 1.44 times broader than long; occipital margin weakly convex in frontal view, ocelli well anterior to margin; inner orbits strongly convergent above, upper frontal width 0.68 times lower frontal width. Mandible slender, tridentate, inner tooth large and its lower edge slightly sinuate. Labrum about 1.4 times broader than long, apical margin broadly rounded; disc shiny between subcontiguous, fine punctures. Clypeus about 1.4 times broader than long; disc shiny across apical margin, otherwise slightly shiny and distinctly tessellate between dense to subcontiguous, fine punctures, impunctate median line narrow and slightly elevated. Frons moderately shiny between dense to subcontiguous, fine to moderate punctures, sparsely punctate areas adjacent to ocelli moderately shiny and distinctly tessellate; preoccipital area shiny between dense subcontiguous, fine to minute punctures; gena shiny between close to dense, fine punctures. Interantennal distance 0.82 times antennal socket diameter; scape robust, 1.97 times longer than wide; scape length 0.70 times length of first flagellar segment; first flagellar segment 5.63 times longer than second, distinctly longer than combined lengths of second to fourth segments. Interocellar distance 1.90 times diameter of anterior ocellus; ocellocular distance 0.55 times diameter of anterior ocellus; ocelloccipital distance 2.84 times diameter of anterior ocellus.

Thorax. Mesoscutum shiny between subcontiguous, fine punctures which become well separated posteromedially; scutellum shiny between scattered, minute to fine punctures; metanotum dull, sharply tessellate and with scattered, minute punctures; mesepisternum and metepisternum shiny between dense to subcontiguous, fine to moderate punctures. Basal area of propodeum shiny and weakly tessellate between sparse to close, moderate punctures; side and disc shiny between close to dense, fine to moderate punctures. Procoxa with narrow, distal, spiniform process; metafemur stout, about twice longer than thick, ventral process stout (Fig. 57); process on anterior margin of metatibia slender, spiniform; metabasitarsus about 3.2 times longer than broad, posterior ridge ending at about midlength.

Abdomen. Dorsal face of first tergite moderately shiny and tessellate between sparse, minute punctures; disc of second tergite shiny and weakly tessellate between sparse to dense, fine punctures, punctures of apical zone minute; third tergite similar, but punctures dense; fourth tergite similar to third, but punctures variably spaced from sparse to subcontiguous; fifth tergite similar to fourth, but punctures sparse; apex of seventh tergite distinctly bilobed, hidden under dense hairs.

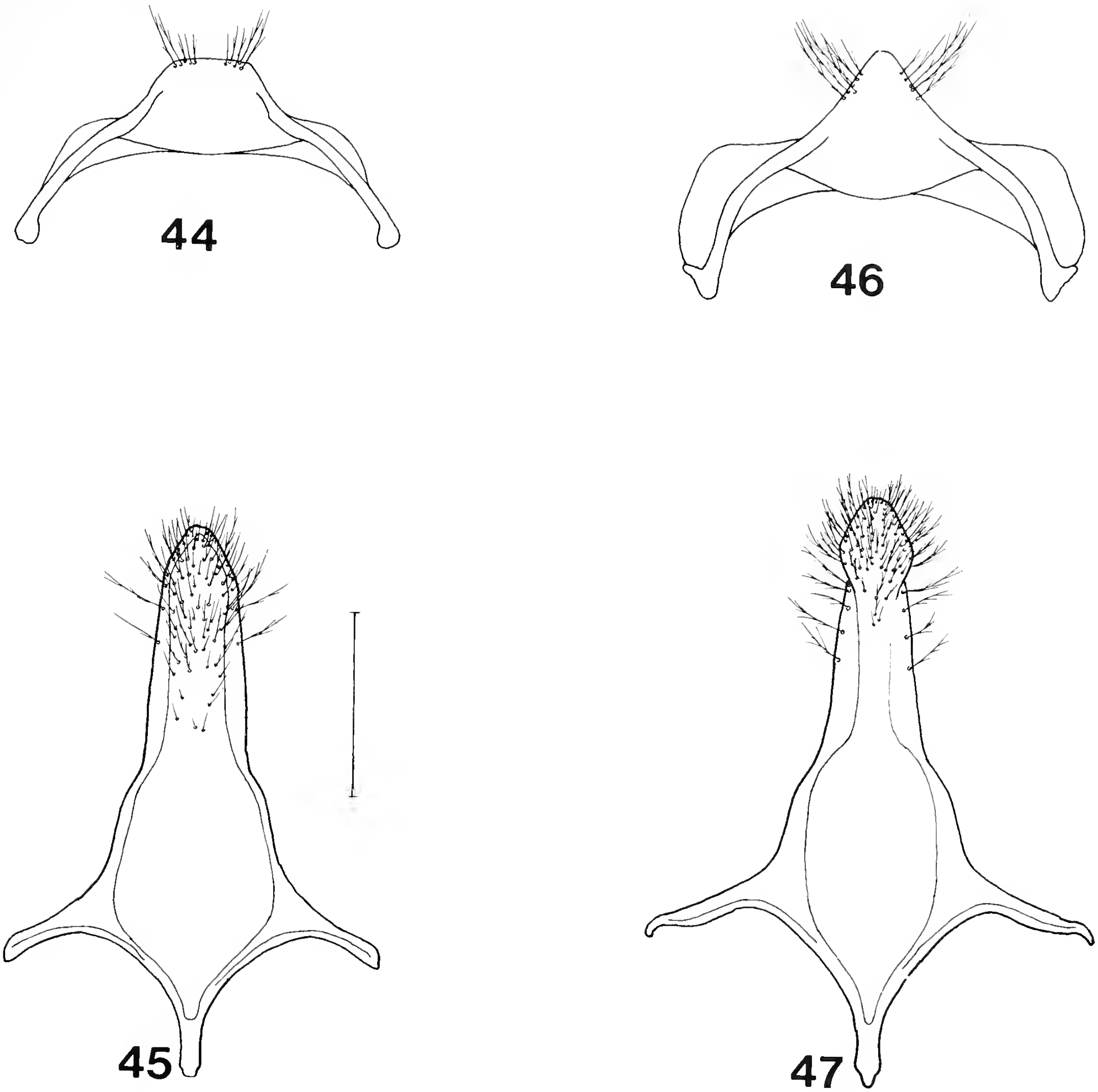
Terminalia. Process of seventh sternite (Fig. 48) short, broad, apical margin convex; margin with long, plumose hairs, disc with a few short, simple hairs. Eighth sternite (Fig. 49) moderately flared preapically, apex acute; hairs fine, plumose. Dorsal process of gonocoxite short, broad, apex rounded; distal tubercles of gonostylus not visible in dorsal view (Figs. 50, 51).

Pilosity. Generally pale ochreous, slightly brownish across vertex, on thoracic dorsum, and on legs, darker on meso- and metatibiae and tarsi; some brown hairs on inner surface of meso- and metatibiae and basitarsi. Second tergite with long, suberect, plumose, blackish brown hairs across base, discs of second to fourth terga with sparse, simple, dark hairs which become progressively longer and more erect on succeeding segments; hairs on fifth to seventh terga long, suberect to erect, slightly yellowish to ferruginous. Ventral abdominal pubescence dense, light yellowish brown.

Color. Head and thorax blackish brown, abdomen ferruginous; antenna and legs variably light to dark reddish brown. The following yellow: mandible, except apical teeth; labrum; clypeus, except a pair of brown submedian spots near base; transverse supraclypeal stripe; paraocular area, upper end constricted and terminating on eye margin at about midlevel of antennal socket; broad ventral stripe on scape; dorsal, apical spot on profemur; basal spot on pro- and mesotibia. Tegula clear yellowish-brown. Wings clear and very light brown basad of vein M, darker brown distad; veins and stigma blackish brown.

FEMALE. Measurements (mm). Head width 5.87–6.10; head length 4.05–4.27; wing length 11.5–12.5; total length 15.0–17.0.

Head. 1.43–1.44 times broader than long; in frontal view, occipital margin gently convex, ocelli well anterior to margin;



Figures 44–47, seventh and eighth sternites of male: **44–45,** *Centris* (*Trachina*) *fuscata*; **46–47,** *C.* (*T.*) *dentata*. Scale line = 0.50 mm.

inner orbits moderately convergent above, upper frontal width 0.87–0.89 times lower frontal width. Mandible tridentate, inner tooth large, blunt. Labrum about 1.5 times broader than long, margin broadly rounded; disc shiny between subcontiguous, fine to moderate punctures. Clypeus about 1.6 times broader than long, otherwise as described for male. Frons and preoccipital area as described for male; gena shiny, punctures close and minute near eye, becoming dense and fine ventrad. Interantennal distance 2.79–3.00 times antennal socket diameter; antennocular distance 1.61–1.71 times antennal socket diameter; scape stout, 2.03–2.17 times longer than wide, scape length 0.67–0.72 times length of first flagellar segment; first flagellar segment 5.63–5.88 times longer than second, longer than following three segments combined. Interocellar distance 2.14–2.30 times diameter of anterior ocellus; ocellocular distance 1.33–1.48 times diameter of anterior ocellus; ocelloccipital distance 2.80–3.00 times diameter of anterior ocellus.

Thorax. As described for male. Procoxa without ventral spine; basitibial plate (Fig. 34) narrowly rounded at apex, posterior margin of secondary plate beyond that of primary plate.

Abdomen. First two terga as described for male, third with punctures of disc minute and sparse, becoming more minute and scattered in apical zone; fourth tergum less shiny than third, punctures very irregularly spaced, moderate and somewhat elongate, close to dense. Pygidial plate with margins strongly convergent distad, apex narrowly truncate; secondary plate obsolete.

Pilosity. About as described for male, but some hairs on disc of fourth tergite at least weakly plumose; scopa pale yellowish; prepygidial fimbria light golden brown.

Color. As described for male, except mandibular apex more extensively dark, dark clypeal spots reaching base, supraclypeal spot greatly reduced or absent and legs approximately concolorous with abdomen. Wings darker brownish.

TYPE MATERIAL

Holotype male: Estación Biologia Chamela, Jalisco, MEXICO, 17 May 1980 (S.H. Bullock, #373), in Natural History Museum of Los Angeles County. Allotype: same locality and collector, 7 Apr. 1982 (#922; LACM). Paratypes (all MEXICO): 1♀, same locality and collector, 12 May 1980 (#372); 2♀♀, 30 mi. E Villa Union, 570 m elev., Sinaloa, 10 Mar. 1980 (J.L. Neff; NEFF). One paratype each in collections of the Estación Biologia de Chamela and in the personal collection of J.L. Neff, the remaining specimens in the Natural History Museum of Los Angeles County.

ETYMOLOGY

The specific epithet combines the Greek *eurys* (broad) and *patanas* (plate), in allusion to the broad secondary basitibial plate of the female.

DISCUSSION

The male is easily distinguished from all previously described species of *Trachina* by the presence of a distinct spine-like process at the apex of the procoxa. It is otherwise very similar to the males of *C. dentata, C. fuscata, C. heithausi,* and *C. xochipillii.* All of these differ from males of *C. eurypatana* in having lighter colored wings, particularly that of *C. heithausi,* which further differs in the paler pubescence of the head and thorax. Males of *C. dentata* have the ventral tooth of the metafemur higher and more slender and the tooth on the anterior margin of the metatibia is stouter than in *C. eurypatana.* The brown, rather than ferruginous, first three abdominal terga will differentiate *C. xochipillii* from *C. eurypatana.*

The female of *C. eurypatana* is best recognized from other members of this complex by the broad secondary basitibial plate, ochreous pubescence, dark wings, and wholly red abdomen. In *C. xochipillii* the first three abdominal segments are brown; in *C. heithausi* the thoracic pubescence is whitish and the wings only faintly brown; in *C. dentata* the median line of the clypeus is shiny and the punctures on either side are moderate rather than fine, and the second tergite is duller, more sharply tessellate and closely punctate. Since the secondary basitibial plate of *C. fuscata* does not overhang the first, this species is easily separated from *C. eurypatana.*

Centris (*Trachina*) *fuscata* Lepeletier

Figures 34, 44, 45

Centris fuscata Lepeletier, 1841:167. ♂.
Centris bimaculata Lepeletier, 1841:168. ♀.

This species, also described from Brazil, is much more common in Central America than the similar *C. dentata.* Females of *C. fuscata,* however, have a narrow secondary basitibial plate (Fig. 35), a feature which will separate this species from superficially similar species. Males most closely resemble those of *C. dentata,* but have the ventral tooth of the metafemur short and stout; in *C. dentata* this tooth is long, slender, and somewhat curved.

I have seen Central American material from Mexico, Guatemala, Costa Rica, and Panama. Michener (1954) has also recorded *C. fuscata* from Panama and Lutz and Cockerell (1920) cite it from Guatemala.

Centris (*Trachina*) *heithausi* Snelling

Figure 56

Centris (*Trachina*) *heithausi* Snelling, 1974:20–23. ♂ ♀.

This species was described from many specimens from Guanacaste Province, Costa Rica. I have seen numerous additional specimens from the same general area. One female, however, was collected 20 km SSE of Chiquimula, Depto. Chiquimula, Guatemala, 25 Feb. 1966 (D.P. Gregory; UCB).

Centris (*Trachina*) *labiata* Friese

Figure 18

Centris labiata Friese, 1904:91. ♂.
Centris schwarzi Cockerell, 1919:192. ♀. NEW SYNONYMY.

This is evidently not a common species. Friese's male type is from San Carlos, Costa Rica. The type of *C. schwarzi* is from Alta Vera Paz, Guatemala. I have seen the type of *C. schwarzi,* in the USNM, and it is the same as females I had already associated with *C. labiata* males. Both sexes are characterized by the dark thoracic pubescence (but pale on the scutellum and metanotum) and the red abdomen.

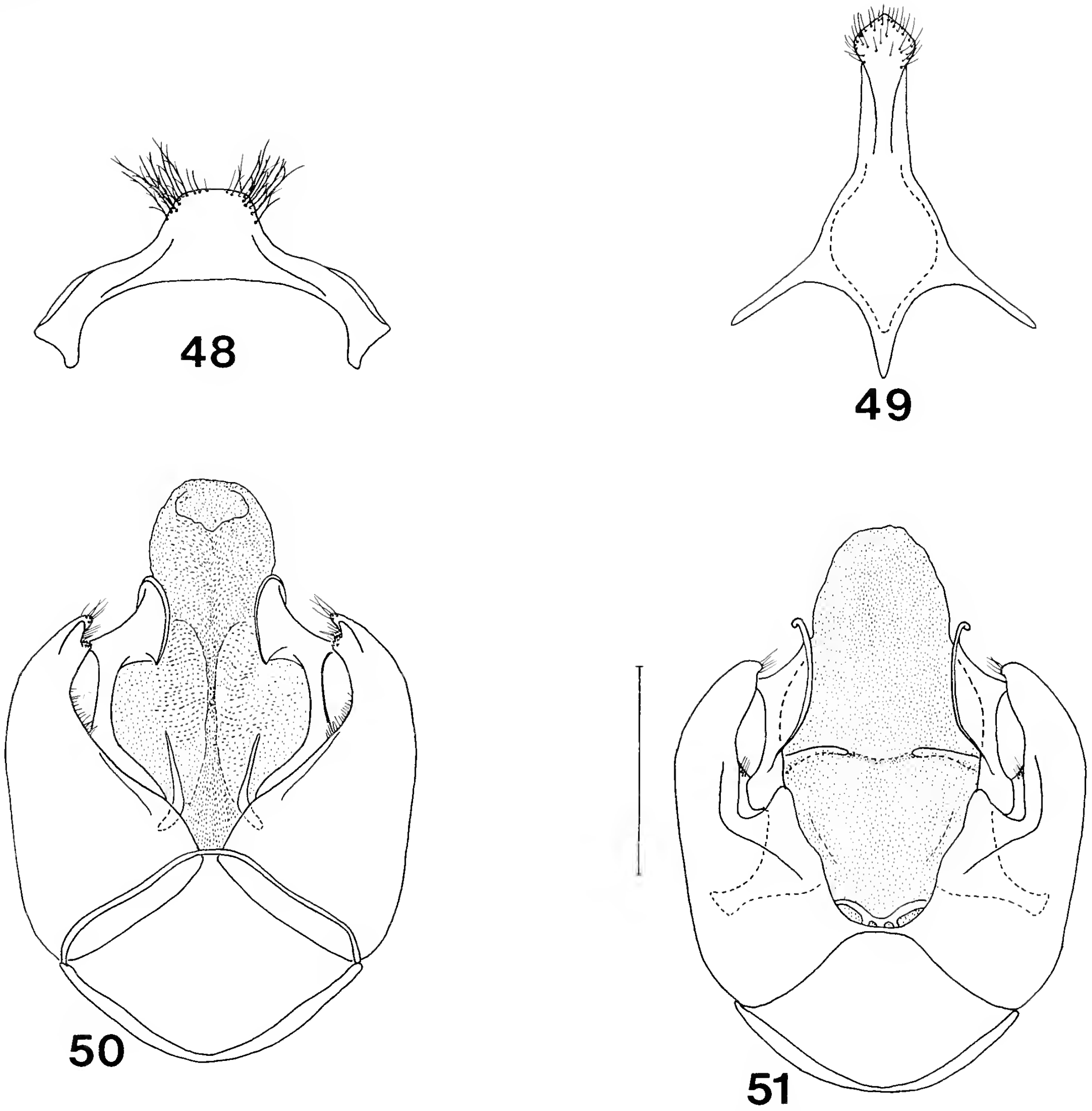
NEW RECORDS

MEXICO, *OAXACA:* 2♂♂, 20 mi. E El Camerón, 21 July 1956 (J.W. MacSwain; UCB); 2♂♂, 19 mi. W Tequisistlan, 29 Aug. 1970 (E.M. and J.L. Fisher; LACM). *VERA CRUZ:* 1♂, El Palmar, 28 Mar. 1954 (D.H. Janzen; LACM). *YUCATÁN:* 1♀, Pisté, 29 June 1967 (E.C. Welling; LACM). BELIZE: 1♀, no further data (LACM).

Centris (*Trachina*) *longimana* Fabricius

Figure 19

Centris longimana Fabricius, 1804:356. ♀ ♂.



Figures 48–51. *Centris* (*Trachina*) *eurypatana*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

Centris personata F. Smith, 1874:362. ♂.

Michener (1954) reported *C. longimana* from several Panamanian localities. In addition to specimens from Panama, I have seen material from Nicaragua and Costa Rica.

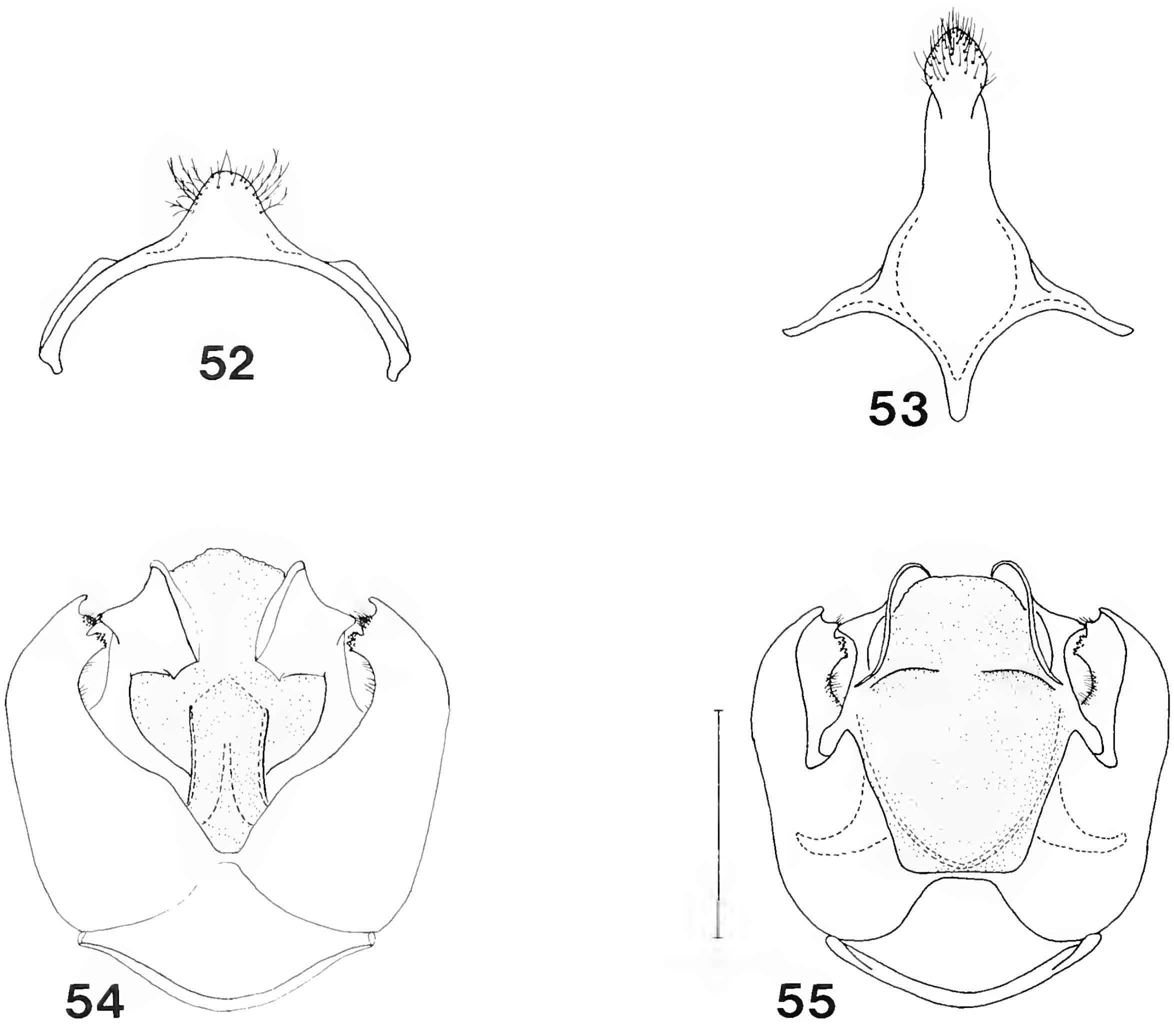
Centris (*Trachina*) *similis* (Fabricius)

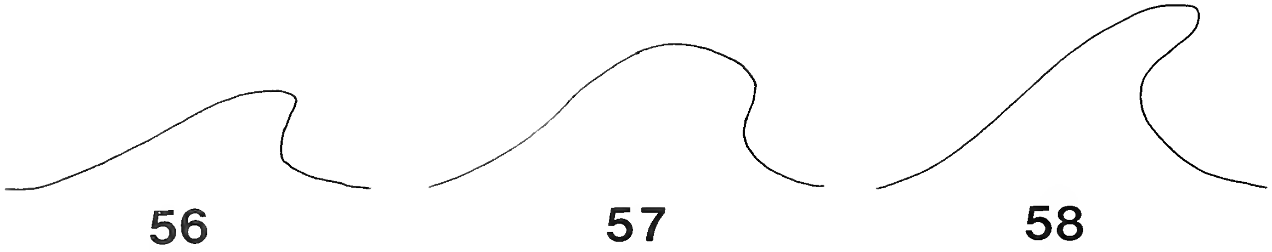
Bombus similis Fabricius, 1804:351. ♀.
Centris lineolata Lepeletier, 1841:158. ♀.
Centris lineolata castaneiventris Mocsáry, *In* Friese, 1899: 288.
Centris (*Paremisia*) *similis:* Moure, 1960b:130–131.

This is a common species in northern South America (Trinidad, Guyana, French Guiana) south to Brazil and Peru. There are no previous reports of its presence in Central America. I have seen the following Central American specimens.

NEW RECORDS

COSTA RICA, *PUNTARENAS:* 1♀, 1.8 mi. W Rincón, 4 Mar. 1971 (J.P. Donahue and C.L. Hogue; LACM). *SAN JOSÉ:* 1♀, Pozo Azul, Junction Ríos Parrita and Candelaria, 85 m elev., 9 Dec. 1961 (A. Wille; UKAN). PANAMA. *PANAMÁ:* 2♂♂, 15 km E Chepo, Llano Carti Rd., 18 Jan.





Figures 52–55. *Centris* (*Trachina*) *xochipillii*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm. Figs. 56–58, outline of ventral metafemoral process of male: **56,** *C.* (*T.*) *heithausi*; **57,** *C.* (*T.*) *eurypatana*; **58,** *C.* (*T.*) *dentata*.

1980 (D. Roubik, #6; ROUB); 2♀♀, 1♂, 15 km NE Chepo, 19 Dec. 1980 (D. Roubik, #48; ROUB).

Centris (*Trachina*) *vidua* Mocsáry

Centris vidua Mocsáry, 1899:252. ♂.

This species was described from Honduras (San Pedro Sula) and has been reported by Friese (1900b) from Orizaba, Vera Cruz, Mexico. I have seen the following specimens of this uncommon bee.

NEW RECORDS

BELIZE: 1♀, Belize (no further data; LACM). COSTA RICA, *CARTAGO:* 1♂, Turrialba, 18 Oct. 1947 (A. Svihla; LACM). PANAMA, *BOCAS DEL TORO:* 1♀, Almirante, Sept. 1963 (LACM). *COLÓN:* 2♀♀, 1♂, 5 km SW Colón, 30 Jan. 1980 (D. Roubik, #12; ROUB).

***Centris* (*Trachina*) *xochipillii*, new species**

Figures 37, 52–55

DIAGNOSIS

At least first three terga brown, apical segments ferruginous; male ocellocular distance less than ocellar diameter, occipital margin at most weakly convex in frontal view, thoracic pubescence ochreous; female with ochreous thoracic pubescence, posterior margin of secondary plate of basitibial plate overhanging that of primary plate, scopa yellowish.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 5.23 (5.13–5.74); head length 3.79 (3.59–4.05); wing length 13.5 (12.0–14.0); total length 15.0 (13.0–17.0).

Head. 1.38 (1.38–1.51) times broader than long; in frontal view, occipital margin flat or slightly convex, ocelli well below margin; inner eye margins strongly convergent above, upper frontal width 0.74 (0.69–0.75) times lower frontal width. Mandible tridentate, inner tooth large, its lower margin slightly concave in outline. Labrum about 1.7 times wider than long, apical margin broadly rounded; disc shiny between subcontiguous, fine to moderate punctures. Clypeus about 1.6 times broader than long; disc dull and densely tessellate at base, shiny and weakly tessellate on about distal one-fourth, median line raised and impunctate, disc otherwise densely to subcontiguously punctate, punctures fine to moderate. Frons and ocellar area closely punctate, except usual nearly impunctate areas near ocelli; postocellar area varying from moderately shiny between minute, dense punctures immediately behind ocelli, to shiny between sparse to close, moderate punctures at posterior margin; gena shiny between sparse to close punctures, minute adjacent to eye and grading to fine over most of area. Interantennal distance 2.30 (2.00–2.56) times antennal socket diameter; antennocular distance 0.85 (0.63–0.88) times antennal socket diameter; scape stout, 1.90 (1.76–2.03) times longer than wide, scape length 0.63 (0.63–0.72) times length of first flagellar segment; first flagellar segment longer than following three segments combined, 5.63 (5.24–6.13) times length of second segment. Interocellar distance 2.15 (1.89–2.11) times diameter of anterior ocellus; ocellocular distance 0.70 (0.57–0.78) times diameter of anterior ocellus; ocelloccipital distance 2.85 (2.50–2.96) times diameter of anterior ocellus.

Thorax. Mesoscutum shiny between dense, fine punctures; dorsal face of scutellum shiny, punctures sparse and minute in center, becoming close and fine laterad, dense and fine on posterior face; metanotum slightly shiny, sharply tessellate between scattered, minute punctures; mesepisternum shiny between dense, fine punctures; metespisternum similar but punctures more crowded toward posterior margin and lower one-third with punctures minute and scattered. Basal area shiny between sparse, fine punctures in middle, becoming dense laterad; side of propodeum similar but punctures scattered to close. Procoxa aspinose; metafemur robust, about 1.8 times longer than thick, ventral process stout; anterior tooth of metatibia acute, moderately stout; metabasitarsus about 3.5 times longer than wide, posterior carina ending at about midlength in slender tooth.

Abdomen. Dorsal face of first tergum moderately shiny and tessellate between sparse, minute punctures; disc of second tergum shiny between sparse, minute punctures which extend across apical zone nearly to margin; disc of third tergum similar, but punctures a little larger and impunctate margin broader; fourth tergum shiny and weakly tessellate between sparse, moderate punctures; fifth and sixth terga similar, but a little more distinctly tessellate.

Terminalia. Seventh sternite (Fig. 52) with distal process longer and more narrowly rounded than in *C. eurypatana* (Fig. 48) and fewer long marginal hairs. Apical swelling of eighth sternite (Fig. 51) shorter than in *C. eurypatana* (Fig. 49), apex less acute. Dorsal process of gonocoxite (Fig. 55) narrower and more acute than in *C. eurypatana*; tubercles at apex of gonostylus visible in dorsal view.

Pilosity. Pubescence generally ochreous, whitish on head, especially on gena; brownish across vertex, anteriorly on mesobasitarsus, externally on metatibia and metabasitarsus; reddish brown on remainder of hind legs; discs of second to fourth terga with hairs simple, blackish and appressed on second, longer and more erect on third, some suberect on fourth; fifth with erect hairs, some plumose, mixed ferruginous and black; sixth and seventh terga with hairs mostly plumose, pale ferruginous, brownish laterad.

Color. Blackish; first three terga, and most of fourth, dark reddish brown; distal margin of fourth, and all of following terga, ferruginous; sternites reddish; legs medium to light reddish brown. The following dull yellow: most of mandible; labrum; narrow median stripe and transverse distal band (broader laterad) on clypeus; paraocular area, constricted above and ending on eye margin at about midlength of antennal socket; linear mark on underside of scape; small basal spot on pro- and mesotibiae. Wings light brown, a little darker apicad; veins and stigma dark brown.

FEMALE. Measurements (mm). Head width 5.79–6.10; head length 4.21–4.36; wing length 11.0–13.0; total length 13.0–17.0.

Head. 1.36–1.42 times broader than long; in frontal view occiput nearly flat and ocelli well anterior to margin; eyes weakly convergent above, upper frontal width 0.88–0.91 times lower frontal width. Mandible tridentate, inner tooth large, subtruncate. Labrum about 1.6 times broader than long, apex broadly rounded; shiny between subcontiguous, moderate punctures, but with distinct, slightly convex basal zone virtually free of punctures. Clypeus about 1.7 times broader than long, otherwise about as described for male, but impunctate median line moderately shiny and moderate-sized punctures clearly dominant. Frons, occipital area, and gena about as described for male. Interantennal distance 2.43–2.77 times antennal socket diameter, antennocular distance 1.47–1.68 times antennal socket diameter; scape robust, scape 1.83–2.06 times longer than broad; scape length 0.70–0.76 times length of first flagellar segment; first flagellar segment longer than following three segments combined, 5.00–5.41 times length of second segment. Interocellar distance 2.06–2.24 times diameter of anterior ocellus; ocellocular distance 1.39–1.48 times diameter of anterior ocellus; ocelloccipital distance 2.50–2.83 times diameter of anterior ocellus.

Thorax. Punctation as described for male. Basitibial plate (Fig. 37) long, apex subacute; posterior margin of secondary plate extending beyond that of primary plate.

Abdomen. First tergum similar to that of male, but with a few moderate punctures across base of dorsal face; second to fifth terga about as described for male. Pygidial plate V-shaped, apex narrowly rounded, secondary plate indistinct.

Pilosity. Generally as described for male, but only first three terga dark reddish brown, last three ferruginous; yellowish marks of face as in male, but scape entirely dark, or with a small, obscure, yellowish blotch.

TYPE MATERIAL (all Oaxaca, MEXICO)

Holotype male, allotype, 2♂♂, 7♀♀ paratypes: Tehuantepec, 18 Feb. 1954 (R.R. Dreisbach), in University of Kansas, Snow Entomological Museum. Additional paratypes: 1♀, 20 mi. W Tehuantepec, 18 Feb. 1954 (R.R. Dreisbach; UKAN): 1♂, 5 mi. W Tehuantepec, 7 Apr. 1953 (E.I. Schlinger; UCB); 8♂♂, 35 mi. N Tehuantepec, 2600 ft. elev., 5 Feb. 1966 (D. Bolinger; ORSU); 1♂, 20 mi. E Juchitan jct., 500 ft. elev., 28 Jan. 1965 (D. Bolinger; ORSU). Two male and two female paratypes in LACM, remainder returned to their respective collections.

ETYMOLOGY

This species is named for the Aztec (Nahuatl) god of Spring and of flowers, *Xochipilli*; in pronoucing the name, the x has an "sh" sound.

DISCUSSION

Aside from the variations in measurements and ratios noted above, the females of this species are all very similar to one another. Even the yellowish face marks appear to be quite stable, but this may be due to the fact that all are from the same locality. Much the same is true of the males. The principal variation involves the extent of the shiny area of the clypeus. In a few males, up to one-half of the discal area is shiny, but generally the shiny portion is less extensive, and may be limited to a very narrow band along the apical margin.

Most males possess a narrow, transverse supraclypeal mark, but in one it is merely a small median spot. Other males, including the holotype, lack a supraclypeal mark. All males seen possess a broad stripe on the underside of the scape which almost attains the apex of the segment. The black laterobasal marks on the clypeus are consistently large.

The combination of pale ochreous pubescence and bicolored abdomen will separate both sexes of *C. xochipillii* from all other species. Males of *C. eurypatana, C. heithausi,* and *C. xochipillii* all have the basal margin of the clypeus more strongly arched upward in the center than at either side; in *C. fuscata* the margin is evenly, very slightly convex between the subantennal sutures; *C. dentata* is intermediate between these two types.

From *C. eurypatana,* males of *C. xochipillii* may be separated by the lack of procoxal spines, the broader clypeus and the reduced yellow areas on the clypeus. In *C. xochipillii* the pubescence is slightly yellowish, the disc of the second tergum is only moderately shiny, and the punctures of the apical zone of the second tergum are not conspicuously finer than those of the disc; these features will separate *C. xochipillii* from *C. heithausi.* Males of *C. dentata* have the punctures of the clypeal disc distinct, rather than obscured by dense tessellation, the disc of the second tergite is densely punctate, and the ventral tooth of the metafemur slender and curved. All of the species differ from *C. xochipillii* in having the abdomen wholly ferruginous.

The female shares with those of *C. dentata, C. heithausi,* and *C. eurypatana* the broad secondary plate on the basitibial plate, thus differing from that of *C. fuscata.* It is separable from all by the bicolored abdomen, from *C. heithausi* by the ochreous rather than whitish pubescence, from *C. dentata* by the immaculate scape and shiny, sparsely punctate disc of the second tergite, and from *C. eurypatana* by the shiny median clypeal line, immaculate scape, and much paler wings.

Subgenus *Hemisiella* Moure

Hemisiella Moure, 1945b:407–408. Type-species: "*Hemisiella lanipes* (Fabricius, 1775)" = *Apis lanipes* Fabricius, 1775; original designation.

Centris subg. *Hemisiella:* Michener, 1951:7–8.

This is a large group, with most of the species occurring in South America, but with one entering the southwestern United States. The distinctions between this subgenus and *Heterocentris* are not great and possibly the two should be merged. A detailed study of the extensive South American fauna might resolve this question, but is beyond the scope of this paper.

In addition to the characters noted in the keys by Michener (1951) and Snelling (1974), *Hemisiella* females may be separated from those of *Heterocentris* by the lack of compressed, blade-like setae on the fourth and fifth sterna and by the acute apex of the secondary pygidial plate.

KEY TO NORTH AMERICAN *HEMISIELLA*

1a. Male, antenna 13-segmented; abdomen with seven visible terga 2
b. Female, antenna 12-segmented; abdomen with six visible terga 6
2a. Hairs of thoracic dorsum with conspicuous black tips 3
b. Hairs of thoracic dorsum without conspicuous black tips 4
3a. Large species, head width over 5.2 mm; face broad, frontal width greater than clypeocellar distance .... *vittata* Lepeletier
b. Smaller species, head width less than 4.7 mm; face narrower, frontal width less than clypeocellar distance .... *dichrootricha* Moure
4a. Midline of clypeus not cariniform; paraocular area with yellow mark; segments 10 and 11 of flagellum dark beneath, contrasting with underside of segments 2–9 5
b. Midline of clypeus low-cariniform; paraocular area without yellow mark; segments 10 and 11 of flagellum beneath not contrasting with color of segments 2–9 .. .. *transversa* Pérez
5a. At least two terga, often entire abdomen, ferruginous, apical hairs ferruginous; first flagellar segment less than 3.7 times second .... *trigonoides* Lepeletier
b. Abdominal terga blackish, apical segments with white hairs; first flagellar segment at least 4.0 times second .... *nitida* F. Smith
6a. Hairs of thoracic dorsum conspicuously black-tipped 7
b. Hairs of thoracic dorsum not black-tipped 8
7a. Clypeus broadly and deeply depressed across lower part of disc; labrum at least twice wider than long; larger species, head width at least 6.0 mm .... *vittata* Lepeletier
b. Clypeus protuberant; disc flat or slightly convex; labrum no more than 1.5 times wider than long; smaller species, head width less than 5.5 mm .... *dichrootricha* Moure
8a. Abdomen and legs blackish; scopa black 9
b. Abdomen and middle and hind legs largely ferruginous; scopa ferruginous .... *trigonoides* Lepeletier
9a. Fifth tergum usually with long, glistening, white hairs; lower margin of clypeal marks parallel to apical margin of clypeus; smaller species, head width 3.9–4.5 mm .... *transversa* Pérez
b. Fifth tergum with brown to black hairs only; lower margin of clypeal marks oblique to apical margin of clypeus; larger species, head width 4.8–5.3 mm .... *nitida* F. Smith

Centris (Hemisiella) dichrootricha (Moure)

Hemisiella dichrootricha Moure, 1945b:408–409. ♀.
Centris (*Hemisiella*) *dichrootricha:* Michener, 1954:143. ♀ ♂ (distr., tax.).

This species was described from the State of Guapore, Brazil; Michener (1954) recorded it from Panama and noted characteristics of the previously undescribed male. I have seen many specimens from Panama and a few from Costa Rica. The species is easily recognized by the characteristics cited in the key.

Centris (*Hemisiella*) *nitida* F. Smith

Centris nitida F. Smith, 1874:368. ♀.
Centris confinis Pérez, 1905:40. ♀. NEW SYNONYMY.

Pérez (1905) described *C. confinis* from "Mexique?" The type specimen, a female, is in the Museum National d'Histoire Naturelle, Paris, and has been examined by me. Although in poor condition, it is unquestionably a specimen of *C. nitida.* The records from southern Arizona cited by Hurd (1979) as *C. confinis* are based on specimens of *C. transversa.*

This is a common species through Central America, extending into northern South America; the type locality is Honduras, without more precise locality. I have seen Central American material of *C. nitida* from Mexico, Belize, Guatemala, Honduras, El Salvador, and Costa Rica. Although I have seen no records from Panama, *C. nitida* must be present there, as it is present in South America (Colombia, Ecuador).

Centris (*Hemisiella*) *transversa* Pérez

Centris transversa Pérez, 1905:39. ♀ ♂.
Hemisiella transversa: Moure, 1945b:408.
Centris (*Melanocentris*) *ruae* Cockerell, 1949:474–475. ♀. NEW SYNONYMY.
Centris (*Hemiesiella*) *transversa:* Snelling, 1966:26–27 (distr.).
Centris (*Hemisiella*) *confinis:* Hurd, 1979:2175 (misidentification).

This primarily Mexican species is found also in Guatemala and Honduras. Although it has been suggested that this is a synonym of *C. nitida* (see Lutz and Cockerell, 1920:560), the two are distinct from one another. In addition to differences noted in the key, females of *C. transversa* have the median impunctate line of the clypeus distinctly raised, the flagellum is uniformly dark, the dorsal thoracic hairs are brownish and the hairs at the sides of the fourth and fifth sternites are whitish. In *C. nitida,* the impunctate median line is not raised or, if a little elevated, the raised area is broadly rounded rather than narrow and sharply defined; the underside of the flagellum is lighter in color than the upper side; the dorsal thoracic hairs are yellowish; the hairs at the sides of the fourth and fifth sternites are uniformly dark.

Males of *C. transversa* possess a somewhat coniform ventral process on the metatrochanter, a prominent ventral process near the base of the metafemur, and the pubescence of the fifth and sixth sternites is mostly pale. The ventral process of the metatrochanter of *C. nitida* is a depressed, narrow apical spine and, in that species, the ventral surface of the metafemur lacks a process and the pubescence of the fourth to sixth sterna is dark.

The type of *C.* (*Melanocentris*) *ruae* is in the USNM (No. 58880) and is from Zamorano, Honduras. I have examined the specimen and it is a normal specimen of *C. transversa,* differing from Mexican specimens only in the reduction in the number of white hairs on the apical terga. In spite of Cockerell's statement to the contrary, the size is normal and the clypeal and labral markings are well within the range for this species. The type agrees with other material from Honduras.

Hurd (1979) reported *C.* (*Hemisiella*) *confinis* from Arizona (Patagonia and Tumacacori) on flowers of *Parkinsonia aculeata.* The specimens on which this report was based are in UCB and I have examined them. They are *C. transversa,* which I had previously (1966) recorded from Arizona. At that time I conjectured that *C. transversa* was possibly adventive in Arizona, a view I no longer hold. Additional material now shows the distribution of *C. transversa* to extend north along the western flanks of the Sierra Madre Occidental through Sonora to southern Arizona.

Centris (*Hemisiella*) *trigonoides* Lepeletier

Centris trigonoides Lepeletier, 1841:167. ♂.
Centris dentipes F. Smith, 1874:366. ♂. NEW SYNONYMY.
Centris hoplopoda Moure, 1943:160. ♂.
Centris rufomaculata Cockerell, 1949:476. ♂. NEW SYNONYMY.
Centris (*Rhodocentris*) *lanipes subtarsata* Cockerell, 1949: 476–477. ♂ ♀. NEW SYNONYMY.
Centris (*Hemisiella*) *hoplopoda:* Michener, 1954:142–143 (distr., tax.).
Centris (*Hemisiella*) *trigonoides subtarsata:* Snelling, 1966: 25–26 (distr., tax.).

Centris trigonoides is a common species, ranging from Mexico to Argentina. Throughout this range it is subject to much variation and some localized phenotypes have been named; presumably there are additional synonyms to be recognized among the many names applied to South American forms of *Hemisiella.* The entire complex of forms in this difficult group will have to be examined.

In an earlier paper (Snelling, 1966), I attempted to justify recognition of *C. lanipes subtarsata* as a Central American subspecies of *C. trigonoides.* Subsequent study of several hundred additional specimens convinced me of the futility of that effort.

The type male of *C. dentipes* (BMNH 17B.919) has been examined and agrees with the current concept of *C. trigonoides.* The type male of *C. rufomaculata* (USNM 58883) is merely an individual with abdomen mostly dark brownish.

Females of *C. trigonoides* consistently have the entire abdomen ferruginous in Central American samples, and cannot be confused with any other species in our area. The abdomen in males varies from wholly ferruginous to dark reddish brown on the basal three or four tergites. The metatrochanter has a prominent, thick, ventral spine, the ventral ridge of the metafemur is high and cariniform, and the ventral pubescence of the abdomen is yellowish to reddish.

Centris (*Hemisiella*) *vittata* Lepeletier

Centris vittata Lepeletier, 1841:168. ♂ ♀.
Centris montezuma Cresson, 1879:213. ♀ ♂.
Centris breviceps Friese, 1899:44. ♂ ♀.
Centris Friesei Crawford, 1906:158. ♀. Preoccupied.
Centris Costaricensis Crawford, 1907:21. New name for *C. friesei* Crawford, 1906, not *C. friesei* Ducke, 1902.
Centris costaricensis var. *erubescens* Friese, 1925:30. ♀. NEW SYNONYMY.

Both sexes of *C. vittata* are easily recognized by the large size (length over 20 mm), black-tipped thoracic hairs, and the transversely depressed clypeal disc. The posteroventral margin of the male metafemur is sharply angled, but is not a cariniform ridge and the ventral spine of the metatrochanter is reduced to an inconspicuous, obtuse tubercle.

This is a widespread species through South America, and in Central America. I have seen specimens from Mexico, Costa Rica, Panama, and Honduras. Friese's *C. costaricensis* var. *erubescens,* described from Costa Rica, is a minor variant, not worthy of recognition.

Subgenus *Heterocentris* Cockerell

Gundlachia Cresson, 1865:195. Type-species: *Centris* ? *cornuta* Cresson, 1865; type by monotypy. Preoccupied.
Heterocentris Cockerell, 1899:14. Type-species: *Centris* ? *cornuta* Cresson, 1865; autobasic. New name for *Gundlachia* Cresson, 1865, not *Gundlachia* Pfeiffer, 1850 (Mollusca), not *Gundlachia* Herrich-Schaeffer, 1866 (Insecta, Lepidoptera).
Centris subg. *Rhodocentris* Friese, 1900b: 244. Type-species: *C. difformis* F. Smith, 1854; designated by Sandhouse, 1943.

Since Cresson's generic name *Gundlachia* was preoccupied, Cockerell (1899) proposed *Heterocentris* as a replacement name; the type-species for *Heterocentris* automatically is *C.* ? *cornuta* which Cockerell (1906) later considered to be the same as *C. difformis.* There is no evidence that he actually saw the type of *C. cornuta,* now in the Gundlach collection of the Academia de Ciéncias in Havana, Cuba. Indeed, there is reason to suppose that he did not, for the original descriptions of *C. cornuta* and *C. difformis* do not agree in several important peculiarities of head structure. Thus, Cresson described the mandible of *C. cornuta* as "very long, narrow and cleft at tip, shining black . . ." as opposed to Smith's ". . . mandibles large, very broad at their base, and *armed above with a stout tooth,* their apex bidentate, having a longitudinal pale testaceus stripe" (italics mine). Of the clypeus, Cresson stated: "clypeus short, very transverse, emarginate on each side, with *a large, very prominent, incurved, subacute tooth on the middle,* pale yellowish white, the anterior and posterior margin and the tooth except its lateral base, black" (italics mine); the labrum is said to possess a "long slender, porrect, subacute spine." According to Smith, the clypeus of *C. difformis* is "short, transverse, elevated, its anterior portion vertical." There is no mention of processes of any sort on either clypeus or labrum. I think it as unlikely that Cresson would have overlooked the very prominent mandibular process as that Smith would have failed to mention such a conspicuous anomaly (in this genus) as a spinose clypeus. It is my opinion that *C. cornuta* and *C. difformis* are very different entities and that *C. cornuta* must be properly considered to be the type-species of *Heterocentris.*

This possibly has unfortunate ramifications since the identity of *C. cornuta* is problematic. However, since the only forms of *Centris* with unusual modifications of mandible, labrum, and clypeus all belong to the accepted interpretation of *Heterocentris,* the question is probably moot.

Just as the type-species of *Heterocentris* should be clearly restricted to *C. cornuta,* so, too, should the type-species of *Rhodocentris* be restricted to *C. difformis. Rhodocentris* was described as a new subgenus of *Centris,* not as a replacement name for *Gundlachia.* It is clear that Sandhouse considered *C. difformis* to be the proper name for the species which she selected as type. It is unclear why she chose to cite the type-species as "(*Centris cornuta* Cresson, 1865) = *Centris difformis* F. Smith, 1854," unless it was to assure that *Rhodocentris* was an automatic junior synonym of *Heterocentris* through isogenotypy. Both specific names were available, since both were originally included in *Rhodocentris* by Friese. Since it is clear that Sandhouse was of the opinion that *C. difformis* was the correct name for the taxon chosen as type-species I think it best to consider that name to be the type; this would eliminate the ambiguity of having two names involved as possible type-species.

Heterocentris, together with *Hemisiella* and *Trachina,* is part of a complex recognized by possessing three-segmented maxillary palps in both sexes and the male with a carina along the posterior margin of the metabasitarsus; this carina usually terminates in a prominent tooth-like process. Males of *Heterocentris* differ from those of both *Trachina* and *Hemisiella* in the form of the dorsal face of the first abdominal tergite: at the extreme side, the dorsal face is extended caudad (most strongly so in *C. labrosa*) and there is a conspicuous patch of erect, plumose, dark setae at the side of the segment, their apices abruptly bent and flattened. This is a feature unique in the genus. Additionally, the middle mandibular tooth is smaller and nearer to the inner tooth than to the apical tooth.

In females of *Heterocentris* the upper inner mandibular carina is elevated near the base and the labrum is large, with the disc depressed and the apical margin more or less flange-like and with a pair of dentiform submedian processes. In both sexes the apicolateral angle of the clypeus is contiguous with the eyes, or nearly so. Females are additionally characterized by the distinct, abruptly truncate secondary pygidial plate and by the presence of large, flattened, spiniform setae near the apical margins of the fourth and fifth abdominal sterna.

The few Central American *Heterocentris* may be separated by the following key. Since no males of *C. difformis* are known to me, I am unable to include this sex in the key.

KEY TO CENTRAL AMERICAN *HETEROCENTRIS*

1a. Male, antenna 13-segmented and basitibial plate absent 2

b. Female, antenna 12-segmented and basitibial plate present 5

2a. Postgradular area of second tergum about four times as long as pregradular area 3

b. Postgradular area of second tergum shorter than pregradular area . . . . *labrosa* Friese

3a. Mandible tridentate 4

b. Mandible bidentate . . . . *bicornuta* Mocsáry

4a. Clypeal disc smooth and shiny between punctures; apical margin of labrum transverse or very weakly concave; lower corner of pronotum with a few long, simple, reddish or yellowish setae among plumose hairs . . . . *analis* (Fabricius)

b. Clypeal disc roughened and slightly shiny between punctures; apical margin of labrum with distinct median emargination; lower corner of pronotum with plumose hairs only . . . . *C.* (*Heterocentris*) species

5a. Clypeus without lateral cornuti; labrum broader than long; mandible tridentate 5

b. Clypeus with pair of long, slender cornuti; labrum longer than broad; mandible bidentate . . . *bicornuta* Mocsáry

6a. Clypeus no more than 1.8 times wider than long in middle, with disc flattened; mandible without long subbasal process on outer face 7

b. Clypeus very short, more than twice wider than long, transversely elevated; mandible with large, tooth-like subbasal process on outer face . . . . *difformis* F. Smith

7a. Lower, lateral angle of pronotum with a cluster of long, yellowish or reddish, simple setae as well as plumose hairs; juncture of anterior and lateral faces of mesepisternum without carina, rounded; hairs of thoracic dorsum rarely dark-tipped . . . . *analis* (Fabricius)

b. Lower, lateral angle of pronotum with long, plumose hairs only; juncture of anterior and lateral faces of mesepisternum with a short, lamelliform carina; hairs of thoracic dorsum always dark-tipped . . . *labrosa* Friese

Centris (*Heterocentris*) *analis* (Fabricius)

Anthophora analis Fabricius, 1804:375. ♀.
Centris totonaca Cresson, 1879:213. ♀.
Centris otomita Cresson, 1879:214. ♂.
Centris minuta Mocsáry, 1899:254. ♂.
Centris labrosa var. *simplex* Friese, 1899:44. ♀.
Centris (*Melanocentris*) *durantae* Cockerell, 1949:474. ♂.
Centris (*Melanocentris*) *petreae* Cockerell, 1949:475. ♂.
Centris (*Melanocentris*) *petreae* var. *rufopicta* Cockerell, 1949: 475. ♂.
Centris (*Heterocentris*) *totonaca:* Michener, 1954:140 (syn.).
Centris (*Heterocentris*) *analis:* Moure, 1960b:132–133 (syn., notes on type).

Moure (1960b) gives very complete literature citations of this common species which ranges from Mexico to Brazil. The presence of long, simple, ferruginous setae on the lower corner of the pronotum is diagnostic for the female. The male has similar setae, but they are less numerous than in the female and are sometimes difficult to see among the more numerous plumose hairs.

Centris (*Heterocentris*) *bicornuta* Mocsáry

Centris bicornuta Mocsáry, 1899:254. ♀.
Heterocentris bicornuta: Moure, 1945b:502.
Centris (*Heterocentris*) *bicornuta:* Michener, 1951:6, 7.

Although widely distributed, *C. bicornuta* does not appear to be a common species, though males are sometimes locally abundant. The bicornute clypeus of the female is diagnostic for that sex. Males may be easily separated from those of *C. analis* and *C. labrosa* by the bidentate mandible. Since I have seen no males of *C. difformis,* which presumably has bidentate mandibles, I am uncertain how to distinguish that species from *C. bicornuta.* Presumably, however, the males of *C. difformis* will be more than 15 mm long and the hairs of the thoracic dorsum will be black-tipped. Males of *C. bicornuta* are not more than about 10 mm long and the hairs of the thoracic dorsum are not black-tipped.

Specimens of *C. bicornuta* have been seen from Mexico, Guatemala, Costa Rica, and Panama, as well as from South America (Brazil and Guyana). The species was described from Brazil.

Centris (*Heterocentris*) *difformis* F. Smith

Centris difformis F. Smith, 1854:374. ♀.
Centris difformis: Crawford, 1906:158. ♀.
Heterocentris difformis: Moure, 1945b: 402, 403.
Centris (*Heterocentris*) *difformis:* Michener, 1951: 6, 7.

As discussed above, I do not believe that *C. cornuta,* described from Cuba, is a synonym of *C. difformis.* The latter species was originally described from Brazil and seems to be rare in collections. According to Cresson (1879) *C. difformis* occurs in Mexico, but I have seen no specimens from there. Crawford (1906) recorded a female from Pozo Azul, Costa Rica, as *C. difformis.* I have examined the specimen and agree with Crawford's identification.

No males have been seen. Presumably the mandibles are bidentate, as in *C. bicornuta* (Moure, 1945b, noted that *C. minuta* and *C. labrosa* differed from his characterization of *Heterocentris* mandibles as bidentate with the statement that the mandible is falsely tridentate in these two species). Based on the females, males of *C. difformis* should be conspicuously larger than those of *C. bicornuta* and the hairs of the thoracic dorsum should have blackish apices.

NEW RECORDS

PANAMA, *CANAL ZONE:* 3♀♀, Barro Colorado Island, 27 Apr. 1980 (K.E. Steiner; UCD), on *Byrsonima crassifolia.*

Centris (*Heterocentris*) *labrosa* Friese

Centris labrosa Friese, 1899:44. ♀ (not ♂).
Centris tarsata: Schwarz, 1934:13. Misidentification.
Heterocentris labrosa: Moure, 1945b:402.
Centris (*Rhodocentris*) *triangulifera* Cockerell, 1949: 477. ♀. NEW SYNONYMY.
Centris (*Heterocentris*) *labrosa:* Michener, 1954:104 (var., distr.).

This is a moderately common species which ranges from Mexico to Brazil. I have seen specimens from throughout Central America. It should be noted that the specimen recorded by Schwarz (1934) from Barro Colorado Island, Panama, as *C. tarsata* F. Smith, is actually *C. labrosa.* The type of *C. triangulifera,* in the USNM (No. 58885), has been examined and is a normal specimen of *C. labrosa.*

The unusually long pregradular area of the males is immediately diagnostic for this sex of *C. labrosa.* Females are likewise immediately recognizable by the presence of a distinct carina separating the anterior and lateral faces on the lower half of the mesepisternum; in all other species, the juncture of the two surfaces is rounded.

Centris (*Heterocentris*) species

A few males from Panama (Canal Zone and Panamá Province) cannot be assigned to any of the above species. It seems unlikely that they are males of *C. difformis* for they are much smaller (less than 15 mm long) than the one female of *C. difformis* (about 20 mm long) I have seen; the two sexes tend to be approximately equal in size in this genus.

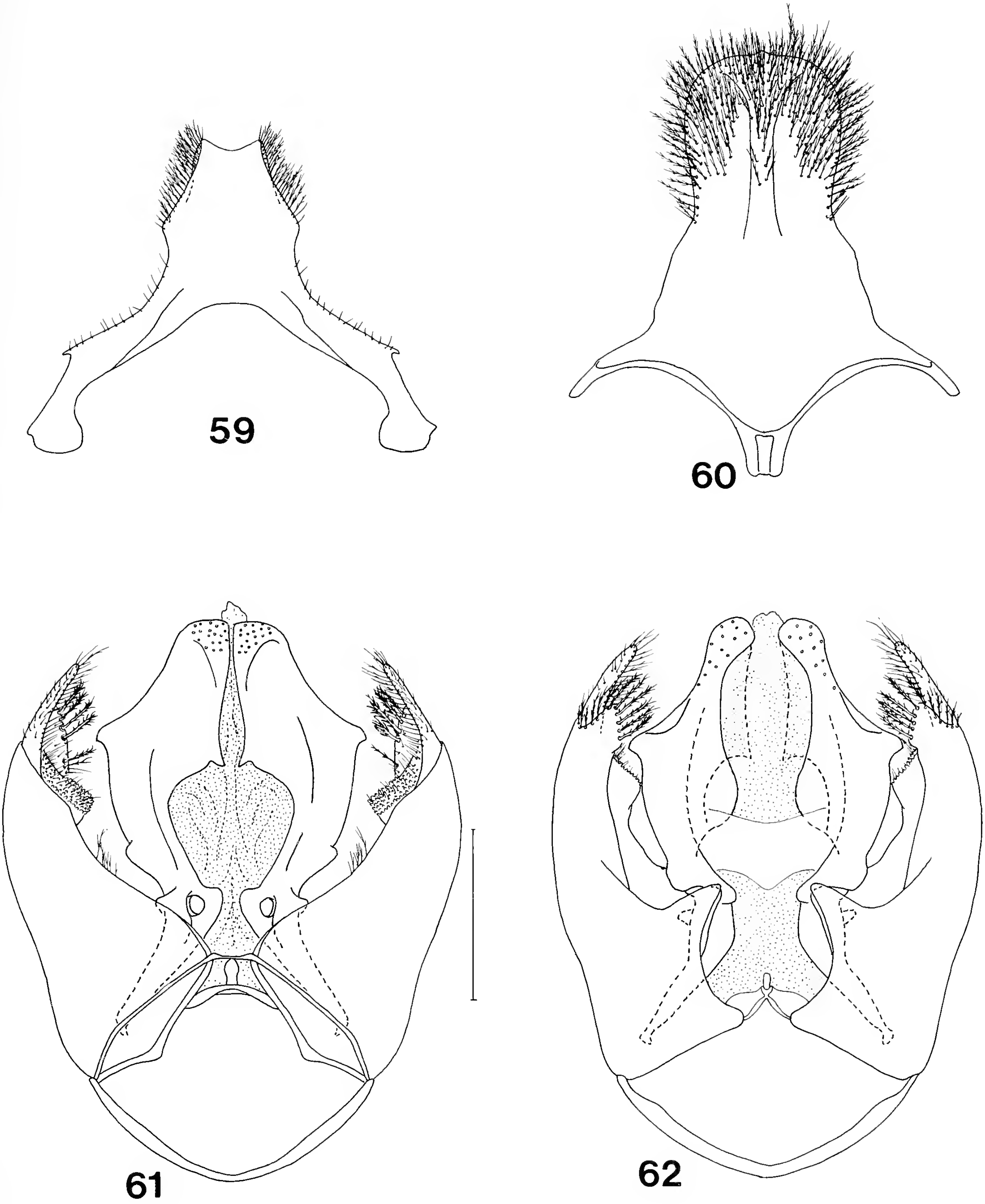
They are very similar to males of *C. analis,* but lack the simple setae on the lower lateral angle of the pronotum, the clypeus is distinctly dull and roughened between the punctures, and the mandible and scape are immaculate or with traces of yellowish markings. Possibly these represent an undescribed species, but the available material is too limited for any decision as to their identity.

Genus *Ptilotopus* Klug

Ptilotopus Klug, 1810:31. Type-species: *Ptilotopus americanus* Klug, 1810; monobasic.
Centris subg. *Ptilotopus:* Michener, 1951:10. Snelling, 1974: 2, 3.

In recent years *Ptilotopus* has usually been treated as a subgenus of *Centris* characterized by the bilobate scutellum with defined bare areas, the prominent hypoepimeral tubercle, the lack of a secondary basitibial plate in the female and the male genitalia without giant branched setae (Michener, 1951; Snelling, 1974). The largest and most spectacular centridines are included in *Ptilotopus.*

Although in general habitus the species of *Ptilotopus* are similar to those of *Centris* and have *Centris*-like wing venation, I am now of the opinion that *Ptilotopus* should be removed from *Centris.* There are a number of features which are not shared with any of the groups presently assigned to *Centris.* Both sexes of *Ptilotopus* possess long, black flagelliform setae on the occipital margin; these setae project well beyond the occipital hair fringe, although they are not as spectacularly developed as in many *Epicharis.*



Figures 59–62. *Ptilotopus zonatus*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

The metatibia of *Ptilotopus* females has a well-defined basitibial plate. There is, however, no secondary plate; instead, the disc of the basitibial plate is moderately depressed, the depression filled with a dense mat of short, fine, subappressed hairs. In *Centris* and *Epicharis* females, a secondary plate is present and usually well defined. When it is not distinct the plate has a discal convexity and is glabrous.

Females of *Ptilotopus* have a distinct tubercle on either side of the midline of the mesosternum, anterior to the mesocoxa. As a rule the tubercles are hidden in an exceptionally dense tuft of short, stiff hairs. Although mesosternal tubercles are known for some *Epicharis* males, they are not known to be present in the females of either *Centris* or *Epicharis.*

A particularly unusual feature is to be seen in the structure of the basal areas of the second and third abdominal tergites of the females. In both *Centris* and *Epicharis* the gradulus of each segment marks off a very narrow basal area across most of the breadth of the segment; laterad, it is either evanescent or deflected distad. In *Ptilotopus* females the gradulus of the second and third tergites is strong and, in the middle, is directed distad as a more or less triangular incursion onto the disc of the segment. The area on either side of this triangular extension is depressed and filled with a compact mat of very short, erect, plumose hairs. This unusual feature is not known to occur in *Centris* and in *Epicharis* is known only in the subgenus *Epicharitides.*

Thus, although *Ptilotopus* is *Centris*-like in many features, particularly in general body form and wing venation, there are features, such as the presence of the flagelliform occipital setae, presence of mesosternal tubercles in the female and the modified structure of the female second and third abdominal terga, which will readily separate *Ptilotopus* from *Centris.* The short marginal cell of the forewing will readily separate *Ptilotopus* from *Epicharis,* as will the mesosternal tubercles and lack of a secondary basitibial plate in the female. Additionally, in *Ptilotopus,* the hypoepimeron has a prominent tubercle and the scutellum has a conspicuous, flattened, bare lobe on either side of the middle. The genitalic structures of *Ptilotopus* are very distinctly *Centris*-like, without the unusual modifications seen in *Epicharis.*

Ptilotopus zonata (Mocsáry)

Figures 59–62

Centris zonata Mocsáry, 1899:251. ♀.
Centris pandora Friese, 1900b:241, 269 (new name for *C. zonata* Mocsáry, not *C. zonata* F. Smith, 1854, now placed in *Epicharis*).

This species, the only known North American *Ptilotopus,* was described from Chiriquí Province, Panama; no additional material has been recorded since the original description.

The females have the pubescence of the head, thorax, and legs bright ferruginous. Except for a broad band of short, erect yellow pubescence across the second tergite, the abdomen is black pubescent. The male pubescence is all black, except for a yellow band across the second tergite.

NEW RECORDS

PANAMA, *PANAMÁ:* 14♀♀, Arraijan, 16 Oct. 1980 (D. Roubik; LACM, ROUB). *VERAGUAS:* 1♂, El Maria, Coibu Island, 22 Oct. 1979 (D. Roubik; LACM). *CANAL ZONE:* 1♀, Gatun, 3 Nov. 1977 (K.E. Steiner; UCD), on *Stigmaphyllon hypargyreum.*

Genus *Epicharis* Klug

Epicharis is an exclusively Neotropical genus of medium- to large-sized bees, often quite colorful, allied to *Centris.* Friese (1900b) monographed these bees, as a subgenus of *Centris,* but most subsequent authors have treated *Epicharis* as a separate genus. Since Friese's monograph most work in this genus has consisted of descriptions of new species and variant forms. Moure (1945a), however, divided *Epicharis* into nine genera, for which he proposed the subtribe Epicharitina within within the Centridini. Michener (1954) recognized Moure's genera as subgenera within the single genus *Epicharis* and subsequent authors have been in accord with this interpretation.

Epicharis was described by Klug (1807), but a type-species was not designated until Latreille (1810) fixed *Apis rustica* Olivier, 1789, as the type-species; *A. rustica* was not one of the originally included species and, hence, is not available. Lutz and Cockerell (1920) selected *Centris umbraculata* Fabricius, 1804, one of the originally included species, as the type-species. Moure (1945a, 1960b) held that the designation made by Latreille is valid since *Apis hirtipes* Fabricius, 1793, one of the originally included names, is a synonym of *A. rustica.*

Sandhouse (1943) accepted the designation of Lutz and Cockerell, as did Michener (1954) when he named *Epicharana* to replace *Epicharis* (s.s.) of Moure (1945a) and placed *Xanthepicharis* Moure in synonymy with true *Epicharis* (s.s.). It is my understanding of the ICZN Code that even though *A. hirtipes* ultimately proved to be a synonym of *A. rustica,* this does not validate the designation made by Latreille, since Latreille was not aware that the two names applied to the same species. There is, additionally, the fact that *A. hirtipes* can never be anything other than a *subjective* synonym of *A. rustica*; the synonym is a generally accepted opinion which has the potential for being incorrect. Stability would be best served by accepting the security of the designation of Lutz and Cockerell.

Of the nine subgenera recognized by Moure (1945a), five are known to be present in North America: *Hoplepicharis* Moure, 1945a; *Epicharana* Michener, 1945 (="*Epicharis*" of Moure, 1945a); *Epicharoides* Radoszkowski, 1884; *Parepicharis* Moure, 1945a; and *Epicharitides* Moure, 1945a. The remaining four subgenera, including *Epicharis* proper (=*Xanthepicharis* Moure, 1945a), are limited to South America: *Anepicharis, Triepicharis,* and *Cyphepicharis,* all Moure, 1945a.

The taxonomy of *Epicharis* is difficult. These bees are generally black or blackish and both sexes usually have conspicuous patterns of white or yellow and/or ferruginous markings on various parts of the body. The species within a subgenus tend to be morphologically very similar and differences often are subtle. Previous descriptive work has tended to emphasize differences in maculations. This, coupled with a scarcity of specimens, has resulted in a confused situation. I expect a reduction in the number of species of *Epicharis* as more material becomes available and the species better known. I have proposed some new synonymy below and pointed out cases where I suspect further synonymy will be in order. Two new species are described, based on morphological characteristics.

The following key to the subgenera of *Epicharis* is modified from that of Moure (1945a).

KEY TO SUBGENERA OF *EPICHARIS*

1a. Female with secondary basitibial plate; male with pygidial plate obsolete, its margins more or less coextensive with margins of seventh tergite, apex thin and bilobate or bidentate 2

b. Female without secondary basitibial plate; male with distinct, sharply marginate pygidial plate, no more than one-half as wide as seventh tergite, its apex narrowly truncate or rounded 4

2a. Lateral margins of female pygidial plate distinctly concave in dorsal view, apex broadly truncate (Fig. 63); female metatibia no longer than metabasitarsus; male without scopa-like hairs on hind legs and metabasitarsus with longitudinal keel on anterior margin which terminates in spiniform process at apex, or without keel . . 3

b. Lateral margins of female pygidial plate nearly straight, apex narrowly truncate (Fig. 64); female metatibia longer than metabasitarsus; hind legs of male with long, scopa-like hairs and metabasitarsus with prominent tooth at basal one-third .... *Hoplepicharis*

3a. *Female:* frontal carina ending more than diameter of anterior ocellus in front of that ocellus; pygidial truncation narrower than diameter of anterior ocellus; disc of fifth tergite with very short hairs mostly simple or barbulate. *Male:* mesosternal tubercles absent; metabasitarsus without carinate ridge on anterior margin; metatrochanter and metafemur without ventral patch of short, dark plumose setae .... *Epicharis,* s.s.

b. *Female:* distance between frontal carina and anterior ocellus less than diameter of anterior ocellus; pygidial truncation broader than diameter of anterior ocellus; disc of fifth tergite with very short hairs distinctly plumose. *Male:* mesosternal tubercles present; metabasitarsus with carinate ridge on anterior margin, terminating in tooth-like process (Fig. 65); metatrochanter and metafemur with ventral patch of short, dark, plumose setae .... *Epicharana*

4a. First flagellar segment short, in female usually no longer than combined second and third but always shorter than following three combined, and in male shorter than scape; posterior margin of dorsal face of scutellum not, or weakly, impressed in middle (if deeply impressed, maxillary palp three-segmented) 5

b. First flagellar segment of female equal to length of next three segments combined, of male longer than scape and longer than following two segments combined; posterior margin of dorsal face of scutellum deeply impressed in middle; maxillary palp two-segmented . . . *Parepicharis*

5a. Lateral ridges of clypeal disc absent or weakly evident only on basal one-half or less; male metabasitarsus with carinate ridge on anterior margin, terminating in large tooth at about midlength 6

b. Lateral ridges of clypeal disc strong and sharply defined to near apical margin; male metabasitarsus without carinate ridge or tooth on anterior margin 7

6a. Maxillary palp two-segmented; flagelliform occipital setae distinct and extending beyond anterior margin of mesoscutum; ocellocular distance of male less than diameter of *lateral* ocellus in dorsal view . . *Anepicharis*

b. Maxillary palp three-segmented; flagelliform occipital setae short, not projecting beyond occipital hairs and not reaching anterior margin of mesoscutum; ocellocular distance of male equal to diameter of *lateral* ocellus in dorsal view .... *Triepicharis*

7a. Dorsal face of scutellum flat; prepygidial fimbria of female preceded by a shiny, nearly glabrous area 8

b. Dorsal face of scutellum bigibbous; female without shiny, glabrous area anterior to prepygidial fimbria .... *Cyphepicharis*

8a. Jugal lobe of posterior wing about half as long as vannal lobe and nearly attaining apex of cubital cell; female metabasitarsus about twice longer than broad, posterior margin nearly straight; male pygidial plate broad, covering most of seventh tergum .... *Epicharoides*

b. Jugal lobe of posterior wing about one-third as long as vannal lobe, its apex well short of that of cubital cell; female metabasitarsus about one-third longer than broad, posterior margin strongly curved; male pygidial plate narrow, covering less than one-half of seventh tergum .... *Epicharitides*

Subgenus *Epicharana* Michener

Epicharis: Moure, 1945a:294–295. Type-species: "*Epicharis rustica* Olivier, 1789" = *Apis rustica* Olivier, 1789. Not *Epicharis* Klug, 1807.

Epicharis subg. *Epicharana* Michener, 1954:144. Type-species: *Apis rustica* Olivier, 1789; original designation.

DESCRIPTION

Maxillary palp three-segmented, third segment a little shorter, and much narrower, than second; lateral ridge of clypeal disc strong; malar area about as long as minimum thickness of first flagellar segment; occipital margin rounded; occipital flagelliform setae long, extending beyond anterior margin of tegula; metanotum bifaced, dorsal face about as long as posterior face, juncture angular or crested; jugal lobe of posterior wing shorter than cubital cell and less than half as long as vannal lobe.

Female. Labrum with low, median longitudinal ridge; outer face of mesobasitarsus, on anterior one-third with mixed long, coarse, simple setae and shorter, fine, plumose hairs, posterior two-thirds with sparse longer, coarse, simple setae and sparse, short, fine, plumose hairs; basitibial plate with secondary plate; metatibia no longer than metabasitarsus; third and fourth terga without basal specialized areas; in dorsal view, margins of pygidial plate concave, apex broadly truncate.

Male. Labrum without median ridge; first flagellar segment shorter than scape, longer than second segment, much shorter then second and third combined; ocellocular distance greater than ocellar diameter; procoxa with flattened distal process; mesosternum with prominent process on each side of midline, anterior to mesocoxa; metatrochanter and base of metafemur with ventral mat of short blackish setae; metatibia with carinate posteroventral ridge; metabasitarsus carinate along anterior margin, ending in prominent tooth-like process at apex of segment; pygidial plate broad, its margins confluent with those of segment, apex bidentate.

This is the group that Moure (1945a) incorrectly interpreted as *Epicharis* s.s., as discussed above. Five species occur in Central America, with a few more in South America.

KEY TO CENTRAL AMERICAN *EPICHARANA*

1a. Abdominal terga blackish and immaculate (except male of one species with dorsal fascia on first and lateral spot on second) or ferruginous and immaculate; male clypeus black 2

b. Abdominal terga reddish brown to ferruginous *and* dorsal face of first segment with narrowly interrupted transverse yellow fascia (sometimes obscure); male clypeus yellow . . . . *elegans* F. Smith

2a. Dorsal segments of abdomen black, first tergite with or without transverse yellow fascia on dorsum; male metatibia moderately convex in middle of anterior margin (Fig. 66); disc of female clypeus, in basal one-third or more, with more or less distinct, weakly depressed, median impunctate line 3

b. Dorsal segments of abdomen bright ferruginous and immaculate; male metatibia strongly, obtusely convex in middle of anterior margin (Fig. 65); disc of female clypeus uniformly, subcontiguously punctate in basal one-third . . . . *bova,* new species

3a. *Female:* scutellum shinier than mesoscutum, punctures of disc both less distinct and more separated than those of mesoscutum; larger punctures of parapsis sparse, separated by more than twice a puncture diameter. *Male:* first tergum without dorsal transverse yellow fascia, mesosternal tubercles nearly prostrate, their inner margins rounded (Fig. 67) . . . . *rustica* (Olivier)

b. *Female:* scutellum no shinier than mesoscutum, micropunctures of disc as sharp and dense as those of mesoscutum; larger punctures of parapsis dense, separated by about a puncture diameter or less. *Male:* first tergite with narrowly interrupted yellow fascia on dorsal face; mesosternal tubercles erect, obtuse, inner margin sharply carinate (Fig. 68) . . . . *angulosa,* new species

Epicharis (*Epicharana*) *angulosa,* new species

Figures 66, 68, 69–72

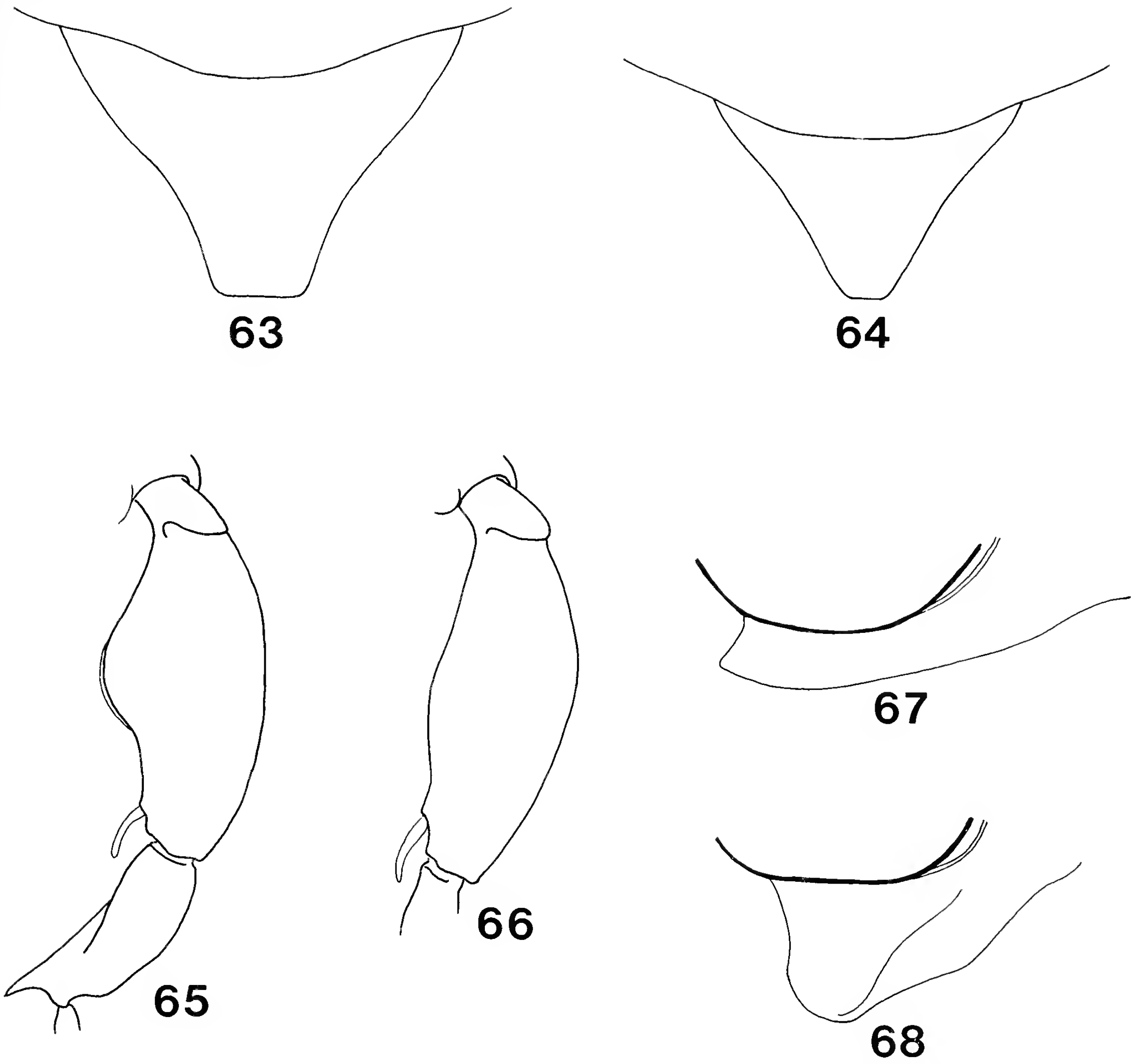
DIAGNOSIS

Separable from other species of *Epicharana* by the following unique combination of features: pubescence, except of hind legs, black; abdomen black, except dorsally on first tergum and laterally on second tergum of male. *Male:* mesosternal tubercles angulate along inner margin, high, long and obtuse in profile; metatibia moderately swollen (Fig. 66), posterior ventral carina low, abruptly reduced beyond midlength. *Female:* shiny area at base of clypeal disc no greater in area than triangular supraclypeal area and basal one-half of disc densely and coarsely punctate, without definite impunctate median line.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 5.95 (5.64–5.90); head length 4.00 (3.90–4.00); wing length 17.0 (15.0–16.5); total length 21.0 (20.0–22.0).

Head. 1.48 (1.45–1.49) times broader than long; in frontal view, occipital margin nearly straight (except ocellar elevation) and slightly below level of tops of eyes; inner eye margins moderately convergent above, upper frontal width 0.77 (0.76–0.79) times lower frontal width. Mandible slender beyond middle, inner tooth large, blunt. Labrum quadrate, slightly broader than long, apical margin transverse, disc shiny and weakly tessellate between sparse to close punctures varying from fine to coarse. Clypeus about 1.7 times broader than long, apicolateral angle removed from eye by slightly less than diameter of antennal socket; disc moderately shiny between dense, coarse punctures except near apical margin where punctures are sparse and fine and integument is more or less "wrinkled," median impunctate line absent; discal carinae moderately convergent above, distance between them at lower end about 1.7 times that at upper end; side slightly shiny and distinctly roughened between variably sparse to subcontiguous, fine to coarse punctures. Frons moderately shiny and distinctly tessellate between dense, mixed fine and moderate punctures; preocellar area slightly bulging on either side, smooth, shiny, and impunctate; ocellocular area dull and densely tessellate, subcontiguously micropunctate and with scattered minute punctures; preocciput moderately shiny between dense, fine punctures; gena moderately shiny to shiny between close to dense punctures, minute near eye, becoming fine near margin. Interantennal distance 1.86 (1.88–2.05) times antennal socket diameter; antennocular distance 0.59 (0.63–0.71) times antennal socket diameter; scape robust, 1.50 (1.50–1.64) times longer than broad, scape length 1.57 (1.53–1.61) times length of first flagellar segment; first flagellar segment 1.31 (1.22–1.32) times longer than broad, much shorter than following three segments combined, 1.15 (1.08–1.13) times longer than second. Interocellar distance 1.70 (1.44–1.64) times diameter of anterior ocellus; ocellocular

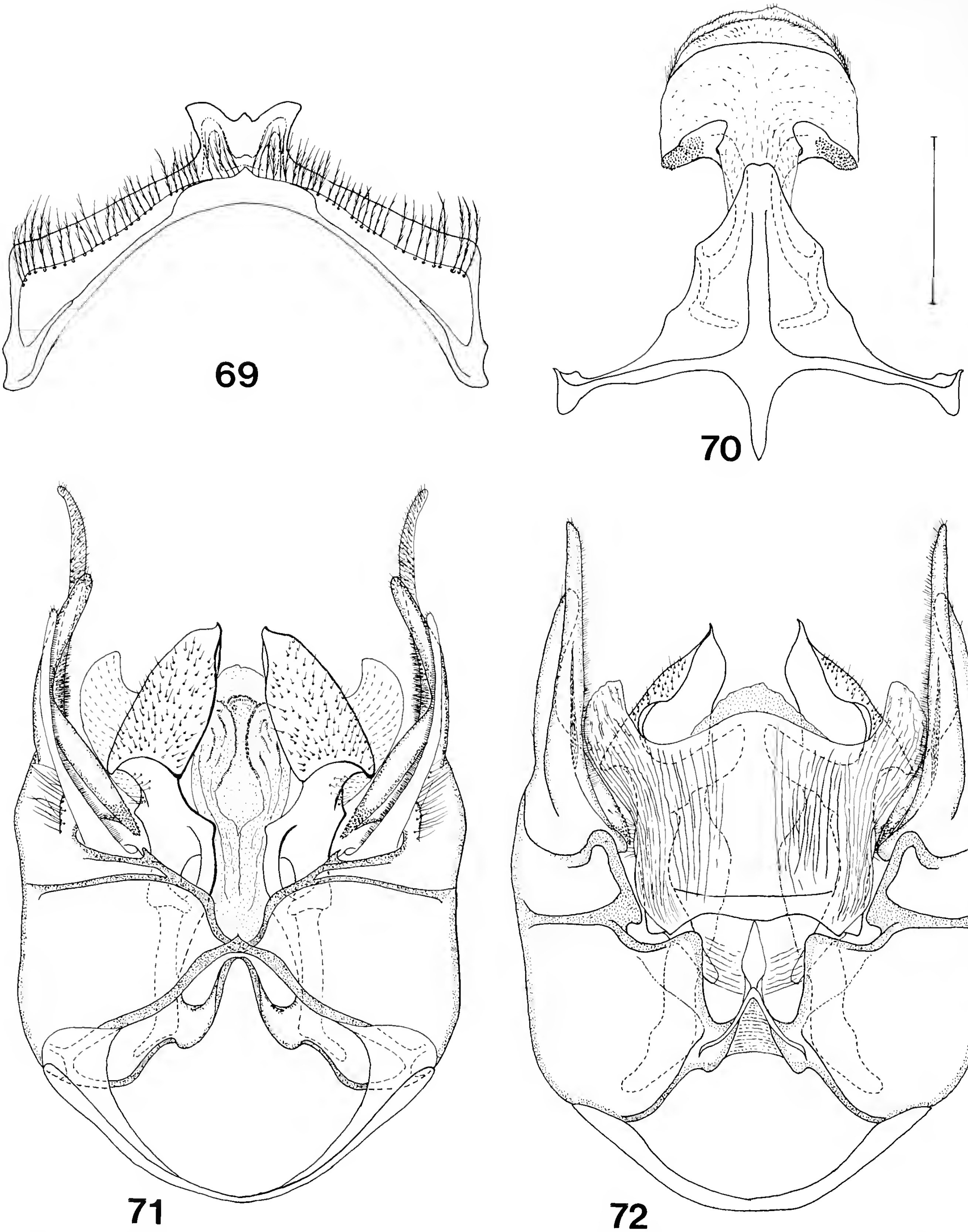


Figures 63–64, pygidial plate of female: **63,** *Epicharis* (*Epicharana*) *rustica*; **64,** *E.* (*Hoplepicharis*) *lunulata.* **Figs. 65–66,** metatibia of male: **65,** *E.* (*Epicharana*) *bova*; **66,** *E.* (*Epicharana*) *angulosa.* **Figs. 67–68,** profile of right mesosternal process of male: **67,** *E.* (*Epicharana*) *rustica*; **68,** *E.* (*Epicharana*) *angulosa.*

distance 1.96 (1.89–1.93) times diameter of anterior ocellus; ocelloccipital distance 1.70 (1.50–1.67) times diameter of anterior ocellus.

Thorax. Mesoscutum slightly shiny, uniformly densely, finely punctate and with sparse moderate punctures which become scattered distad; dorsal face of scutellum broadly depressed in middle, punctation as scutum, but fine punctures scattered; metanotum moderately shiny in median area, dull elsewhere, roughened and tessellate, with minute obscure punctures. Mesepisternum moderately shiny and tessellate between sparse, shallow, fine punctures; metepisternum moderately shiny between subcontiguous, minute punctures (appearing finely reticulopunctate at certain angles). Mesosternal process, in profile, suberect and obtusely triangular (Fig. 68); in ventral view, inner margin carinate. Propodeum moderately shiny, minutely reticulopunctate and with sparse to scattered fine punctures. Procoxal process broadly elliptical, with acute apex; mesofemur stout, twice longer than thick, greatest thickness a little basad of midlength; anterobasal ventral depression of metafemur subcarinate along its posterior margin; anterior edge of metatibia evenly curved (Fig. 66), posterior carina low throughout, abruptly reduced distad of middle.

Abdomen. Tergal discs moderately shiny between minute



Figures 69–72. *Epicharis* (*Epicharana*) *angulosa*, male seventh and eight sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

punctures which are dense on basal segments, becoming progressively coarser and less close on succeeding segments; discs also with scattered fine punctures on basal segments, becoming progressively coarser (but still fine) on succeeding segments. Seventh tergite weakly raised in middle (broader basad) to form a weakly differentiated median plate; apex bidentate, teeth long, slender, acute, emargination longer than a semicircle.

Terminalia. Apical margin of distal lobe of seventh sternite (Fig. 69) broadly, shallowly concave; setae long, some conspicuously plumose. Shoulders of disc of eighth sternite (Fig. 70) angular and sides of apical lobe of disc strongly convergent. Genitalia as in Figs. 71 and 72.

Pilosity. Generally blackish brown; sides of pronotal collar, pronotal lobe, mesoscutum (especially anteriorly and at side) with admixed very pale brown hairs; hairs on side of tergites and on abdominal venter mixed medium and light brown. Hairs mostly long, erect, plumose and dense, but labrum nearly bare. Metatibia and metabasitarsus with long yellowish hairs. Abdominal terga, beyond first, with sparse discal hairs which are short, simple and suberect on second segment, becoming progressively longer and more abundant caudad; terga also with abundant minute, appressed, scale-like hairs (arising from minute punctures) which become progressively longer on succeeding segments.

Color. Blackish brown. The following pale yellow: oblique, linear mark near base of mandible; labrum; oblique, linear mark from clypeal margin, at tentorial pit, to malar area; triangular supraclypeal mark; underside of scape; spot on procoxal process; anterodistal spot on pro- and mesofemora; large distal spot on metafemur; stripe on anterior margin of protibia nearly to apex; broad stripe on anterior margin of mesotibia nearly to apex, constricted in middle; anterior and outer face of metabasitarsus; large, anterior spots on dorsal face of first tergum, narrowly separated in middle; small laterobasal spot on second tergum. Underside of flagellum light brown; apical tarsal segments reddish. Wings uniformly dark brown, veins and stigma blackish.

FEMALE. Measurements (mm). Head width 6.31; head length 4.15; wing length 16.5; total length 23.0.

Head. 1.52 times broader than long; in frontal view, occipital margin straight, except ocellar elevation; inner eye margins moderately convergent above, upper frontal width 0.84 times lower frontal width. Mandible stout, tridentate, inner teeth obtuse and margin between them broadly concave. Labrum about 1.1 times longer than broad, apex subangularly rounded in middle; disc moderately shiny, roughened and tessellate between dense to subcontiguous, mixed fine and coarse punctures, median line slightly raised. Clypeus about 1.6 times broader than long, apicolateral angle separated from eye by 0.5 times diameter of antennal socket; discal carinae moderately convergent basad, intercarinal distance at base about 0.66 times that at their distal end; sculpture as described for male, but with shiny basal area which is no greater than supraclypeal area. Punctation of frons, preoccipital area, and gena as in male. Interantennal distance 2.20 times antennal socket diameter; antennocular distance 0.88 times antennal socket diameter; scape robust, 1.91 times longer than wide, scape length 1.05 times length of first flagellar segment; first flagellar segment shorter than following three combined, 3.81 times longer than second. Interocellar distance 1.44 times diameter of anterior ocellus; ocellocular distance 1.78 times diameter of anterior ocellus; ocelloccipital distance 1.56 times diameter of anterior ocellus.

Thorax. Punctation as in male. Metanotum with horizontal basal face separated from vertical posterior face by a cariniform ridge on either side of middle. Apex of basitibial plate acute; secondary plate about twice longer than wide.

Abdomen. Punctation as described for male. Disc of pygidial plate not visible.

Pilosity. About as described for male, but pronotal collar and lobe without pale hairs; bristles of thoracic venter with pale tips; scale-like hairs of fifth tergum becoming longer, more erect and plumose toward prepygidial fringe; hairs of prepygidial fringe reddish brown and pale tips; scopal hairs pale yellowish.

Color. Generally blackish brown; mandible (except golden apical blotch), underside of flagellum, apical segments, reddish brown; paraocular area with small, obscure yellowish blotch near clypeal margin, below level of tentorial pit (larger and more distinct on left side). Wings as in male.

TYPE MATERIAL

Holotype male, allotype, and one male paratype: Monteverde, 1500 m elev., Puntarenas Prov., COSTA RICA, 12 Sept. 1978 (G.W. Frankie), in LACM. Paratypes: 1♂, same locality, 19 Aug. 1974 (D. Janzen; UKAN); 2♂♂, 4 km E San Ignacio de Acosta, 4000 ft. elev., San José Prov., COSTA RICA, 8 July 1963 (C.D. Michener et al.; UKAN).

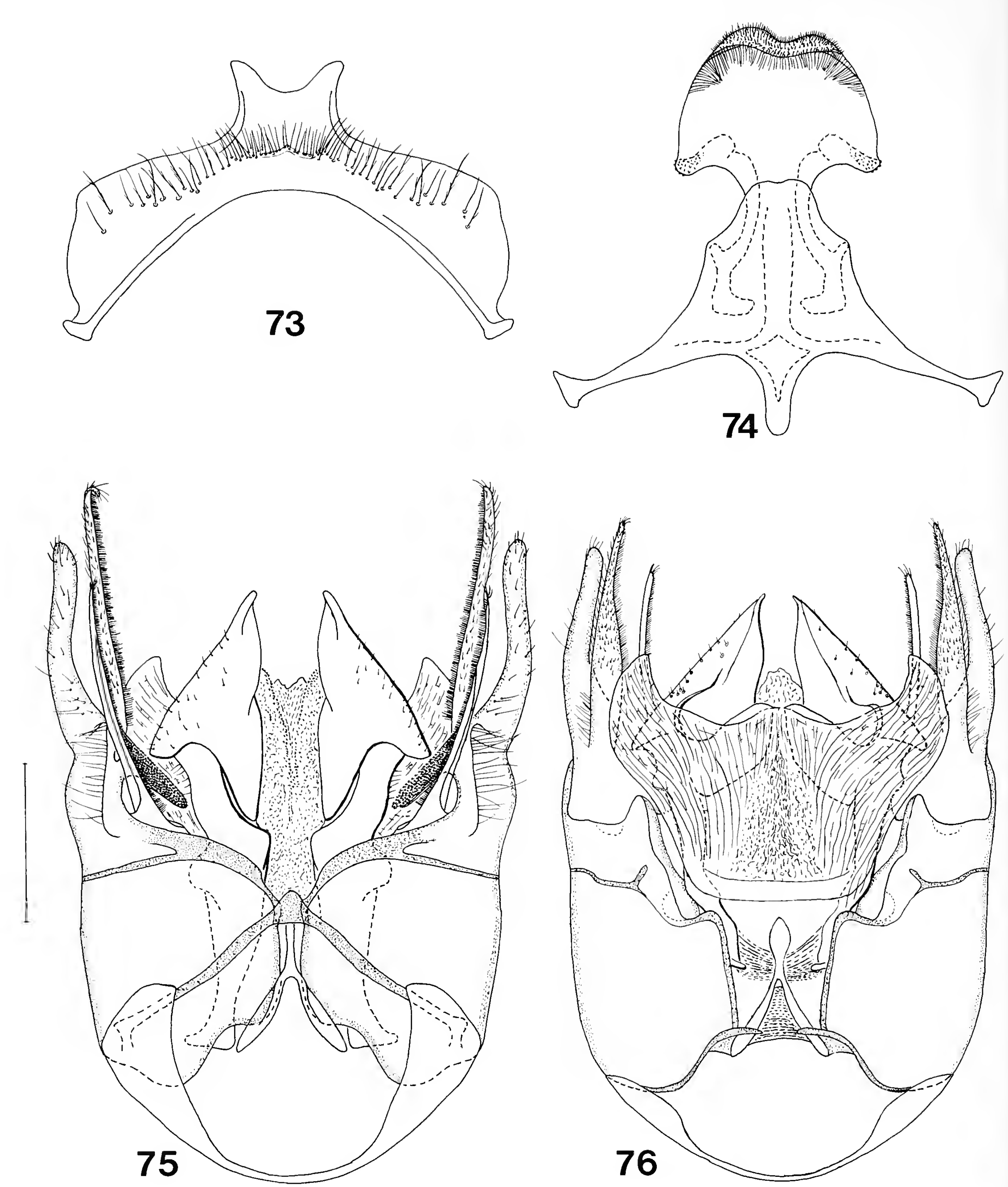
ETYMOLOGY

The specific epithet is a Latin word meaning with corners, referring to the angulate mesosternal processes of the male.

DISCUSSION

Aside from the variations noted above in the measurements and proportions, the males available are very similar to one another. The laterobasal spot on the second tergite may extend mesad as a narrow line and/or a short distance distad. The procoxal process is immaculate in three paratypes and in these specimens the mesotibial stripe is divided into a basal spot and two narrowly separated stripes along the segment. One male has a narrow yellow stripe on the anterior face of the metadistitarsus and yellow blotches on the outer face of the metamediotarsi.

Males of this species are easily recognized by the combination of black abdomen with contrasting pale marks, suberect and internally carinate mesosternal tubercles and black labrum. Females are considerably less distinctive, but differ from such species as *E. elegans, E. rustica,* and *E. bova* in possessing an immaculate abdomen and largely black thoracic pubescence. The lack of a median impunctate line on



Figures 73–76. *Epicharis* (*Epicharana*) *bova*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

the clypeal disc will also separate *E. angulosa* from *E. elegans* and *E. rustica.*

Epicharis (Epicharana) bova, **new species**

Figures 65, 73–76

DIAGNOSIS

Separable from all other species of *Epicharana* by the following unique combination of characters. Abdomen ferruginous, immaculate; pubescence of head and thorax medium brown to blackish brown, mesoscutum without pale hairs; clypeus black. *Male:* mesosternal processes, in profile, suberect but low and rounded, not carinate on inner margin; anterior margin of metatibia strongly produced (Fig. 65). *Female:* clypeal disc subcontiguously to densely punctate, without median impunctate line.

DESCRIPTION

HOLOTYPE MALE. Measurements (mm). Head width 5.95; head length 4.15; wing length 16.0; total length 25.0.

Head. 1.43 times broader than long; in frontal view, occipital margin very weakly concave, except for ocellar elevation; ocelli on occipital margin; upper frontal width 0.71 times lower frontal width. Mandible slender, inner tooth small, obtuse. Labrum about 1.2 times broader than long, apical margin broadly rounded; disc moderately shiny, weakly tessellate between irregularly spaced (mostly sparse), fine and coarse punctures. Clypeus about 1.5 times broader than long, apicolateral angle separated from inner eye margin by about 0.8 times diameter of antennal socket; clypeus shiny and very weakly tessellate between subcontiguous to dense, coarse punctures which become moderate distad, median impunctate line absent; discal carinae about twice as far apart distad as at base; side shiny between dense, moderate to coarse, elongate (especially distad) punctures. Frons moderately shiny and distinctly tessellate between dense, mixed fine and moderate punctures; preocellar area slightly protuberant on either side, shiny and nearly impunctate; ocellocular area dull and densely tessellate, subcontiguously, shallowly micropunctate and with scattered minute punctures; preocciput moderately shiny to shiny between close to dense punctures, minute near eye, becoming fine near margin. Interantennal distance 2.00 times antennal socket diameter; antennocular distance 0.63 times antennal socket diameter; scape robust, 1.74 times longer than wide, scape length 1.52 times length of first flagellar segment; first flagellar segment shorter than following three segments combined, 1.37 times longer than second segment. Interocellar distance 1.61 times diameter of anterior ocellus; ocellocular distance 1.96 times diameter of anterior ocellus; ocelloccipital distance 1.61 times diameter of anterior ocellus.

Thorax. Mesoscutum slightly shiny, uniformly densely, finely punctate, and with sparse, moderate punctures which become scattered distad; dorsal face of scutellum broadly depressed in middle, punctures as on mesoscutum, but fine punctures scattered; dorsal face of metanotum moderately shiny and distinctly tessellate between dense, fine punctures, posterior face dull, densely tessellate and with scattered fine punctures. Mesepisternum moderately shiny and tessellate between sparse, fine punctures; metepisternum moderately shiny between subcontiguous, minute punctures. Mesosternal process suberect in profile, its apex narrowly rounded; in ventral view, inner margin rounded. Propodeum moderately shiny, subcontiguously micropunctate between sparse to scattered, fine punctures. Procoxal process subcircular, apex not produced; mesofemur stout, about twice longer than thick, greatest thickness a little basad of midlength; anterobasal ventral depression of metafemur subcarinate along its posterior margin; anterior margin of metatibia abruptly convex at about midlength and anterior carina plainly visible (Fig. 65), posterior carina low throughout, highest distad of middle and abruptly reduced beyond highest point.

Abdomen. Tergal discs moderately shiny between minute punctures which are dense on basal segments, becoming progressively coarser and less close on succeeding segments; discs also with scattered fine punctures on basal segments, becoming progressively coarser (but still fine) on succeeding segments. Seventh tergite with very weakly differentiated pygidial plate which is depressed along midline; apex bidentate, teeth stout and acute, emargination between them semicircular.

Terminalia. Apical margin of distal lobe of seventh sternite (Fig. 73) deeply, angularly incised; setae long, widely spaced, mostly simple. Shoulders of disc of eighth sternite (Fig. 74) obtuse and sides of apical lobe of disc weakly convergent distad. Genitalia as in Figs. 75 and 76.

Pilosity. Generally blackish brown on head, thorax, and legs, but yellowish on metatibia and metabasitarsus; suberect hairs and appressed scaliform hairs of terga two to six golden brown, but fringes of fifth and sixth segments brown and a few brown, simple, suberect hairs scattered on discs. Scale-like hairs very short basad, becoming longer and more erect on succeeding segments. Hairs of abdominal sterna golden brown to blackish brown.

Color. Head, thorax, and legs blackish brown; abdominal terga ferruginous, sterna light brown. The following yellowish: large triangular mark near base of mandible; labrum; narrow, oblique stripe on side of face, from tentorial pit to malar area; small, triangular supraclypeal spot; small spot on underside of scape; basal spot on protibia; dorsal, apical spot on metafemur; outer face of metatibia and metabasitarsus (metatibia black at base). Inner leg surfaces dark ferruginous; tarsi ferruginous. Wings blackish brown, veins and stigma black.

FEMALE. Measurements (mm). Head width 6.41; head length 4.26–4.31; wing length 16.5; total length 24.0–27.0.

Head. 1.49–1.51 times broader than long; in frontal view, occipital margin nearly straight, ocellar elevation anterior to margin; upper frontal width 0.79–0.81 times lower frontal width. Mandible stout, tridentate, inner teeth obtuse, margin between them broadly concave. Labrum about 1.1 times longer than broad, apex subangularly rounded in middle; disc moderately shiny, roughened, and tessellate between dense to subcontiguous, mixed fine and coarse punctures, median line slightly raised. Clypeus about 1.4 times broader than long, apicolateral angle separated from inner eye margin by about 0.75 times antennal socket diameter; intercarinal distance at base about 0.36 times that at their distal end; sculpture as described for male. Remaining cephalic sculpture as described for male. Interantennal distance 2.28–2.37 times antennal socket diameter; antennocular distance 0.92–0.95 times antennal socket diameter; scape robust, 1.86–1.91 times longer than broad, scape length 1.04–1.08 times length of first flagellar segment; first flagellar segment shorter than following three segments combined, 3.45–3.85 times length of second segment.

Thorax. Punctation as in male. Dorsal and posterior faces of metanotum separated on either side of middle by short, convex, cariniform ridge. Basitibial plate subacute at apex, secondary plate about 2.8 times longer than wide.

Abdomen. Punctation as in male. Pygidial plate broadly truncate at apex, secondary plate very weak.

Pilosity. About as described for male, with following differences: discs of third, fourth, and fifth terga with some suberect to erect dark brown, bristle-like hairs, longer and more abundant on succeeding segments; prepygidial fringe golden brown. Scopa of metatibia and metabasitarsus yellowish.

Color. As described for male, but wholly without yellowish markings and pronotum and propodeum reddish brown.

TYPE MATERIAL

Holotype male: Cerro Campana, Panamá Prov., PANAMA, 4 May 1960 (W.J. Hanson), in Snow Entomological Museum, University of Kansas. Allotype: 4 mi. S San Vito de Java, Puntarenas Prov., COSTA RICA, 15 Aug. 1967 (R.W. McDiarmid; LACM). Paratypes: 1♀, N of El Vallé de Anton, Coclé Prov., PANAMA, 12–13 Sept. 1964 (R.L. Dressler; UKAN); 1♀, O.T.S. Field Station, Finca La Selva, Heredia Prov., COSTA RICA, mid Aug. 1980 (J.M. MacDougal; LACM), on *Passiflora lobata,* 0900.

ETYMOLOGY

The specific epithet is a Latin word for a swelling of the legs and alludes to the swollen metatibia of the male.

DISCUSSION

Both sexes are easily separated from others in the subgenus *Epicharana* by the features listed above in the Diagnosis. The male is especially distinctive in the shape of the metatibia, the anterior margin of which is conspicuously and abruptly convex at about midlength. The low posterior carina of the metatibia is like that of *E. angulosa,* as is the posteriorly subcarinate anterobasal depression on the underside of the metafemur. The abdomen of *E. angulosa* is black and the mesosternal tubercles are acute at their apices and sharply carinate on their inner margins.

The only other species with a reddish abdomen is *E. elegans,* in both sexes of which the abdomen is distinctly yellowish red and the first tergum is yellowish maculate on the disc. In males of *E. elegans,* and those of *E. flava* and *E. rustica,* the clypeus is pale, the metatibia is regularly convex along its anterior margin, there is no inner, anterior metatibial carina, and the inner posterior metatibial carina is expanded beyond midlength and folded mesad. In both sexes of these species, *E. elegans, E. flava,* and *E. rustica,* there is considerable pale pubescence intermixed with blackish on the thoracic dorsum. Females of these three species have a definite median impunctate line on the clypeus and the minute punctures of the scutellum are usually coarser and less distinct than those of the mesoscutum.

Epicharis (*Epicharana*) *elegans* F. Smith

Epicharis elegans F. Smith, 1861:152. ♀ ♂.
Epicharis elegans: Moure, 1945a:296 (tax.).
Epicharis salazari Cockerell, 1949:480–481. ♀. NEW SYNONYMY.

This is a common black and red species in Mexico and ranges south to Costa Rica. Specimens from southern Mexico (Chiapas and Yucatán), Guatemala, El Salvador, and Costa Rica have the abdomen more brownish and correspond to *E. salazari,* described from El Salvador. These are minor variants and not worthy of separation from *E. elegans.*

NEW RECORDS

MEXICO, *CHIAPAS:* 4♀♀, La Revancha, 20 Aug. 1972 (T.W. Taylor; LACM). *GUERRERO:* 6♀♀, 12.7 mi. N Iguala, 5200 ft. elev., 1 Aug. 1969 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 23 mi. N Taxco, 1700 ft. elev., 8 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 3.7 mi. W Río Balsas, 5 Aug. 1965 (G.W. Byers and party; UKAN); 2♂♂, Iguala, 2400 ft. elev., 8 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN). *JALISCO:* 1♂, Guadalajara, no date (Crawford; LACM); 3♀♀, Cocula, 4450 ft. elev., 27 Sept. 1957 (H.A. Scullen; ORSU); 2♀♀, Puente Grande, 5000 ft. elev., 20 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN). *MORELOS:* 5♀♀, 8♂♂, Lake Tequisquetengo, 5000 ft. elev., 13 Sept. 1957 (H.A. Scullen; ORSU); 1♂, Rancho Tetela, Cuernavaca, 24 June 1974 (K.E. Donahue and S. Adams; LACM); 1♀, 1♂, Cuernavaca, no date (Crawford; LACM); 2♂♂, Alpuyeca, 27 June and 3 July 1951 (P.D. Hurd; UCB); 1♀, 7.3 mi. S Yautepec, 3000 ft. elev., 16 Aug. 1962 (Ordway and Naumann; UKAN); 3♀♀, 4 mi. SW Yautepec, 3800 ft. elev., 2 July 1961 (C.D. Michener; UKAN), on *Cassia* sp.; 2♀♀, 4.3 mi. W Yautepec, 4000 ft. elev., 17 Aug. 1962 (Ordway and Marston; UKAN); 1♂, 7 mi. NE Yautepec, 4000 ft. elev., 18 Aug. 1962 (Univ. Kans. Mex. Exped.; UKAN); 1♂, 14 mi. S Yautepec, 16 Aug. 1962 (Marston and Roberts; UKAN). *OAXACA:* 1♀, 25 mi. SE Oaxaca, 5600 ft. elev., 27 June 1963 (Scullen and Bolinger; ORSU); 1♀, 1♂, 47 mi. SE Oaxaca, 13 July 1952 (E.E. Gilbert and C.D. MacNeil; UCB); 2 ♀♀, 5 mi. NW Totolapan, 4000 ft. elev., 29 July 1970 (E.M. Fisher and P. Sullivan; LACM); 47♀♀, 5 mi. NW Totolapan, 3800 ft. elev., 6 July 1953 (Univ. Kans. Mex. Exped.; UKAN), on *Malpighia mexicana*; 1♀, Salina Cruz, no date (F.K. Knab; USNM); 2♀♀, Mixtla, 5600 ft. elev., 22 Aug. 1963 (Scullen and Bolonger; ORSU); 4♂♂, Monte Alban, 6000 ft. elev., 27 June 1961 (Univ. Kans. Mex.

Exped.; UKAN); 1♂, same, except 15 July 1955; 1♀, Tamazulapan, 6000 ft. elev., 28 June 1961 (Univ. Kans. Mex. Exped.; UKAN); 1♀, 2 mi. NW Tamazulapan, 6000 ft. elev., 28 June 1961 (Univ. Kans. Mex. Exped.; UKAN). *PUEBLA:* 9♀♀, 22 km NW Izúcar de Matamoros, 1158 m elev., 21 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Cassia laevigata*; 16♀♀, 16.1 km NW Izúcar de Metamoros, 1280 m elev., 17 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Caesalpinia cacalaco*; 9♀♀, 7♂♂, 6.9 km S Izúcar de Matamoros, 1250 m elev., 17 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Solanum rostratum* (♀♀) and *Martynia annua* (♂♂); 3♀♀, 3♂♂, Atlixco, 9 July 1970 (R.E. Beer and party; UKAN); 2♀♀, 3 mi. NW Petlalcingo, 4600 ft. elev., 29 Aug. and 5 Sept. 1972 (Byers and Thornhill; UKAN); 1♀, 12 mi. NW Tehuitzingo, 4050 ft. elev., 29 June 1961 (Univ. Kans. Mex. Exped.; UKAN); on *Cassia* sp.; 1♀, 10 mi. SE Tehuitzingo, 3900 ft. elev., 3 July 1953 (Univ. Kans. Mex. Exped.; UKAN). *SAN LUIS POTOSÍ:* 6♂♂, El Salto, 1600 ft. elev., 24 Aug. 1954 (Univ. Kans. Mex. Exped.; UKAN). *TAMAULIPAS:* 1♀, 38 mi. N El Mante, 1050 ft. elev., 11 Oct. 1957 (H.A. Scullen; ORSU). *YUCATÁN:* 5♀♀, Pisté, 24 June 1967 (E.C. Welling; LACM). GUATEMALA: 2♀♀, "1923 F.4696" (UKAN); 1♀, "env. de Guatemala" (R. Guerin; MNHN). EL SALVADOR: 1♀, Dept. Santa Tecla, Feb. 1947 (M. Salazar; USNM; type of *E. salazari*); 4♀♀, Santa Tecla, 900 m elev., 25 Apr.–6 May 1972 (S. and L. Steinhaus; DPIF). COSTA RICA, *GUANACASTE:* 1♀, Comelco, 8 km NW Bagaces, 31 March 1971 (P.S. Opler; UCB), on *Tabebuia rosea*; 1♀, same, except 25 Nov. 1972; 1♂, same, except 5 Mar. 1971; 1♂, La Pacifica, 4 km NW Cañas, 14 Mar. 1972 (P.A. Opler; UCB), on *Inga vera*; 1♂, Hacienda Comelco, 24 km NW Cañas, 21 Mar. 1971 (E.R. Heithaus; LACM), on *Stachytarpheta jamaicense,* 0815; 1♂, same locality, 13 Mar. 1971 (E.R. Heithaus; LACM), on *Centrosoma pubescens,* 0750.

Epicharis (*Epicharana*) *rustica* (Olivier)

Figures 63, 67

Apis rustica Olivier, 1789:64.
Apis hirtipes Fabricius, 1793:325. ♀.
Epicharis rustica: F. Smith, 1854:368.
Centris (*Epicharis*) *rustica:* Friese, 1900b:253. ♀ ♂.
Centris (*Epicharis*) *rustica* var. *flava* Friese, 1900b:254. ♂. NEW SYNONYMY.
Epicharis rustica: Moure, 1945a:295–296. ♂ ♀ (syn.).
Epicharis (*Epicharana*) *rustica:* Michener, 1954:144 (distr.).
Epicharis (*Epicharis*) *rustica:* Moure, 1960b:119–120 (syn.).
Epicharis (*Epicharis*) *flava:* Moure, 1960b:120 (status).

Moure (1960b) reexamined the type female of *Apis hirtipes* and reaffirmed its traditional place in the synonymy of *E. rustica.* He concluded ". . . that with this discovery, the true meaning of *Epicharis* is to be restored as in my revision of *Epicharis* (1945) and *Epicharana* Michener, 1954, with the same type species is to be considered a synonym." I have already alluded to be unavailability of *Apis rustica* to be the type-species of *Epicharis.*

In point of fact, Moure's determination is inconclusive. Moure synonymized *A. hirtipes* under ". . . *Epicharis rustica* as interpreted by older authors and Friese in his Monographie der Bienengattung *Centris* (s. lat.)." This is by no means the same as placing *A. hirtipes* in synonymy with Olivier's species. Moure admitted that he had been unable to find Olivier's type. In truth the identity of *E. rustica* is unknown and the current interpretation of this species rests upon the very insecure foundation of assumptions made over a century ago by workers whose concepts of species were different from those of the present and who may not actually have seen the relevant specimens.

For the present, it would seem best to continue to accept the traditional interpretation of *E. rustica* and its appended synonymy, as published by Moure (1960b). The alternative would be to regard Olivier's species as unidentifiable and to use the next available name (*A. hirtipes*), suffering the resultant nomenclatural confusion. I adhere to the traditional understanding, which includes the unavailability of *E. rustica* as the type species for this genus.

This is a common bee, ranging from Costa Rica and Panama to Brazil and Peru. Friese's var. *flava,* with whitish cinereous pubescence on the thorax, was thought by Moure (1960b) to be probably a good species. In general, specimens from northeastern South America have almost entirely black thoracic pubescence and would correspond to the "typical" form of *E. rustica.* Similar dark specimens are also found in Costa Rica, but most populations have considerable pale pubescence on the dorsum and sides of the thorax. There are, however, many variants, the most common being a form with dark mesepisternal hairs, those of the mesoscutum and scutellum pale, or largely so. These specimens of an intermediate character occupy geographical areas between the two extremes, as would be expected if *E. rustica* and *E. flava* were conspecific, which I believe to be the case.

NEW RECORDS

COSTA RICA, *GUANACASTE:* 1♀ [Hacienda] Comelco, 5 Mar. 1971 (P.A. Opler; UCB), on *Tabebuia rosea. HEREDIA:* 1♀, Finca La Selva, 500 m elev., 23 June 1979 (D.R. Perry; LACM). *PUNTARENAS:* 1♀, Monteverde, 1400 m elev., 17 Sept. 1982 (C.D. Nagano and M. Hayes; LACM). PANAMA, *CANAL ZONE:* 1♀, Barro Colorado Island, 15 July 1980 (H. Wolda; ROUB); 1♀, same, except 1 Aug. 1980. *CHIRIQUÍ:* 3♀♀; 1♂, Dolega, 15 Mar. 1980 (D.W. Inouye; ROUB). *PANAMÁ:* 3♀♀, Arraijan, 16 Oct. 1980 (D. Roubik; ROUB); 4♀♀, Chilibre Cave, 26 July 1966 (R.D. Sage; UCB); 1♂, San Miguelito, 16 May 1974 (M. Gonzalez; LACM).

Subgenus *Parepicharis* Moure

Parepicharis Moure, 1945a:307–308. Type-species: "*Parepicharis zonata* (Smith, 1854)" = *Epicharis zonata* F. Smith, 1854; monobasic and original designation.

DESCRIPTION

Maxillary palp two-segmented, second segment much longer than first, more than five times longer than wide, gradually narrower distad; lateral ridges of clypeal disc weak; malar space linear, eye margin nearly contiguous with mandible base; frontal carina ending before attaining anterior ocellus; occipital margin abruptly rounded; flagelliform occipital setae reaching about to level of anterior margin of tegula; posterior margin of dorsal face of scutellum impressed; metanotum vertical; jugal lobe of posterior wing about as long as cubital cell and one-half as long as vannal lobe.

Female. Labrum with median ridge weak or absent; outer face of mesobasitarsus with mixed long, coarse plumose setae and long, fine plumose hairs on anterior half, posterior half with long, coarse plumose setae only; basitibial plate without secondary plate; metatibia no longer than metabasitarsus; third and fourth terga without specialized basal areas; margins of pygidial plate, in dorsal view, nearly straight, apex broadly truncate.

Male. Labrum without median ridge; first flagellar segment longer than scape and longer than following two segments combined; ocellocular distance less than ocellar diameter; procoxa without apicoventral process; mesosternal protuberances absent; metatrochanter and metafemur without ventral seta patch; metatibia without carinate posteroventral ridge; metabasitarsus with or without anterior carina-like ridge, when present terminating in tooth a little beyond midlength; pygidial plate narrower than seventh tergite, margins cariniform, apex narrow, rounded or truncate.

Parepicharis was proposed as a monotypic genus for *Epicharis zonata*. Subsequently, Moure and Seabra (1959) added *E. metatarsalis* to *Parepicharis*. Of the two species, only *E. metatarsalis* is found in Central America. I have seen material of *E. zonata* from Guyana, Brazil, and Bolivia and there are records of the species from Peru and Trinidad.

KEY TO SPECIES OF *PAREPICHARIS*

1a. Male, antenna 13-segmented and ocellocular distance less than diameter of anterior ocellus 2
 b. Female, antenna 12-segmented and ocellocular distance greater than diameter of anterior ocellus 3
2a. Metabasitarsus about twice as long as broad and with distinct tooth on anterior margin .. *metatarsalis* Friese
 b. Metabasitarsus about six times longer than broad and without tooth on anterior margin .... *zonata* F. Smith
3a. First abdominal segment blackish, remaining segments dull ferruginous, immaculate; prepygidial fimbria consisting of long, closely ranked, plumose hairs .... *metatarsalis* Friese
 b. Abdomen brown, with conspicuous yellow maculations on at least first three terga; prepygidial fimbria weak, consisting of short, discretely separated, short-plumose hairs which do not conceal underlying surface .... *zonata* F. Smith

Epicharis (*Parepicharis*) *metatarsalis* Friese

Epicharis metatarsalis Friese, 1899:40. ♂.
Epicharis phenacura Cockerell, 1917:200. ♂. NEW SYNONYMY.
Epicharis conura Cockerell, 1917:200. ♀. NEW SYNONYMY.
Epicharis (*Parepicharis*) *metatarsalis:* Moure and Seabra, 1959:126 (distr., tax.).

The male of *E. metatarsalis* differs from that of *E. zonata* most obviously by the metabasitarsus, which is only twice as long as broad and with a distinct tooth on the anterior margin beyond the middle. Males of *E. zonata* lack a tooth on the metabasitarsus and the segment is about six times longer than broad. Females of *E. metatarsalis* have the first tergite blackish and the remaining segments dull yellowish red; in *E. zonata* there are yellow maculae, of variable extent, on the first three tergites which usually are dark brown to blackish. Both sexes of *E. metatarsalis* are larger (25–27 mm versus 20–23 mm).

Friese (1900b) recorded males of this species from St. Parime, Venezuela (type locality), and "Darien (=Colombia)," now in Panama. Another male was reported by Moure and Seabra (1959) from San José, Costa Rica. San Carlos, Costa Rica is the type locality for both *E. phenacura* and *E. conura*. The material now available indicates that *E. phenacura* and *E. conura* are the opposite sexes of one species and that the males are inseparable from *E. metatarsalis*.

NEW RECORDS

COSTA RICA, *HEREDIA:* 23♀♀, 6♂♂, Finca La Selva, near Puerto Viejo, 5 June–24 July (D.R. Perry; LACM), on *Hymenolobium* sp. (8♀♀, 2♂♂), *Dipteryx panamensis* (11♀♀, 2♂♂), *Tabebuia* sp. (1♂), *Dussia* sp. (1♂), and *Byrsonima* sp. (4♀♀).

Subgenus *Hoplepicharis* Moure

Hoplepicharis Moure, 1945a:300–301. Type-species: "*Hoplepicharis fasciata* (Lepeletier & Serville, 1828)" = *Epicharis fasciata* Lepeletier and Serville, 1828; original designation.
Epicharis subg. *Hoplepicharis:* Michener, 1954:145.

DESCRIPTION

Maxillary palp two-segmented, second segment shorter than first, flattened; lateral ridges of clypeal disc strong; malar space distinct, slightly longer than minimum thickness of first flagellar segment; frontal carina sharp but ending well in front of anterior ocellus; occipital margin abruptly rounded; flagelliform occipital setae extending nearly to level of posterior tegular margin; posterior margin of dorsal face of scutellum not impressed; metanotum bifaced, juncture sharply angulate to crested; jugal lobe of posterior wing about as long as cubital cell and about one-half as long as vannal lobe.

Female. Labrum with weak median ridge; outer face of mesobasitarsus, on anterior half, with long, coarse, simple setae and shorter, fine, plumose hairs, posterior half with sparse long, coarse, simple setae and scattered short, fine, plumose hairs; secondary basitibial plate present; metatibia a little longer than metabasitarsus; third and fourth terga without specialized basal areas; margins of pygidial plate nearly straight and strongly convergent to narrowly truncate apex.

Male. Labrum without median ridge; first flagellar segment shorter than either scape or second flagellar segment; ocellocular distance greater than diameter of anterior ocellus; procoxa with short, inconspicuous apicoventral process; mesosternum without tubercles; metatrochanter and metafemur without ventral seta patch; metatibia without posteroventral ridge; metabasitarsus with anterior carinate ridge terminating in sharp tooth basad of midlength; pygidial plate broad and indistinct, weakly bilobate at apex.

This is a small group, with two species known from South America and two in Central America.

KEY TO CENTRAL AMERICAN *HOPLEPICHARIS*

a. Second abdominal tergite with basal yellow band, narrowed across middle, followed by narrow blackish brown band; most of remainder of this segment, and all of following segments, ferruginous (except short, yellow longitudinal stripe at side of third segment) .... *lunulata* Mocsáry

b. Similar, but second tergite, beyond yellow basal band, and all of following segments, blackish (except short, yellow longitudinal stripe at side of third segment) .... *monozona* Mocsáry

Epicharis (*Hoplepicharis*) *lunulata* Mocsáry

Figure 64

Epicharis lunulata Mocsáry, 1898:499. ♂ ♀.
Hoplepicharis lunulata: Moure, 1945a:302 (distr., syn.).
Epicharis (*Hoplepicharis*) *lunulata:* Miehener, 1954:145 (distr.).

This attractive Central American species appears to be less common than the superficially similar *E. elegans.* Its range extends from Mexico to Panama.

NEW RECORDS

MEXICO, *CHIAPAS:* 1♀, Simojovel, 18–31 July 1958 (J.A. Chemsak; UCB). *JALISCO:* 1♀, Estación Biologia UNAM, Chamela, 11 Sept. 1981 (S.H. Bullock; LACM), on *Psidium sartorianum. NAYARIT:* 2♀♀, 16 mi. NW Tepic, 19 July 1953 (Univ. Kans. Mex. Exped.; UKAN). *OAXACA:* 1♀, 6 mi. W Zanatepec, 150 ft. elev., 9 July 1953 (Univ. Kans. Mex. Exped.; UKAN), on *Malpighia mexicana*; 2♀♀, 5 mi. NW Totolapan, 3800 ft. elev., 6 July 1953 (Univ. Kans. Mex. Exped.; UKAN), on *Malpighia mexicana. VERA CRUZ:* 1♀, 1♂, Cordóba, 1–10 Sept. (♀), 1 Oct. 1964 (♂) (LACM). GUATEMALA: 1♀, Cayuga, Nov. (Schaus and Barnes; USNM); 1♀, "F.4694" (UKAN). HONDURAS: 1♂, Tegucigalpa, 12 May 1981 (F.J. Dyer; USNM). COSTA RICA, *GUANACASTE:* 4♀♀, 1♂, Hacienda Comelco, 8 km NW Bagaces and 24 km NW Cañas, dates between 7 Mar. and 14 Oct. (E.R. Heithaus [1♀], P.A. Opler [3♀♀, 1♂]; LACM, UCB), on *Byrsonima* sp. (1♀), *Stachytarphe frantzii* (1♀), *Petastoma patelliferum* (♂) and Bignonaceae, 0700 (1♀); 1♀, near Turin (10°20′N, 84°50′W), 1 Feb. 1960 (C.W. Palmer; UKAN). *PUNTARENAS:* 1♀, 1 mi. ESE jct. Río Cañas and Hwy 2, 1000 ft. elev., 23 July 1965 (R.D. Sage and S.J. Arnold; UCB), on *Bixa orellana,* 1000–1100. *SAN JOSÉ:* 1♂, 4 km E San Ignacio de Acosta, 4000 ft. elev., 8 July 1963 (C.D. Michener et al.; UKAN); 1♀, Playón, 8 km N Parrita, 30 ft. elev., 14–19 Aug. 1962 (C.D. Michener and A. Wille; UKAN); 1♂, San José, 25 July 1913 (UKAN).

Epicharis (*Hoplepicharis*) *monozona* Mocsáry

Epicharis monozona Mocsáry, 1898:498. ♀.
Hoplepicharis monozona: Moure, 1945a:392 (distr., tax.).
Epicharis (*Hoplepicharis*) *monozona:* Michener, 1954:145 (distr.).

This species was based on a female from an unspecified Panamanian locality. Moure (1945a) recorded another female from Muzo, Río Cantinero, Colombia, and Michener (1954) reported two additional Panamanian specimens, both from the Canal Zone: Las Cruces trail, near Corozal, and Fort Clayton.

The male of *E. monozona* has not been previously reported. It is separable from that of *E. lunulata* by the black, rather than ferruginous, abdomen. Aside from the differences in color, *E. monozona* and *E. lunulata* appear to be identical and I suspect they will ultimately be found to be conspecific.

NEW RECORDS

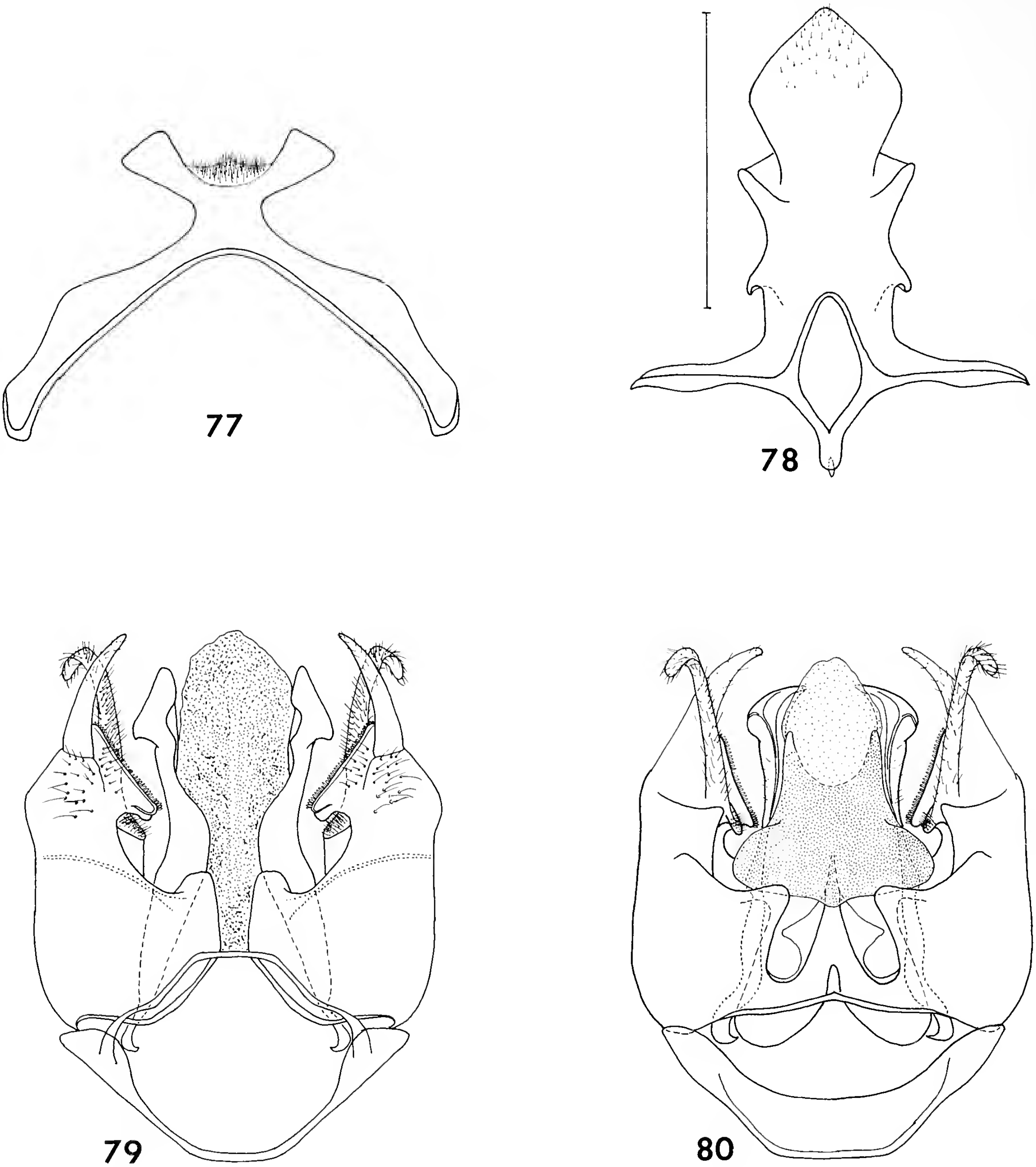
PANAMA, *PANAMÁ:* 3♀♀, Arraijan, 16 Oct. 1980 (D. Roubik; LACM, ROUB); 1♀, Chepo, 15 km E Carti, 8 June (D. Roubik; ROUB); 1♂, Cerro Campana, 13 Apr. 1960 (W.J. Hanson; UKAN); 1♀, Cerro Azul, N of Tocumen, 15 June 1958 (W.J. Hanson; UKAN). *CANAL ZONE:* 1♀, Pipeline Road, Gamboa, 12 Jan. 1980 (D. Roubik; ROUB); 1♀, same, except 10 June 1980; 1♀, 7♂♂, Pipeline Road, 20 Sept., 6 Oct. 1979 (K. Steiner; UCD), on *Drymonia serrulata*; 5♀♀, 1♂, Gamboa, 28 Sept. 1979, same collector and host; 1♂, Barro Colorado Island, 15 July 1958 (W.J. Hanson; UKAN); 3♂♂, same locality, 15 Sept., 12 Oct., 28 Oct. 1979 (K. Steiner; UCD), on *D. serrulata. COLÓN:* 1♀, Portobello, 30 Sept. 1979 (K. Steiner; UCD), on *D. serrulata.*

Subgenus *Epicharoides* Radoszkowski

Epicharoides Radoszkowski, 1884:20. Type-species: (*Epicharoides bipunctatus* Radoszkowski, 1884) = *Epicharis maculata* F. Smith, 1874; monobasic and original designation.
Epicharoides: Moure, 1945a:309–310.
Epicharis subg. *Epicharoides:* Michener, 1954:144.

DESCRIPTION

Maxillary palp three-segmented, second segment longer than first, third segment narrower and shorter than second; lateral ridges of clypeal disc strong; malar space distinct, about as long as minimum thickness of first flagellar segment; frontal carina sharp, nearly reaching anterior ocellus; occipital margin slightly compressed but not ridge-like; flagelliform oc-



Figures 77–80. *Epicharis* (*Epicharoides*) *albofasciata,* male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

cipital setae short and curved laterad, not extending beyond anterior margin of mesoscutum; posterior margin of dorsal face of scutellum not impressed; metanotum wholly vertical; jugal lobe of posterior wing about as long as cubital cell and about one-half as long as vannal lobe.

Female. Labrum without median ridge; mesobasitarsis externally with evenly distributed long coarse setae (some plumose) and short, fine, long-plumose hairs; secondary basitibial plate absent; metatibia no longer than metabasitarsus; third and fourth terga without specialized basal areas; margins of pygidial plate, in dorsal view, slightly concave, apex narrowly truncate, disc depressed.

Male. Labrum without median ridge; scape unusually robust, slightly longer than wide, first flagellar segment shorter than either scape or second flagellar segment; ocellocular distance greater than diameter of anterior ocellus; procoxa without apicoventral process; mesosternal tubercles absent; metatrochanter and metafemur without ventral seta patch; metatibia without posteroventral ridge; metabasitarsus without carinate anterior ridge; pygidial plate about one-half as broad as seventh tergite, sharply margined, apex narrowly rounded.

Moure (1945a) recognized three species in this subgenus, and a fourth was added by Moure and Seabra (1959). Two of these species are present in Central America and two are confined to South America. The two Central American species are black, with abundant, very variable yellow markings.

KEY TO CENTRAL AMERICAN *EPICHAROIDES*

a. Male clypeus with irregular black blotch on disc; female with basal yellow band of second tergite broadly interrupted, but if complete, it is much shorter in middle than black band following it and basal bands of following terga are broadly interrupted .... *albofasciata* F. Smith

b. Male clypeus without black blotch on disc; female with basal yellow band of second tergum as long in middle as black band following it or, if a little shorter, third and fourth terga with complete transverse yellow fasciae ... . *maculata* F. Smith

Epicharis (*Epicharoides*) *albofasciata* F. Smith

Figures 77–80

Epicharis albofasciata F. Smith, 1874:321. ♂.
Epicharis maculata var. *nigroclypeata* Friese, 1899:40.
Epicharoides albofasciata: Moure, 1945a:310 (syn., distr.).
Epicharis (*Epicharoides*) *maculata:* Michener, 1954:145 (in part).

This species and *E. maculata* are so similar as to be virtually inseparable and records from the literature under either name must be treated with caution. There are, however, consistent differences in the male terminalia (compare Figs. 77–80 with Figs. 81–84).

Females of the two species are especially difficult to separate. Those of *E. albofasciata* have either lateral spots on the second tergite or a subbasal fascia which is shorter than the black area following the band; the third and fourth tergites apparently never possess entire transverse subbasal bands, though the margins of the segments may be broadly ferruginous. On the other hand, females of *E. maculata* possess a subbasal band on the second segment which is usually, though not always, at least as long as the dark band following it; a shorter transverse band, often attenuated in the middle, is present on the third tergite; a transverse band is also present on the fourth segment, usually longer than that of the third.

Aside from the differences in genitalic structures, males of *E. albofasciata* are recognizable by the presence of a black blotch on the the clypeal disc, the very short fasciae of the second to fourth tergites (evanescent or absent on third and often on fourth as well) and the pronotum black, except two widely separated spots on the collar.

From Central America, I have seen material of *E. albofasciata* only from Costa Rica and Panama. At least some of the specimens from Panama recorded by Michener (1954) as *E. maculata* are this species; his figures 141–143 are based on *E. albofasciata.*

NEW RECORDS

COSTA RICA, *GUANACASTE:* 2♀♀, Hacienda Comelco, 24 km NW Cañas, 6–13 Mar. 1972 (E.R. Heithaus; LACM), 1 on *Securidaca tenuifolia*; 1♀, Hacienda Comelco, 8 km NW Bagaces, 5 Mar. 1971 (P.A. Opler; UCB), on *Delbergia retusa*; 1♂, same locality, 28–31 Jan. 1972 (P.A. Opler; UCB), on *Securidaca sylvestris*; 1♂, Finca La Pacifica, 4 mi. NW Cañas, 10 July 1971 (P.A. Opler; UCB), on *Petastoma patelliferum*; 1♀, Liberia, 15–16 Feb. 1972 (P.A. Opler; UCB), on *Andira inermis. HEREDIA:* 5♀♀, 16♂♂, Finca La Selva, near Puerto Viejo, 6 May to 18 June (D.R. Perry; LACM), on *Dipteryx panamensis* (3♀♀, 8♂♂), *Vochysia* sp. (1♂), *Byrsonima* sp. (1♀), *Dussia* sp. (6♂♂), and *Hymenolobium* sp. (1♂). PANAMA, PANAMÁ: 1♀, 24 Mar. 1980 (D. Roubik; ROUB); 4♀♀, same, except 2 Apr. 1980; 2♀♀, same except 13 Apr. 1980; 1♀, Curundu, 31 Mar. 1981 (D. Roubik; ROUB). *CANAL ZONE:* 1♀, Barro Colorado Island, 2 June 1981 (H. Wolda; ROUB).

Epicharis (*Epicharoides*) *maculata* F. Smith

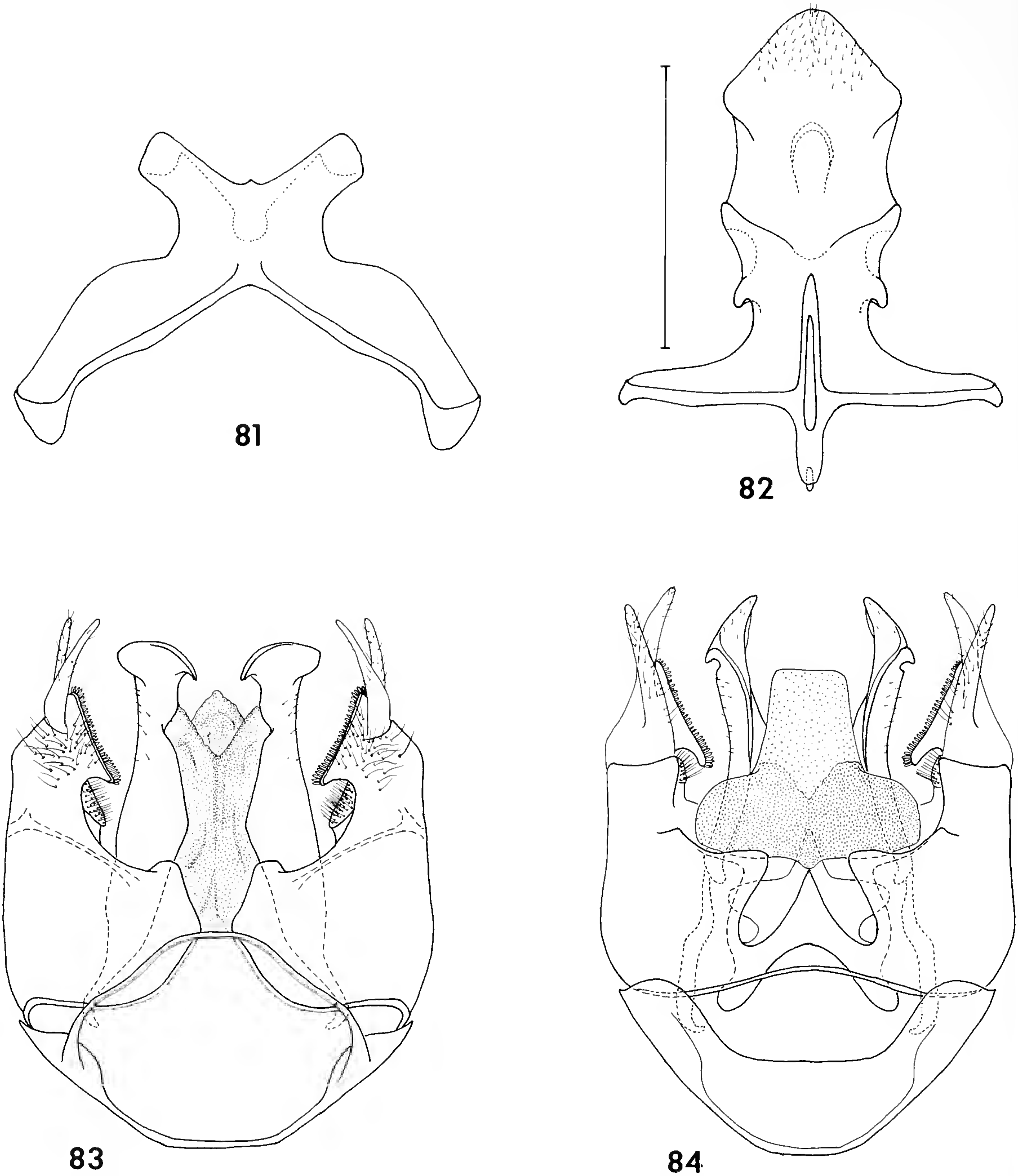
Figures 81–84

Epicharis maculata F. Smith, 1874:320. ♀.
Epicharoides bipunctatus Radoszkowski, 1884:20.
Centris (*Epicharis*) *variabilis* Friese, 1900b:351. (New name for *C. maculata* F. Smith, not *C. maculata* (Lepeletier.)
Epicharoides maculata: Moure, 1945a:310 (syn., distr.).
Epicharis (*Epicharoides*) *maculata:* Michener, 1954:145 (syn., distr.) (in part).

This species was described from Oaxaca, Mexico, and ranges south to Venezuela and Colombia. In Central America it is much more common than *E. albofasciata,* a primarily South American species.

NEW RECORDS

GUATEMALA: 1♀, Secanquim, June 1984 (USNM); 1♀, Quirigua, Aug. (Schaus and Barnes; USNM). MEXICO, *OAXACA:* 2♀♀, Salina Cruz, 10 Aug. 1964 (E. Fisher and D. Verity; LACM). *QUINTANA ROO:* 1♀, 3♂♂, 8–14 May 1963 (E.C. Welling; LACM). *SINALOA:* 1♀, 5 mi. N Mazatlan, 29 July 1973 (J.A. Chemsak, E.G. Linsley, A.E. and M.M. Michelbacher; UCB), on *Turnera diffusa. VERA CRUZ:* 5♀♀, Tecolutla, 19 June 1951 (P.D. Hurd; UCB). *YUCATÁN:* 1♀, Piste, July 1967 (E.C. Welling; LACM). COSTA RICA, *GUANACASTE:* 1♀, Liberia, 15–16 Feb. 1972 (P.A. Opler; UCB), on *Andira inermis*; 2♀♀, Finca La Pacifica, 4 km NW Cañas, 17–20 Nov. 1972 (P.A. Opler; UCB), on "pink malp.



Figures 81–84. *Epicharis* (*Epicharoides*) *maculata*, male seventh and eighth sternites and genitalia (ventral and dorsal views). Scale line = 1.00 mm.

vine"; 1♀, same except 30 Nov. 1972, on *Bixa orellana*; 11♂♂, Hacienda Comelco, 24 km NW Cañas, 13–14 Mar. 1971 (E.R. Heithaus; LACM), on *Securidaca tenuifolia*; 3♂♂, Hacienda Comelco, 8 km NW Bagaces, 28–31 Jan., 6 Mar. 1971 (P.A. Opler; UCB), on *Secridaca sylvestris*. *HEREDIA:* 10♀♀, 71♂♂, Finca La Selva, near Puerto Viejo, 25 Apr. to 19 June (D.R. Perry; LACM), on *Vochysia* sp. (5♂♂), *Byrsonima* sp. (5♀♀), *Dipteryx panamensis* (5♀♀, 60♂♂), *Dussia* sp. (3♂♂), and

Hymenolobium sp. (1♂). PANAMA, *PANAMÁ:* 2♂♂, Capira, Cerro Campana, 12 Aug. 1980 (D. Roubik; ROUB); 1♂, 15 km E Chepo, Llano Carti Rd., 22 Feb. 1980 (D. Roubik; ROUB).

Subgenus *Epicharitides* Moure

Epicharitides Moure, 1945a: 311. Type-species: "*Epicharitides cockerelli* (Friese, 1900)" = *Epicharis cockerelli* Friese, 1900a; original designation.

DESCRIPTION

Maxillary palp three-segmented, second segment broad, longer than first, third segment narrower and a little shorter than second; lateral ridges of clypeal disc strong; malar space distinct, but shorter than minimum thickness of first flagellar segment; frontal carina sharp but short, ending in front of anterior ocellus by much more than diameter of anterior ocellus; occipital margin compressed and ridge-like or crested; flagelliform occipital setae short and curved laterad before reaching anterior margin of mesoscutum; posterior margin of dorsal face of scutellum not impressed; metanotum wholly vertical, jugal lobe of posterior wing shorter than cubital cell and less than one-half as long as vannal lobe.

Female. Labrum without median ridge; outer face of mesobasitarsus with mixed long, coarse, simple setae and short, fine, long-plumose hairs on anterior half, posterior half with sparse long, coarse, simple setae only; secondary basitibial plate absen; metatibia no longer than metabasitarsus; gradulus of third and fourth terga, in middle, broadly deflected apicad and area on either side depressed and covered with dense mat of very short, plumose hairs; margins of pygidial plate, in dorsal view, nearly straight, apex narrowly truncate, disc depressed.

Male. Labrum without median ridge; first flagellar segment shorter than either scape or second flagellar segment; ocellocular distance greater than diameter of anterior ocellus; procoxa without apicoventral process; mesosternal tubercles absent; metatrochanter and metafemur without ventral seta patch; metatibia without posteroventral ridge; metabasitarsus without carinate ridge on anterior margin; pygidial plate less than one-half as wide as seventh tergite, margins sharp, apex narrowly truncate.

Moure (1945b) recognized five species in this subgenus and gave a key for their separation. Two additional species were described from Brazil by Moure and Seabra (1959). All the included species were known, at that time, only from South America, especially Brazil. One species is now known to occur in Central America.

Epicharis (*Epicharitides*) species

Two females from Cerro Campana, Panamá Province, Panama, 9 June 1960 (W.J. Hanson; UKAN) possibly represent an undescribed species. In the key to species of *Epicharitides* by Moure (1945b) they fail at couplet 7, failing to agree with the characteristics cited for either *E. obscura* Friese or *E. duckei* Friese. The abdomen is black ventrally as well as dorsally, there is a narrow transverse lateral stripe on each side of the dorsal face of the first tergum and the second tergum has a broad basal yellow band, slightly expanded on either side. The distal margin of this band is broadly curved inward, but in the middle of the segment, the band is one-half as long as the segment. The face is wholly black except for the yellow basal portion of the labrum and a minute median spot on the lower paraocular area.

These specimens may represent a previously undescribed species, but in the absence of associated males, no nomenclatural action is possible at this time.

These specimens differ from *E. duckei* in the color pattern of the abdominal terga. The first tergite bears a short, sublateral yellow stripe and the second is yellow across the entire base, with the distal one-third blackish, the yellow band a little shorter in the middle one-half. The remainder of the abdomen is blackish. Pubescence is wholly dark, except the pale scopa and some pale hairs around the pronotal lobe. Females of *E. obscura* agree with the Panamanian specimens in having the pubescence largely dark, but the first tergum is immaculate and the second to fourth or fifth terga are maculate only at the sides.

Superficially, these females resemble unusually dark individuals of *E. maculata,* but may be readily separated by the shorter jugal lobe of the hind wing, by the characteristic shape of the metabasitarsus and by the presence of the modified areas on the abdominal terga. These differences will also distinguish this bee from *E. albofasciata.*

SYNONYMIC LIST OF NORTH AND CENTRAL AMERICAN CENTRIDINI

Centris Fabricius

Subgenus *Xerocentris* Snelling, 1974. Type-species: *C. californica* Timberlake, 1940.

01. *californica* Timberlake, 1940. Calif., Nev.
02. *griseola* Snelling, n. sp. Mexico (Guerrero).
03. *hoffmanseggiae* Cockerell, 1897. N. Mex., Ariz., Calif.
    = davidsoni Cockerell, 1904.
04. *pallida* W. Fox, 1899. Southwestern U.S., northwestern Mexico.
    = callognatha Cockerell, 1923.
    = trichosoma Cockerell, 1923.
05. *rhodomelas* Timberlake, 1940. Calif.
06. *tiburonensis* Cockerell, 1923. Calif., Ariz., Son., B. Calif.
07. *vanduzeei* Cockerell, 1923. Mexico (B. Calif., B. Calif. Sur).

Subgenus *Paracentris* Cameron, 1902. Type-species: *C. fulvohirta* (Cameron, 1902).
    = Penthemisia Moure, 1950. Type-species: *C. chilensis* Spinola, 1851.
    = Trichocentris Snelling, 1956. Type-species: *C. rhodoleuca* Cockerell, 1923.
08. *angustifrons* Snelling, 1966. Ariz., Son.
09. *aterrima* F. Smith, 1854. Ariz. to central Mexico.
10. *atripes* Mocsáry, 1899. Southwestern U.S. to Costa Rica.
    = atriventris W. Fox, 1899.

= limbata Friese, 1899. N. SYN.
= Foxi Friese, 1900b.
11. *caesalpiniae* Cockerell, 1897. Tex. to Ariz., northern Mexico.
= morsei Cockerell, 1897.
= marginata W. Fox, 1899.
12. *cockerelli* W. Fox, 1899. Southwestern U.S., northern Mexico.
= resoluta Cockerell, 1923. N. SYN.
13. *ectypha* Snelling, 1974. B. Calif.
14. *ferrisi* Cockerell, 1924. B. Calif. Sur.
15. *fisheri* Snelling, 1974. B. Calif., B. Calif. Sur.
16. *harbisoni* Snelling, 1974. B. Calif.
17. *laevibullata* Snelling, 1966. Central Mexico.
18. *lanosa* Cresson, 1872. Fla. to Tex., Okla., Kans.
= subhyalina W. Fox, 1899.
= birkmanii Friese, 1900a.
19. *mexicana* F. Smith, 1854. Texas to Ariz., south to Oaxaca, Mexico.
20. *nigrocaerulea* F. Smith, 1874. Central Mexico to Panama.
= clypeata Friese, 1899. Preoccupied. N. SYN.
= anthracina Snelling, 1966. N. SYN.
21. *rhodopus* Cockerell, 1897. Southwestern U.S., northern Mexico.
= pulchrior Cockerell, 1900.
= rhodoleuca Cockerell, 1923.
22. *zacateca* Snelling, 1966. Ariz., N. Mex., central Mexico.

Subgenus *Xanthemisia* Moure, 1945b. Type-species: *C. bicolor* Lepeletier, 1841.
23. *carolae* Snelling, 1966. Mexico to Costa Rica.
24. *lutea* Friese, 1899. Central Mexico to Panama; South America.
25. *rubella* F. Smith, 1854. Panama; South America.

Subgenus *Exallocentris* Snelling, 1974. Type-species: *C. anomala* Snelling, 1966.
26. *anomala* Snelling, 1966. Central Mexico.

Subgenus *Acritocentris* Snelling, 1974. Type-species: *C. ruthannae* Snelling, 1966.
27. *agameta* Snelling, 1974. Northeastern and central Mexico.
28. *albiceps* Friese, 1899. Northeastern and central Mexico.
= strawi Snelling, 1966. N. SYN.
29. *ruthannae* Snelling, 1966. Ariz., Son.
30. *satana* Snelling, n. sp. Southern Arizona to central Mexico.

Subgenus *Centris* Fabricius, 1804. Type-species: *C. haemorrhoidalis* (Fabricius, 1775).
= Hemisia Klug, 1807. Type-species: *C. haemorrhoidalis* (Fabricius, 1775).
= Cyanocentris Friese, 1900b. Type-species: *C. versicolor* (Fabricius, 1775).
= Poecilocentris Friese, 1900b. Type-species: *C. fasciatella* Friese, 1900b.
31. *adanae* Cockerell, 1949. Southern Mexico to Panama.
32. *aethiocesta,* Snelling, n. sp. El Salvador to Panama.
33. *aethyctera* Snelling, 1974. Southern Mexico to Panama.
34. *decolorata* Lepeletier, 1841. Texas to Panama; Caribbean; northern South America.
= obscuriventris Friese, 1899?
35. *eisenii* W. Fox, 1899. Arizona to Panama.
36. *errans* W. Fox, 1899. Florida.
37. *flavifrons* (Fabricius, 1775) Central America; South America.
= brasiliana Christ, 1791.
= citrotaeniata Gribodo, 1894. N. SYN.
= nigritula Friese, 1899. N. SYN.
= rufescens Friese, 1899. N. SYN.
38. *flavofasciata* Friese, 1900a. Central America, northern South America.
39. *inermis* Friese, 1899. Central America, northern South America.
= segregata Crawford, 1906. N. SYN.
= gualanensis Cockerell, 1912.
= robusta Cockerell, 1949. N. SYN.
= pallidifrons Cockerell, 1949.
40. *meaculpa* Snelling, n. name. Eastern Mexico.
= erubescens Snelling, 1974. Preoccupied.
41. *obscurior* Michener, 1954. Southern Mexico to Panama.

Subgenus *Ptilocentris* Snelling, n. subg. Type-species: *C. festiva* F. Smith, 1854.
42. *festiva* F. Smith, 1854. Costa Rica to Venezuela and Peru.
= chlorura Cockerell, 1919. N. SYN.

Subgenus *Melanocentris* Friese, 1900b. Type-species: *C. atra* Friese, 1899.
43. *agilis* F. Smith, 1874. Mexico to Honduras.
= ignita F. Smith, 1874. N. SYN.
= bakeri Friese, 1912. N. SYN.
= bakerella Friese, 1913. N. SYN.
= Epicharis cisnerosi Cockerell, 1949. N. SYN.
44. *agiloides* Snelling, n. sp. Mexico to Costa Rica.
45. *flavilabris* Mocsáry, 1899. Costa Rica to South America.
= boliviensis Mocsáry, 1899.
46. *fusciventris* Mocsáry, 1899. Costa Rica to South America.
= scutellata Friese, 1900b. N. SYN.
47. *gelida* Snelling, n. sp. Mexico, Guatemala.
48. *obsoleta* Lepeletier, 1841. Mexico to South America.
= melanochlaena F. Smith, 1874. N. SYN.
= Epicharis zamoranensis Cockerell, 1949. N. SYN.
49. *plumipes* F. Smith, 1854. Costa Rica to South America.
50. *sericea* Friese, 1899. Central Mexico.

Subgenus *Trachina* Klug, 1810. Type-species: *C. longimana* Fabricius, 1804.
= Paremisia Moure, 1945b. Type-species: *C. lineolata* Lepeletier, 1841.
51. *dentata* F. Smith, 1854. Southern Mexico to South America.
= proxima Friese, 1900a.
52. *eurypatana* Snelling, n. sp. Mexico (Jalisco).
53. *fuscata* Lepeletier, 1841. Southern Mexico to South America.

54. *heithausi* Snelling, 1974. Guatemala to Costa Rica.
55. *labiata* Friese, 1904. Mexico to Costa Rica.
    = schwarzi Cockerell, 1919. N. SYN.
56. *longimana* Fabricius, 1804. Nicaragua to South America.
    = personata F. Smith, 1874.
57. *similis* (Fabricius, 1804). Costa Rica to northern South America.
    = lineolata Lepeletier, 1841.
58. *vidua* Mocsáry, 1899. Belize to Panama.
59. *xochipillii* Snelling, n. sp. Mexico (Oaxaca).

Subgenus *Hemisiella* Moure, 1945b. Type-species: *C. lanipes* (Fabricius, 1775).

60. *dichrootricha* Moure, 1945b. Panama; South America.
61. *nitida* F. Smith, 1874. Mexico to Panama; northern South America.
    = confinis Pérez, 1905. N. SYN.
62. *transversa* Pérez, 1905.
    = ruae Cockerell, 1949. N. SYN.
63. *trigonoides* Lepeletier, 1841. Southern Mexico to South America.
    = dentipes F. Smith, 1874. N. SYN.
    = hoplopoda Moure, 1943.
    = rufomaculata Cockerell, 1949. N. SYN.
    = subtarsata Cockerell, 1949. N. SYN.
64. *vittata* Lepeletier, 1841. Mexico to South America.
    = montezuma Cresson, 1879.
    = breviceps Friese, 1899.
    = friesei Crawford, 1906. Preoccupied.
    = costaricensis Crawford, 1907.
    = erubescens Friese, 1925. N. SYN.

Subgenus *Heterocentris* Cockerell, 1899. Type-species: *C. cornuta* Cresson, 1865.

65. *analis* (Fabricius, 1804). Mexico to South America.
    = totonaca Cresson, 1879.
    = otomita Cresson, 1879.
    = minuta Mocsáry, 1899.
    = simplex Friese, 1899.
    = durantae Cockerell, 1949.
    = petreae Cockerell, 1949.
    = petreae var. rufopicta Cockerell, 1949.
66. *bicornuta* Mocsáry, 1899. Mexico to South America.
67. *difformis* F. Smith, 1854. Costa Rica; South America.
68. *labrosa* Friese, 1899. Costa Rica to South America.
    = triangulifera Cockerell, 1949. N. SYN.

Ptilotopus Klug

Ptilotopus Klug, 1810. Type-species: *P. americanus* Klug, 1810.

69. *zonatus* Mocsáry, 1899. Panama.
    = pandora Friese, 1900b.

Epicharis Klug

Subgenus *Epicharana* Michener, 1954. Type-species: *E. rustica* (Olivier, 1789).

70. *angulosa* Snelling, n. sp. Costa Rica.
71. *bova* Snelling, n. sp. Costa Rica, Panama.
72. *elegans* F. Smith, 1861. Mexico to Costa Rica.
    = salazari Cockerell, 1949. N. SYN.
73. *rustica* (Olivier, 1789). Costa Rica to South America.
    = flava Friese, 1900b. N. SYN.

Subgenus *Hoplepicharis* Moure, 1945a. Type-species: *E. fasciata* Lepeletier and Serville, 1828.

74. *lunulata* Mocsáry, 1899. Mexico to Panama.
75. *monozona* Mocsáry, 1899. Panama.

Subgenus *Parepicharis* Moure, 1945a. Type-species: *E. zonata* F. Smith, 1854.

76. *metatarsalis* Friese, 1899. Costa Rica to Venezuela.
    = phenacura Cockerell, 1917. N. SYN.
    = conura Cockerell, 1917. N. SYN.

Subgenus *Epicharoides* Radoszkowski, 1884. Type-species: *E. maculata* F. Smith, 1874.

77. *albofasciata* F. Smith, 1874. Costa Rica to South America.
    = nigroclypeata Friese, 1899.
78. *maculata* F. Smith, 1874. Mexico to northern South America.
    = bipunctatus Radoszkowski, 1884.
    = variabilis Friese, 1900b.

Subgenus *Epicharitides* Moure, 1945a. Type-species: *E. cockerelli* Friese, 1900a.

79. undetermined species near *obscura* Friese. Panama.

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LITERATURE CITED

Alcock, J., C.E. Jones, and S.L. Buchmann. 1976. Location before emergence of the female bee, *Centris pallida*, by its male (Hymenoptera: Anthophoridae). Journal of Zoology 179:189–199.

———. 1977. Male mating strategies in the bee *Centris pallida* Fox (Anthophoridae: Hymenoptera). The American Naturalist 111:145–155.

Cameron, P. 1903. Descriptions of new species of Hymenoptera taken by Mr. Edward Whymper on the "Higher Andes of the Equator." Transactions, American Entomological Society, 29:225–238.

Cheesman, L.E. 1929. Hymenoptera collected on the "St. George" expedition in Central America and the W. Indies. Transactions, Entomological Society of London 77: 141–154.

Cockerell, T.D.A. 1899. Note on the nomenclature of some Hymenoptera. The Entomologist 32:14.

———. 1906. The North American bees of the family Anthophoridae. Transactions, American Entomological Society 32:63–116.

———. 1912. New bees from Brazil. Psyche 19:41–61.

———. 1917. New bees from Costa Rica (Hym.). Entomological News 28:200–201.

———. 1919. Bees in the collection of the United States National Museum.—3. Proceedings, United States National Museum 55:167–221.

———. 1923. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The Bees (I). Proceedings, California Academy of Sciences (ser. 4) 12: 73–103.

———. 1924. Anthophorid bees in the collection of the California Academy of Sciences. Pan-Pacific Entomologist 1:49–56.

———. 1949. Bees from Central America, principally Honduras. Proceedings, United States National Museum 98: 429–490.

Coville, R.E., G.W. Frankie, and S.B. Vinson. 1983. Nests of *Centris segregata* (Hymenoptera: Anthophoridae) with a review of the nesting habits of the genus. Journal, Kansas Entomological Society 56:109–122.

Crawford, J.C. 1906. Some Costa Rican bees. Transactions, American Entomological Society 32:157–163.

———. 1907. Preoccupied names of bees. Canadian Entomologist 39:21.

Cresson, E.T. 1865. On the Hymenoptera of Cuba. Proceedings, Entomological Society of Philadelphia 4:1–200.

———. 1872. Hymenoptera Texana. Transactions, American Entomological Society 4:153–292.

———. 1879. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. Transactions, American Entomological Society 7:201–214.

Ducke, A. 1902. Beobachtungen über Blutenbesuch, Erscheinungszeit etc. der bei Para vorkommenden Bienen. Allegemeine Zeitschrift für Entomologie 7:321–325, 360–367, 400–404, 417–421.

———. 1907. Contribution à la connaissance de la fauna hyménoptérologique du nord-est du Brésil. Revue d'Entomologie, Caen 26:73–76.

Fabricius, I.C. 1775. Systema entomologie. Flensburg and Leipzig, xxx + 832 pp.

———. 1793. Entomologia systematica emendata et aucta. Copenhagen, viii + 519 pp.

———. 1804. Systema Piezatorum. Braunschweig, 439 + 30 pp.

Fox, W.J. 1899. Synopsis of the United States species of the hymenopterous genus *Centris* Fabr. with description of a new species from Trinidad. Proceedings, Academy of Natural Sciences of Philadelphia 51:63–70.

Friese, H. 1899. Neue Arten der Bienengattungen *Epicharis* Klug und *Centris* Fabr. Természetrajzi Füzetek 22:39–48.

———. 1900a. Neue Arten der Bienengattungen *Centris* und *Epicharis*. Természetrajzi Füzetek 23:117–122.

———. 1900b. Monographie der Bienengattung *Centris* (s. lat.). Annalen, K.K. Naturhistorische Hofmuseums, Wien 14:237–350.

———. 1904. Nachtrag zur Monographie du Bienengattung *Centris*. Annales Musei nationalis Hungarici 2: 90–92.

———. 1912. Neue und wenig bekannte Bienenarten der neotropischen Region. Archiv für Naturgeschichte 78(6): 198–226.

———. 1913. Über einige neue Apiden. Archiv für Naturgeschichte 78(12):85–89.

———. 1925. Neue neotropische Bienenarten, zuglich II. Nachtrag zur Bienenfauna von Costa Rica (Hym.). Stettiner Entomologische Zeitung 86:1–41.

Gribodo, G. 1894. Note imenotterologiche. Nota II, continuazione. Bolletino, Società Entomologica Italiana 26: 262–312.

Harris, R.A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, California Department of Food and Agriculture, 28, 31 pp.

Hurd, P.D., Jr. 1979. *In* K.V. Krombein et al. Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution, Washington 2:xvi + 2209 pp.

International Commission of Zoological Nomenclature. 1959. Opinion 567. (*Centris* placed on Official List of Generic Names in Zoology.)

Klug, J.C.F. 1807. Vergleichung der Gattungen der Hautflugler Piezata Fabr. Hymenoptera Linn. Jur. Magazin für Insektenkunde 6:189–199.

———. 1810. Einige neue Piezatengattungen. Magazin Gesellschaft Naturforschender Freunde zu Berlin 4:31–45.

Latreille, P.A. 1810. Considérations générales . . . des insectes. Paris, 444 pp.

Lepeletier de Saint-Fargeau, A. 1841. Histoire naturelle des insectes, hyménoptères. Paris, 2:1–680.

Lepeletier de Saint-Fargeau, A., and A. Serville. 1842. *In* P. A. Latreille, Encyclopédie méthodique. Histoire naturelle, Entomologie. Paris.

Lutz, F.E., and T.D.A. Cockerell. 1920. Notes on the distribution and bibliography of North America bees of the families Apidae, Meliponidae, Bombidae, Englossidae and Anthophoridae. Bulletin, American Museum of Natural History 42:491–641.

Michener, C.D. 1944. Comparative external morphology, phylogeny and a classification of the bees (Hymenoptera). Bulletin, American Museum of Natural History 82:151–326.

———. 1951. Subgeneric groups of *Hemisia* (Hymenoptera, Apoidea). Journal, Kansas Entomological Society 24:1–11.

———. 1954. Bees of Panamá. Bulletin, American Museum of Natural History 104:1–176.

———. 1965. A classification of the bees of the Australian and South Pacific Regions. Bulletin, American Museum of Natural History 130:1–362.

Mitchell, T.B. 1962. Bees of the eastern United States. Technical Bulletin, North Carolina Agricultural Experiment Station, 152, 557 pp.

Mocsáry, A. 1898. Species novae generum: *Euglossa* Latr. et *Epicharis* Klug. Természetrajzi Füzetek 21:497–500.

———. 1899. Species novae generis *Centris* Fabr. Természetrajzi Füzetek 22:251–255.

Moure, J.S. 1943. Abelhas de Batatais (Hym., Apoidea). Arquivas, Museo do paranaense, Curitiba 3:145–203.

———. 1945a. Notas sôbre as Epicharitina (Hymenop., Apoidea). Revista de Entomologia 16:293–314.

———. 1945b. Apoidea da Coleção de Conde Amadeu A. Barbiellini. II (Hym. Apoidea). Revista de Entomologia, 16:394–414.

———. 1950. Alguns agrupamentos novos de abelhas Neotropicais. Dusênia 1:385–394.

———. 1960a. Abelhas da Região Neotropical descritas por G. Gribodo (Hymenoptera-Apoidea). Boletim, Universidade do Parana 1:1–18.

———. 1960b. Notes on the types of the Neotropical bees described by Fabricius (Hymenoptera: Apoidea). Studia Entomologia 3:97–160.

Moure, J.S., and C.A.C. Seabra. 1959. Notas sôbre abelhas do gênero *Epicharis* (Hym., Apoidea). Studia Entomologia 2:119–127.

Neff, J.L., and B.B. Simpson. 1981. Oil-collecting structures in the Anthophoridae (Hymenoptera): morphology, function, and use in systematics. Journal, Kansas Entomological Society 54:95–123.

Olivier, G.A. 1789. Encyclopédie Méthodique, histoire naturelle . . . Insectes. Paris and Liege, 4:cclxxxviij + ccclxxiij + 331 pp.

Pérez, J. 1905. Hyménoptères nouveaux du Mexique. Bulletin, Museum d'Histoire Naturelle, Paris 11:39–41.

Radoszkowski, O. 1884. Quelques nouveaux Hyménoptères d'Amérique. Horae Societe Entomologique Rossicae 18:17–22.

Sandhouse, G.A. 1943. The type species of the genera and subgenera of bees. Proceedings, United States National Museum 92:519–619.

Schwarz, H.F. 1934. The solitary bees of Barro Colorado Island, Canal Zone. American Museum Novitates 722: 1–24.

Smith, F. 1854. Catalogue of Hymenopterous insects in the collection of the British Museum. II, Apidae. British Museum, London, 465 pp.

———. 1861. Descriptions of new genera and species of exotic Hymenoptera. Journal of Entomology 1:146–155.

———. 1874. A revision of the genera *Epicharis*, *Centris*, *Eulaema*, and *Euglossa* belonging to the family Apidae, section Scopulipedes. Annals and Magazine of Natural History (ser. 4) 13:357–373.

Snelling, R.R. 1956. Bees of the genus *Centris* in California (Hymenoptera: Anthophoridae). Pan-Pacific Entomologist 32:1–8.

———. 1966. The taxonomy and nomenclature of some North American bees of the genus *Centris* with description of new species (Hymenoptera: Anthophoridae). Los Angeles County Museum Contributions in Science 112: 1–33.

———. 1974. Notes on the distribution and taxonomy of some North American *Centris* (Hymenoptera: Anthophoridae). Contributions in Science, Los Angeles County Museum of Natural History 259:1–41.

———. 1980. New bees of the genus *Hylaeus* from Sri Lanka and India (Hymenoptera: Colletidae). Contributions in Science, Los Angeles County Museum of Natural History 328:1–18.

Timberlake, P.H. 1940. The genus *Centris* in California (Hymenoptera, Apoidea). Pan-Pacific Entomologist 16: 138–141.

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Number 348
18 April 1984

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SALAMANDERS OF THE NORTHWESTERN HIGHLANDS OF GUATEMALA

Paul Elias[1]

ABSTRACT. The salamander faunas of the Cordillera de los Cuchumatanes and the Montañas de Cuilco of western Guatemala are reviewed in light of extensive new collections. Thirteen species are reported from the Cuchumatanes including one new member of the *Bolitoglossa mexicana* species group, herein described as *Bolitoglossa jacksoni* sp. nov., and four recognized species never before collected in the massif (*Bolitoglossa hartwegi, B. mulleri, B. rufescens* and *Dendrotriton rabbi*). Four species are reported from the Cuilco including two hitherto unknown from that mountain range (*Bolitoglossa morio* and *Pseudoeurycea rex*).

Bolitoglossa resplendens (*sensu lato*) lacks the features purported to differentiate it from *B. lincolni* and is considered a junior synonym. Based on gross morphological similarity, the *Bolitoglossa helmrichi* and *B. rostrata* species groups are divided and reconstituted into four species groups (*dunni, franklini, morio* and *veracrucis* groups).

The Cuchumatanes support fewer salamander species but a larger number of species groups and genera than do the Pacific Uplands. The diversity differences are correlated with greater age and connectedness among high elevation salamander habitats in the Cuchumatanes relative to the Pacific Uplands.

Salamander species on the Cuchumatanes and Cuilco occur in narrow elevational belts as they do on the Pacific Uplands. Conspecific populations or related species tend to occur at comparable elevations wherever found. Within-group variation in elevational range does exist, however, and much of it is correlated with geographic variation in the elevation of the cloud line. The *Bolitoglossa veracrucis* species group is exceptional among Nuclear Central American salamander groups in the extreme breadth of the combined elevational ranges of its three member species (2,800 m; the next broadest is 1,200 m). The great ecological scope of the *Bolitoglossa veracrucis* group may have been a crucial factor in the invasion of the lowlands by *Bolitoglossa* beta.

RESUMEN. Las faunas de salamandras de la Cordillera de los Cuchumatanes y de las Montañas de Cuilco en el oeste de Guatemala se revisan en base a las extensas nuevas colecciones realizadas. Trece especies se encuentran en los Cuchumatanes, incluyendo una nueva especie, *Bolitoglossa jacksoni,* miembro del grupo específico de *Bolitoglossa mexicana,* y cuatro especies ya descritas pero nunca encontradas en esta sierra previamente (*Bolitoglossa hartweig, B. mulleri, B. rufescens* y *Dendrotriton rabbi*). Cuatro especies se encuentran en el Cuilco incluyendo dos anteriormente desconocidas en esta región (*Bolitoglossa morio* y *Pseudoeurycea rex*).

Bolitoglossa resplendens (*sensu lato*) no tiene las características que supuestamente la diferencian de la *B. lincolni,* y consecuentemente *B. resplendens* es un sinónimo. En base de similaridades en morfología externa, los grupos específicos de *Bolitoglossa helmrichi* y *B. rostrata* descritos por Wake y Lynch (1976) son divididos y redefinidos en cuatro grupos (*dunni, franklini, morio* y *veracrucis*).

En los Cuchumatanes habitan menos especies de salamandras pero un número mayor de grupos específicos y géneros, en comparación con las montañas del lado Pacífico. Estas diferencias de diversidad están correlacionadas con una edad geológica mayor y con una mayor conexión entre regiones de alta elevación en comparación con las montañas del lado Pacífico.

Las especies de urodelos en los Cuchumatanes y el Cuilco se localizan en estrechas bandas elevacionales al igual que en las montañas del Pacífico. Poblaciones de la misma especie, o especies relacionadas, generalmente se encuentran en la misma zona elevacional. Pero, si se encuentra variación al nivel de intra-grupo, la mayor parte de esta variación está correlacionada con la variación geográfica a la altura de la zona nublada. El grupo específico de *Bolitoglossa veracrucis* es una excepción entre todos los grupos de Centro America Nuclear debido a la extrema distribución elevacionál de las tres especies miembros (2,800 m); la segunda distribución mas amplia es 1,200 m. El gran alcance geológico de este grupo puede tener un papel importante en la historia de la invasión de las tierras bajas por *Bolitoglossa* beta.

INTRODUCTION

Nuclear Central America (NCA), the landmass bounded to the northwest by the Isthmus of Tehuantepec and to the southeast by the Nicaraguan depression, contains six major highland masses isolated from one another by deep dry valleys (Fig. 1). The Cordillera de los Cuchumatanes and the Montañas de Cuilco are two limestone capped ranges, respectively about 3,000 and 400 square kilometers in extent and 4,000 and 3,400 meters at greatest elevation (Fig. 2).

On the Caribbean slope of the Cuchumatanes, tropical rain forest (following the ecological terminology of Schmidt, 1936) extends from near sea level to a 1,300 m "cloud line" (that characteristic elevation at which the water carried by rising

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[1] Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.

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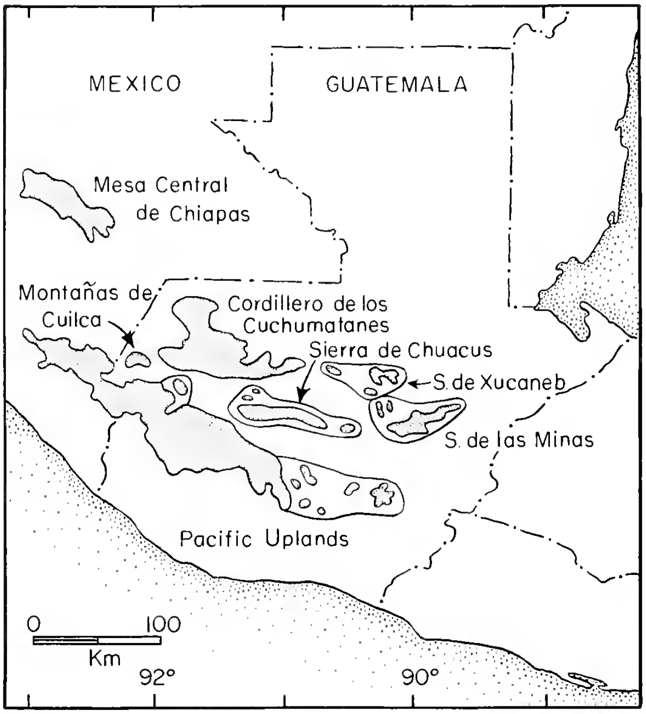

Figure 1. Nuclear Central America. The 2,100-m contour interval is stippled.

humid air condenses in the form of fog). Above the cloud line is a zone of extremely wet broadleaf and treefern forest, the subtropical zone cloud forest, which grades upward into drier but still humid subtropical forest that is frequently composed of oak. At about 2,700 m, varying locally, the pine and cypress temperate zone forests commence, continuing to the 3,400-m treeline, above which bunchgrass predominates.

The above vegetational series is found on the unobstructed face of the Caribbean slope; but, in the protected interior valleys, variably drier systems occur, typically dominated by pine-oak forest even at low elevation. Because of their protected position, the Montañas de Cuilco have an abbreviated form of the ecological pattern found on the open escarpment: as in the Cuchumatanes, pine and cypress dominate down to about 2,700 m, where a wet broadleaf forest begins; however, a high cloud line occurs at about 2,000 m, and dry scrubby pine-oak growth predominates below this level.

The salamander faunas of the Cordillera de los Cuchumatanes and the Montañas de Cuilco of western Guatemala have been little sampled or reported upon. In the Cuchumatanes Stuart (1943a, 1943b) made the first collections and reported four species referred to *Oedipus*: *lincolni, cuchumatanus, rostratus,* and *rex.* From later collections Stuart (1952) described *Magnadigita omniumsanctorum.* The next discovery in the Cuchumatanes was recorded by Lynch and

Figure 2. Montañas de Cuilco and the Cordillera de los Cuchumatanes with the 2,100-m contour interval and regional landmarks.

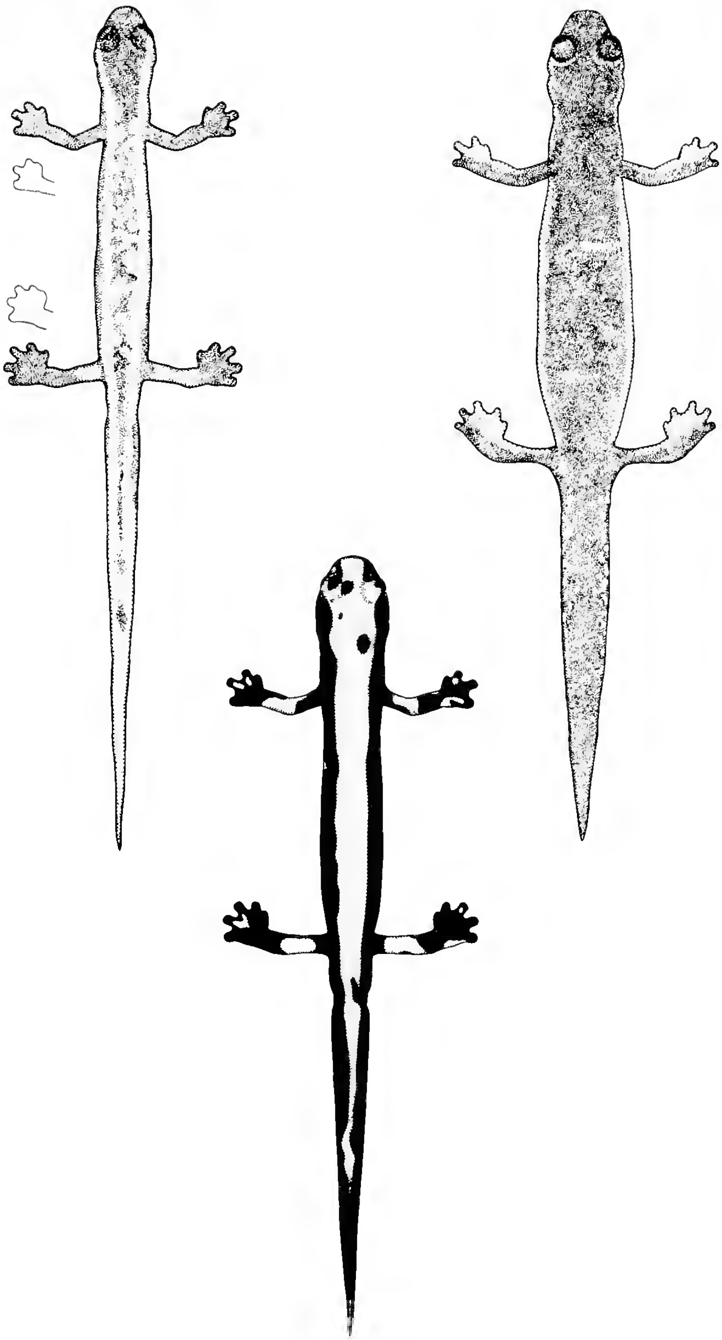

Figure 3. *Bolitoglossa rostrata, B. cuchumatana, B. morio,* and *B. lincolni,* life size. UPPER LEFT: *Bolitoglossa rostrata,* body, legs, and flanks dark brown, bilateral shoulder stripes lighter brown with middorsal brown mottling. A unicolor brown morph also is found. UPPER LEFT INSET: Feet of *B. cuchumatana.* Overall coloration like that of *B. rostrata.* UPPER RIGHT: *B. morio,* dark slate grey all over except for light speckling on flanks and anterior surfaces of limbs, and light lateral spotting on tail (Cuilco specimen figured; Cuchumatan specimens have light spotting on flanks as well as tail). BOTTOM CENTER: *B. lincolni,* black ground color with a coral red dorsal swath and spotting on limbs and (occasionally) venter. In some specimens, the dorsal swath is reduced to a series of red spots.

Wake (1975) with the naming of *Chiropterotriton cuchumatanus.* Finally, Elias and Wake (1983) and Wake and Elias (1983) named two new monotypic genera, *Nyctanolis pernix* and *Bradytriton silus,* both from the cordillera.

Prior to the present study the only salamanders that had been collected in the Montañas de Cuilco were *Bolitoglossa resplendens* (*sensu lato*) and *Chiropterotriton rabbi,* both first reported by Lynch and Wake (1975).

Bolitoglossa stuarti was described from the valley separating the Cuilco from the Cuchumatanes (Wake and Brame,

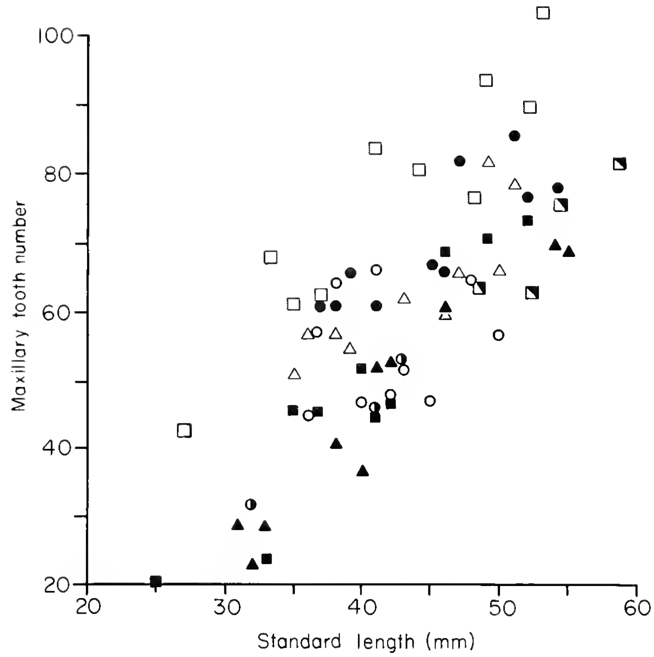

Figure 4. Relationship between maxillary tooth number (both sides summed) and standard length in the *Bolitoglossa dunni* complex. Solid triangle = *B. cuchumatana* (Eastern Cuchumatanes); open triangle = *B. cuchumatana* (Western Cuchumatanes); half-filled circle = *B. helmrichi* (Chuacús); solid circle = *B. helmrichi* (Western Minas); open circle = *B. helmrichi* (Xucaneb); solid square = *B. engelhardti* (Pacific Uplands); open square = *B.* sp. (Eastern Cuchumatanes); half-filled square = *B. dunni* (Honduras).

1969) and is the only salamander species known from the valley. As a low elevation form this species will be mentioned only in the discussion.

In the course of the present study twelve salamander species were documented for the Cuchumatanes, bringing the total number of known forms from six to thirteen for the mountain range. Among the seven species previously unknown from the massif were the two new monotypic genera described elsewhere (Elias and Wake, 1983; Wake and Elias, 1983) and the one new member of the *Bolitoglossa mexicana* species group described below. Four species were taken in the Montañas de Cuilco during this work. All of these were recognized forms, but two were previously unknown from those mountains.

This paper provides a species account for each of the salamander species now known from the Cuchumatanes and Cuilco, including taxonomic synonymies, type locality, geographic range, habits and habitat preferences and a discussion of the geographic variation and possible evolutionary relationships of the taxon. The discussion section is divided into three parts. In the first part, the species groups within *Bolitoglossa* beta (*sensu* Wake and Lynch, 1976) are redefined. In the second part, contemporary patterns of distribution and differentiation are examined to provide insight into the history of the salamander fauna. In the third part, patterns of elevational distribution are presented for the Cuchumatanes and Cuilco and are discussed relative to the results of Wake and Lynch (1976) for the Pacific Uplands.

SPECIES ACCOUNTS

Bolitoglossa cuchumatana (Stuart, 1943)

Figure 3

Oedipus cuchumatanus Stuart, 1943a:14.
Magnadigita cuchumatana: Taylor, 1944:218.
Bolitoglossa cuchumatana: Wake and Brame, 1963:386.

TYPE LOCALITY. Oak woods 2 km N Nebaj, Depto. Quiché, Guatemala, 1,900 m elevation.

RANGE. Stuart collected this form only at the type locality. Wake, Houck, and Lynch next found the species 25 years later about 15 km to the south and 600 m higher in elevation. I found *B. cuchumatana* at two additional sites in the western Cuchumatanes near Chiapas and at the easternmost end of the range, near San Miguel Uspantán.

HABITAT AND HABITS. *B. cuchumatana* have been taken on the ground, under bark, and in arboreal bromeliads where they have been found active on surface debris on wet evenings from the 1,200-m cloud line through the subtropical cloud forest to 2,500 m.

SYSTEMATICS. A series of species, including *Bolitoglossa engelhardti* in the Pacific Uplands, *B. helmrichi* in the Xucaneb and Western Minas, a newly discovered population (possibly representing a new species) in the Eastern Minas, *B. cuchumatana* in the Cuchumatanes, and *B. dunni* in Hon-

Table 1. Geographic variation in subcaudal coloration and degree of interdigital webbing among the species of the *Boltioglossa dunni* complex.

Species and population	Subcaudal coloration	Degree of interdigital webbing
B. helmrichi (Chuacus)	no data	high
B. helmrichi (Xucaneb)	orange	high
B. helmrichi (Western Minas)	orange	high
B. sp. (Eastern Minas)	tan	low
B. cuchumatana (Western Cuchumatanes)	tan	medium
B. cuchumatana (Eastern Cuchumatanes)	tan	medium
B. engelhardti (Pacific Uplands)	tan	medium
B. dunni (Honduras)	no data	medium

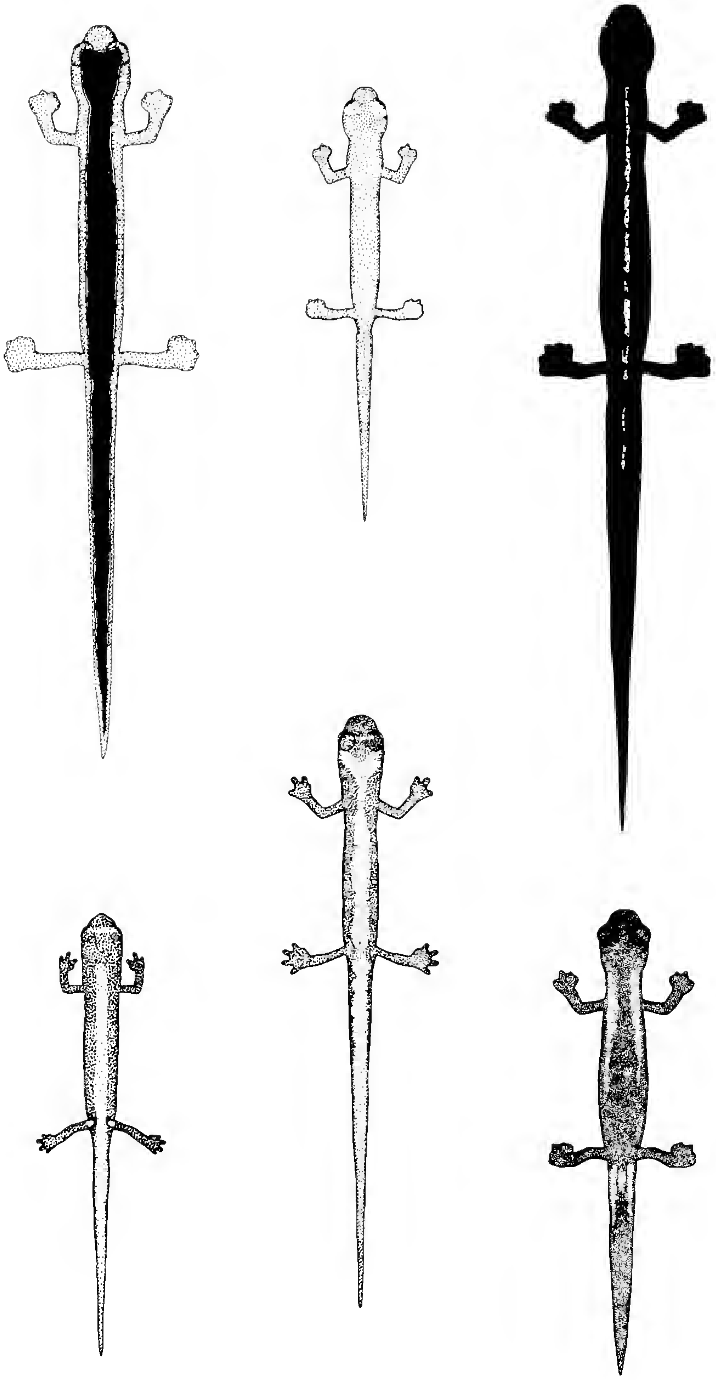

Figure 5. *Bolitoglossa jacksoni, B. rufescens, B. mulleri, Dendrotriton rabbi, D. cuchumatanus,* and *Bolitoglossa hartwegi,* life size. UPPER LEFT: *Bolitoglossa jacksoni* (holotype figured), background yolky yellow, middorsal swath dark brown with narrow white border. TOP CENTER: *B. rufescens,* tan overall with a slightly darker brown snout and flanks. Tone varies from light to dark brown both between individuals and for one individual at different times of day. UPPER RIGHT: *B. mulleri,* black overall except for a narrow broken vertebral stripe of tan. In some Cuchumatan specimens, the stripe is reduced or absent. LOWER LEFT: *Dendrotriton rabbi,* pattern composed of various shades of brown. Note light interorbital bar. Animals may have a reddish or even greenish cast. Pattern and tone variable between individuals. BOTTOM CENTER: *D. cuchumatanus,* similar to *D. rabbi* above. LOWER RIGHT: *Bolitoglossa hartwegi,* dark brown overall with lighter paired shoulder and pelvic stripes. Animals may be without markings altogether or may have small light streaks on dorsum at random.

Figure 6. *Bolitoglossa jacksoni* sp. nov., an adult female (escaped) from the type locality.

duras, appears to form a relatively homogeneous assemblage of related congeners. The group, which I shall call the *dunni* complex, was first outlined by Stuart (1943a) and is characterized by a moderate degree of foot webbing; by well-developed subdigital pads and the associated hypertrophy of the terminal phalanges; by a generally brown dorsal color frequently differentiated into light shoulder stripes and darker flanks; and by a common microhabitat (see Wake and Lynch, 1976, for information on the ecology of *B. engelhardti*).

The species in this series are most similar to *Bolitoglossa rostrata,* but differences in foot morphology (*B. rostrata* has little interdigital webbing) usually permit separation (see *B. rostrata* and compare inset *B. cuchumatana* feet, Fig. 3). *B. rostrata* occurs in limited sympatry with *B. cuchumatana* with no hybridization.

Despite the general similarities, variation between the species of the *B. dunni* complex is pronounced in the coloration of the subcaudal surface, the number of maxillary teeth, and the morphology of the foot. Data were collected for eight populations from the five *B. dunni* complex species (Fig. 4, Table 1). *B. helmrichi* can be defined on the basis of its high degree of interdigital webbing and orange subcaudal coloration to include populations in the Xucaneb, the Western Minas, and the Chuacús. *B. cuchumatana,* including all Cuchumatan specimens, and *B. engelhardti* are similar in their intermediate degree of interdigital webbing, tan subcaudal surface, and moderate tooth number, and are distinguishable from one another both on the basis of adult size (*B. engelhardti* is smaller than any other member of the complex) and in frequency of shoulder striping (*B. engelhardti* is usually unmarked, while *B. cuchumatana* almost always has bilateral light striping). *Bolitoglossa dunni* occurs in both a pink and dark morph, the latter with light spotting (Schmidt, 1933), and it achieves larger size than any other member of the complex and has little webbing and low tooth numbers. The population from the Eastern Minas differs sharply from all other members of the *B. dunni* complex (and from all known *B. rostrata* populations as well) in having extremely high numbers of maxillary teeth. It has almost as little webbing as *B. rostrata.* That this population belongs in the *B. dunni* complex rather than to *B. rostrata* is suggested only by its occurrence at relatively low elevation.

Bolitoglossa hartwegi Wake and Brame, 1969

Figure 5

Bolitoglossa hartwegi Wake and Brame, 1969:10.

TYPE LOCALITY. 4.5 mi. W San Cristobal de Las Casas, Chiapas, Mexico. 7,000 ft elevation.

RANGE. *B. hartwegi* has been known only from the general vicinity of its type locality on the Mesa Central de Chiapas. It is here reported from Guatemala, both in the western Cuchumatanes at Finca Chiblac, and in the easternmost reaches of the range, near San Miguel Uspantán.

HABITAT AND HABITS. Specimens have been collected under bark on logs and stumps, under cover objects on the ground, in rock crevices, and in arboreal bromeliads; the species is active on rainy nights. *B. hartwegi* have a broad elevational range, occurring from the 1,200-m cloud line to the lower temperate forest at over 2,700 m.

SYSTEMATICS. When these populations were discovered in the Cuchumatanes during this study they were assigned to the *Bolitoglossa veracrucis* species group (see Discussion) based upon their well-ossified skull with a broad pars dentalis of the premaxillary, and a derived foot morphology. They were assigned to the species *B. hartwegi* based on a mainly unicolor dorsum (*B. veracrucis* is streaked and mottled), a small size (*B. stuarti* is larger), and a mottled venter (unicolor in *B. stuarti*).

Bolitoglossa jacksoni new species

Figures 5 and 6

HOLOTYPE. MVZ 134634, a young adult female from the Las Nubes sector of Finca Chiblac, approximately 12 km NNE of Santa Cruz Barillas, Depto. Huehuetenango, Guatemala, at about 1,400 m elevation, collected by Jeremy L. Jackson, 1 September 1975.

DIAGNOSIS. The new taxon is a large species of *Bolitoglossa* (the young adult holotype is 49.1 mm and another specimen was approximately 65 mm in standard length) with low numbers of maxillary teeth (31 in the holotype) and moderate numbers of vomerine teeth (21 in the holotype). The species is a member of the *Bolitoglossa* alpha group on the basis of its simple vertebral tail autotomy mechanism (Wake and Dresner, 1967; Wake and Lynch, 1976). It is distinguished from *B. salvinii, B. mexicana, B. mulleri, B. odonnelli, B. platydactyla,* and *B. flaviventris* in having dark coloration restricted to the middorsal region; separated from all other Nuclear Central American *Bolitoglossa* both by color pattern and its tail autotomy mechanism.

DESCRIPTION (OF HOLOTYPE). Nostril small; labial protuberances of nasolabial grooves small and poorly developed; canthus rostralis moderate in length, rounded and gently arched. Standard length 6.6 times head width; standard length 4.5 times snout-gular fold length (head length). Deep, unpigmented groove below eye extends almost full length of opening, following curvature of eye, but does not extend to lip. Eye moderate in size, slightly protuberant in life. Lightly indicated postorbital groove extends posteriad and slightly ventrad as a shallow depression for 2.7 mm, thence proceeds directly ventrad and passes behind posterior end of mandible to produce a shallow but definite nuchal groove parallel to and 4.0 mm anterior to the clearly defined gular fold. The 21 vomerine teeth are arranged in single arched rows on either side of the midline and extend laterally to the level of the midpoint of the internal nares. The two rows of 31 maxillary teeth extend posteriad to a level one-third of the way through the eye. Five small undifferentiated premaxillary teeth protrude from well behind the lip. The tail is round in cross section and is 0.8 times the standard length from base to tip; the postiliac gland is not evident. Limbs are of moderate length, three costal grooves are exposed between the toetips of the adpressed fore and hind limbs; standard length is 4.4 times right hind limb length and 4.9 times right fore limb length. Standard length is 10.0 times the hind foot width and both fore and hind feet are fully webbed and lack subdigital pads; the toetips are rounded in dorsal aspect. The fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

MEASUREMENTS (OF HOLOTYPE). Head width (maximum), 7.4 mm; head length (snout to gular fold), 11.0 mm; head depth at posterior angle of jaw, 4.1 mm; eyelid length, 3.0 mm; eyelid width, 1.9 mm; anterior rim of orbit to snout, 2.6 mm; horizontal orbital diameter, 2.2 mm; interorbital distance, 3.0 mm; distance between vomerine teeth and parasphenoid tooth patch, 0.3 mm; snout to fore limb, 13.6 mm; distance separating internal nares, 2.2 mm; distance separating external nares, 2.1 mm; snout projection beyond mandible, 0.6 mm; snout to posterior angle of vent (standard length), 49.1 mm; snout to anterior angle of vent, 45.6 mm; axilla to groin, 27.4 mm; tail length, 43.4 mm; tail width at base, 3.7 mm; tail depth at base, 3.3 mm; fore limb length, 10.0 mm; hind limb length, 11.2 mm; width of hand, 3.7 mm; width of foot, 4.9 mm.

COLORATION IN ALCOHOL. The ground color is pale yellow with a broad middorsal swath of dark brown. The brown marking originates on the head at the level of the eyelids and extends in breadth from the center of one eyelid to the center of the other in a straight edge across the head. Posteriorly the brown stripe diminishes gradually until it disappears near the tail tip. Aside from the brown swath, the animal is unmarked (Fig. 5).

COLORATION IN LIFE. This animal was a brilliant yolky yellow. The dorsal swath was chocolate brown and was entirely bordered by an edging of immaculate white less than a millimeter in width. The eye was metallic gold (Fig. 6).

OSTEOLOGY. As the animal was preserved flat in standard pose, accurate measurements from a radiograph could be taken. Skull, from the anterior border of the premaxilla to the medial edge of the occipital condyles, 8.0 mm; width of pars dentalis of the premaxilla, 1.3 mm; maximum width of braincase (anterior to the otic capsules) 3.0 mm; maximum width of skull base (across otic capsules) 4.9 mm; longest axis of otic capsule, 2.6 mm; and straight line length of the maxilla from anterior to posterior tip, 4.5 mm.

The preorbital process of the vomer extends well lateral to the internal narial opening as a slender sliver that tapers to a point. The frontal processes of the premaxilla arise and continue well separated from one another, spreading gradually as they rise dorsad and posteriad. Septomaxillae are absent. Trunk vertebrae number 14, caudosacral 2, and caudal 30. No tibial spur is evident; phalangeal formulae are 1, 2, 3, 3, 2 for the foot and 1, 2, 3, 2 for the hand. Phalanges are broadened and slightly irregular in outline, and the terminals of the three outer fingers and four outer toes are laterally expanded such that each is broader than it is long. The innermost toe and finger have terminals that are pointed and curved along the rim of the pad toward the other digits.

VARIATION. Two specimens of this form were collected, but one, a large adult female, escaped before it could be preserved. Knowledge of variation is thus restricted to aspects of color and pattern that were preserved in photographs

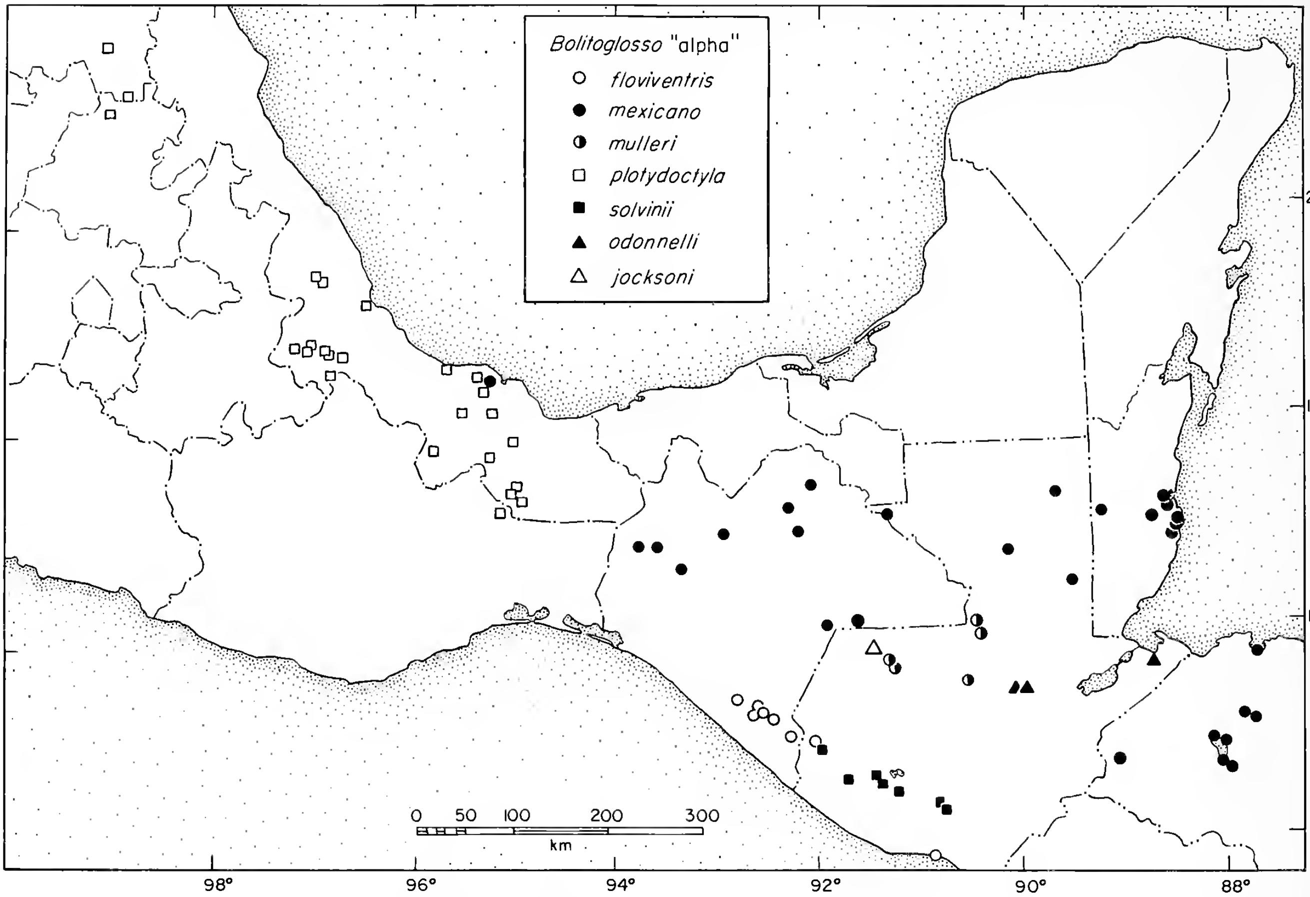

Figure 7. Distribution of the *Bolitoglossa mexicana* species group (modified from Wake and Lynch, 1976).

of the escaped animal (Fig. 6, and Hanken et al., 1980). All the hues described for the holotype were similar in the other individual, but the latter had a more irregular dorsal pattern. The brown dorsal swath was interrupted by a large yellow nape spot and a break on the tail, and the white border was incomplete. In addition a spot of brown was present on the dorsal surface of the right hind foot.

RANGE. *Bolitoglossa jacksoni* has been taken only within 1 km of the type locality on the Caribbean escarpment of the western Cuchumatanes (Fig. 7).

HABITAT AND HABITS. Both individuals were taken under bark of felled hardwood logs in clearings in a subtropical forest, which receives upward of 6 m of rain annually.

SYSTEMATICS. *Bolitoglossa jacksoni* is a member of the *B. mexicana* species group (*sensu* Wake and Lynch, 1976) which also includes *B. flaviventris, B. mexicana, B. mulleri, B. odonnelli, B. platydactyla,* and *B. salvinii.* The members of the group share a variety of structural and ecological traits; all have the primitive (alpha type) vertebral tail autotomy mechanism (Wake and Dresner, 1967); all have fully webbed feet that lack subdigital pads but have expanded terminal phalanges; all are large species, each represented by specimens exceeding 65 mm standard length; and they occur only in the tropical and low subtropical forests.

The species of the *B. mexicana* group are similar in general structure and have been defined mainly on the basis of coloration. The color patterns of the six species are described below; their geographic ranges are indicated in Figure 7.

Bolitoglossa flaviventris typically has paired dorsolateral light stripes that begin on each eyelid and join to produce a light snout. In the extreme condition, these stripes are paired all the way onto the tail, but often they are irregularly developed and may form a light reticulation, especially posteriorly. This species differs from others with dark flanks in having a light colored and unmarked ventral surface. The light ventral coloration sometimes invades the dorsal surfaces of the legs as well, but the flanks are always dark and sharply set off from the light belly (see Wake and Lynch, 1976, fig. 24). The eye is golden.

Bolitoglossa mexicana has a broad middorsal light swath that is typically broken into three longitudinal stripes by the invasion of dark ground color onto the dorsal surface. The dorsal pattern may range from virtually a single swath (as in *B. platydactyla*) to triple stripes, and then, through loss of the vertebral line, to a bilinear pattern much as seen in *B. odonnelli* (described below). The snout is heavily flecked, and light flecking extends over all of the dark regions of the body (see Wake and Lynch, 1976, frontispiece; Taylor and

Smith, 1945, fig. 58; Stuart, 1943a, plate II, fig. 2). The eye is dark.

Bolitoglossa mulleri typically has a narrow vertebral light stripe. When maximally developed, the stripe extends from the tail tip to the nape of the neck where it bifurcates before terminating on the eyelids. The light pigmentation is frequently reduced, and may be absent altogether leaving a uniformly black animal (see Fig. 5 and Stuart, 1943a, plate II, fig. 4). The eye is dark.

Bolitoglossa odonnelli has narrow paired light stripes. At their maximum development, these stripes extend continuously from the eyelids to the tip of the tail, but frequently they are broken into rows of dots or may not extend as far anteriorly or posteriorly. The body, including the snout, is otherwise unmarked black (see Stuart, 1943a, plate II, fig. 3). The eye is dark.

Bolitoglossa platydactyla has a single broad middorsal light swath on a generally dark ground. The snout is dark and speckled with light flecks; additional flecking may occur on the fore limbs. A light swath begins on the eyelids and extends almost to the tip of the tail (see Wake and Lynch, 1976, fig. 43; Stuart, 1943a, plate II, fig. 1); the eye is dark.

Finally, *B. salvinii* has the same distribution of light dorsal markings as *B. flaviventris*: paired dorsolateral lines that join anteriorly to produce a light-colored snout and that frequently meet across the dorsal midline or break into reticulation. In this species, the ventral surfaces are dark and undifferentiated from the dark flanks, although a light ventral blotch occasionally occurs (see Wake and Lynch, 1976, fig. 24; Schmidt, 1936, fig. 17). The eye may be either light or dark.

Relationships among the *B. mexicana* group species remain obscure. The animals are scarce, and more samples would be needed for a comprehensive analysis of the entire assemblage. While primitive–derived polarities are not understood for the color characters separating the species, the seven taxa cluster in two basic color and pattern groups. Stuart (1943a) considered *B. platydactyla, B. mexicana, B. mulleri,* and *B. odonelli* to form a group united by aspects of their coloration, and the remaining three taxa, *B. jacksoni, B. flaviventris,* and *B. salvinii,* themselves form a cluster. All three of the latter forms have (1) some white edging between dark and light areas; (2) at least some individuals with golden eyes; (3) the same basic hues, yellow (to tan) and chocolate brown; and (4) a dorsal swath of brown bordered bilaterally and on the snout by yellow. These three species are the only members of the *mexicana* group that ever have light ventral coloration (apparently universal in *B. jacksoni* and *B. flaviventris* and occasionally, as small blotches, in *B. salvinii*). An additional unique feature of the *jacksoni-flaviventris-salvinii* assemblage is that each is marked only with solid colors, the light regions a single uniform yellow and the dark regions an equally pure brown; speckling and mottling are never observed.

ETYMOLOGY. I name this rare and beautiful new species for Jeremy L. Jackson, the friend who aided me in long moldy months of wet season collecting, and the captor of the first, and now sole, representative of this species.

Bolitoglossa lincolni (Stuart, 1943a)

Figure 3

Oedipus lincolni Stuart, 1943a:9.
Magnadigita lincolni: Taylor, 1944:218.
Bolitoglossa lincolni: Wake and Brame, 1963:386.
Bolitoglossa resplendens McCoy and Walker, 1966:1.

TYPE LOCALITY. Monte at Salquil Grande, Depto. El Quiché, Guatemala, 2,450 m elevation.

RANGE. Including the range of *B. resplendens* (herein synonymized with *B. lincolni*), this is one of the widest ranging of Central American salamanders. It occurs on the Pacific Uplands, in the Cuilco, in the Cuchumatanes, and on the Mesa Central de Chiapas. *B. lincolni* is herein reported from one new locality in the Cuchumatanes and one in the Cuilco.

HABITAT AND HABITS. *Bolitoglossa lincolni* were taken in bromeliads and under logs and bark (see Wake and Lynch, 1976, fig. 30). In addition they were found to be active on wet nights. The species occurs in the upper subtropical

Table 2. Summary of geographic variation in *Bolitoglossa lincolni*.

Population	Dorsal pattern	Ventral spotting	Foot webbing	Max. standard length (millimeters)*
Pacific Uplands	Swath to spots	>95% of pop.	Reduced	m 76 f 74
Cuilco	Swath to spots	<60% of pop.	Intermediate	m 58 f 79
Cuchumatanes	Swath	>95% of pop.	Extensive	m 66 f 78
Mesa Central	Swath	>95% of pop.	Reduced	m 62.3** f 78.4**

* Males (m), females (f).

** Data from McCoy and Walker (1966).

forest from well above the cloud line up to the lower temperate zone.

SYSTEMATICS. The diagnostic characters differentiating *Bolitoglossa resplendens* from *B. lincolni* are its greater standard length and proportionately shorter limbs. In the description of *B. resplendens* it was reported that a higher incidence of ventral spotting and less extensive interdigital webbing also distinguish *B. resplendens* from *B. lincolni* (McCoy and Walker, 1966).

Examination of specimens from the four known populations indicates that the two supposedly diagnostic features of *B. resplendens* reflect comparison to a limited sample of unusually small *B. lincolni*. Nominate *B. lincolni* from the Cuchumatanes are fully as large as the specimens in the *B. resplendens* type series (McCoy and Walker, 1966) from the Mesa Central de Chiapas (Table 2), and both populations have proportionately longer limbs at smaller standard length (Fig. 8). Specimens from the Cuilco and Pacific Uplands have the same maximum size (Table 2) and limb/body length allometry (Fig. 8) as the other two populations.

Color pattern, both dorsal and ventral, and degree of interdigital webbing vary between the four populations (see Table 2 and Fig. 3 for dorsum of Cuchumatan specimen) but not in concordant patterns that suggest species level differentiation. Thus, I refer the name *Bolitoglossa resplendens* to the synonymy of *Bolitoglossa lincolni*.

Wake and Lynch (1982) reported the results of morphometric and electrophoretic analysis of the *Bolitoglossa franklini* species group. While there is general agreement with my conclusions, they choose to continue to recognize *Bolitoglossa resplendens* as a distinct species based upon the large genetic distance between the Cuilco population and those from the Cuchumatanes and Pacific Uplands. The genetic affinities of the nominate populations of *Bolitoglossa resplendens* on the Mesa Central de Chiapas remain unknown.

Bolitoglossa morio (Cope, 1869)

Figure 3

Geotriton carbonarius (part) Cope, 1868:313.
Oedipus morio Cope, 1869:103.
Geotriton morio: Smith, 1877:64.
Spelerpes morio: Boulenger, 1882:70.
Spelerpes bocourti Brocchi, 1883:111.
Magnadigita morio: Taylor, 1944:218.
Magnadigita omniumsanctorum Stuart, 1952:4.
Bolitoglossa omniumsanctorum: Wake and Brame, 1963:386.
Bolitoglossa morio: Wake and Brame, 1963:386.

TYPE LOCALITY. Mountains of Guatemala.

RANGE. This species occurs throughout the Pacific Uplands, in the Chuacús, and in the Cuchumatanes. It is here reported for the first time from the Cuilco.

HABITAT AND HABITS. *B. morio* were taken under logs, in logs, and in bromeliads and were found to be active on rainy nights. They occur in the upper subtropical and lower temperate zone forests between roughly 1,800 and 3,000 m.

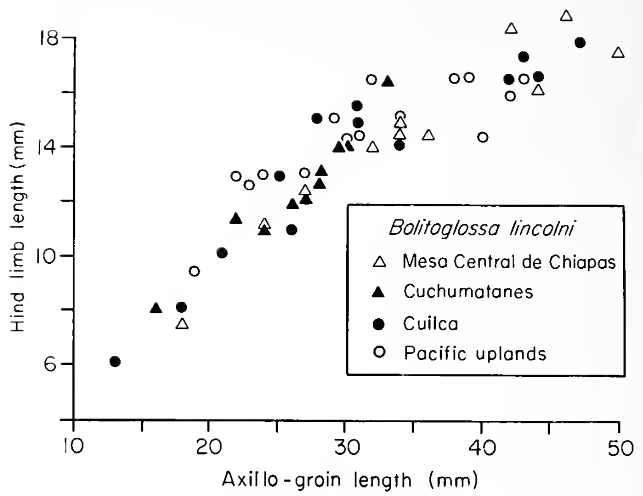

Figure 8. Relationship between hind limb length and axilla-groin length in four populations of *Bolitoglossa lincolni*.

SYSTEMATICS. Relationships of this species are obscure, but its closest relative appears to be *B. flavimembris* (see species group section, below). The characters that unite the populations of this species are the presence of large light (whitish, cream, or pink) blotches on the flanks and/or sides of the tail; the slate grey to brownish ground color of the dorsum; salt and pepper belly mottling; reduced webbing such that all toes of the hind foot are free at their tips; and the robust body form.

The newly discovered Cuilco population has all of the specific characters, except that the lateral markings are reduced to small flecks (diameters less than that of the eye), which are restricted to the sides of the tail rather than extending onto the trunk.

Bolitoglossa mulleri (Brocchi, 1883)

Figure 5

Spelerpes mulleri Brocchi, 1883:116.
Oedipus platydactylus (part) Dunn, 1926:400.
Oedipus mulleri: Schmidt, 1936:150.
Bolitoglossa mulleri: Taylor, 1944:219.
Oedipus mexicanus mulleri: Stuart, 1948:19.
Bolitoglossa moreleti mulleri: Duellman, 1963:220.
Bolitoglossa mexicana mulleri: Wake and Brame, 1963:386.

TYPE LOCALITY. Several localities in Alta Verapaz, restricted by Stuart (1943a) to "les montagnes qui dominent Coban."

RANGE. This form had been taken only in the Xucaneb complex until discovered in the Cuchumatanes during the study described here. It is now known from Santa Cruz Barillas and from a finca 3 km to the NE at 1,500 m (Fig. 7).

HABITAT AND HABITS. This species occurs in the low pine-broadleaf cloud forest border in the Xucaneb and was found in the Cuchumatanes in the cutover Barillas valley, which was once a mix of the two forest types. This area is at the elevation of the lower subtropical zone but is drier because of its protected position. Of the ten or so specimens taken from the Cuchumatanes, all but one were found under stones in a well-watered garden in the town of Barillas. The other specimen was found under a piece of wood in a stand of coffee. In the Xucaneb the species has been taken between 1,000 and 1,500 m.

SYSTEMATICS. The new population has a somewhat reduced middorsal light stripe relative to animals from the type locality: markings never extend anterior to the nape, and some individuals are unmarked black.

Bolitoglossa mulleri is a member of the *Bolitoglossa mexicana* species group (*sensu* Wake and Lynch, 1976). Variation and relationships among the *mexicana* group species are discussed in the *B. jacksoni* account above.

Bolitoglossa rostrata (Brocchi, 1883)

Figure 3

Spelerpes rostratum Brocchi, 1883:112.
Oedipus rostratum: Dunn, 1924:99.
Oedipus rostratus: Dunn, 1926:384.
Magnadigita rostrata: Taylor, 1944:218.
Bolitoglossa rostrata: Wake and Brame, 1963:386.

TYPE LOCALITY. The mountains of Totonicapan, Guatemala.

RANGE. This species is one of the most broadly ranging forms in Nuclear Central America, from the Mesa Central de Chiapas through the Cuchumatanes and into the Pacific Uplands. A newly discovered population at the eastern extremity of the Cuchumatanes indicates that the species may be distributed throughout that cordillera.

HABITAT AND HABITS. *B. rostrata* were taken in and under logs, under bark, in bunchgrass, and under rocks, and were found to be active on rainy nights. The species occurs only above 2,700 m and up to about 3,000 m, in temperate forests and above the treeline in bunchgrass associations.

SYSTEMATICS. The species is distinguished by the following characters: it has almost unwebbed toes (as unwebbed as any member of the genus); it is brown, typically with a middorsal swath of light color or light shoulder stripes; and it has a uniform light beige to dull yellow ventral and subcaudal color.

B. rostrata appears to be most closely related to the *B. dunni* series (see *B. cuchumatana* account above) and where it occurs in sympatry with *B. cuchumatana* the two species are separated with difficulty. *Bolitoglossa rostrata* is distinguishable from *B. cuchumatana* on a number of subtle characters; it occurs in an unstriped morph, is slightly less robust, has a longer tail, and shows reduced interdigital webbing (Fig. 3).

Bolitoglossa rufescens (Cope, 1869)

Figure 5

Oedipus rufescens Cope, 1869:104.
Geotriton rufescens: Smith, 1877:76.
Spelerpes rufescens: Boulenger, 1882:71.
Bolitoglossa rufescens: Taylor, 1941:145.
Palmatotriton rufescens: Smith, 1945:4.

TYPE LOCALITY. Orizaba, Veracruz, Mexico.

RANGE. The range of this species is broad, extending along the Atlantic versant throughout western Honduras, Guatemala, and Chiapas, Mexico, and continuing up the Atlantic coastal plain through the Mexican state of Veracruz to San Luis Potosi. The species is well known from Chiapas and the low Xucaneb on both sides of the Cuchumatanes, but this is the first report of its occurrence in the Cuchumatanes proper. It occurs just below the cloud line at Finca Chiblac in the northwestern Cuchumatanes.

HABITAT AND HABITS. This species almost always occurs in the leaf bases of banana plants. All but one of the four *B. rufescens* taken in the Cuchumatanes were found in this situation. The exception was found crossing a trail on a sultry, overcast afternoon at about 1400 h. The species occurs throughout the tropical zone forest from near sea level (Stuart, 1943a) up to the 1,200-m cloud line.

SYSTEMATICS. Specimens from the Cuchumatanes were assigned to *B. rufescens* based upon derived skull and foot structure and the absence of maxillary teeth.

Bradytriton silus Wake and Elias, 1983

Figure 9

Bradytriton silus Wake and Elias, 1983:3.

TYPE LOCALITY. Finca Chiblac, 15 km NE Barillas, Huehuetenango, Guatemala, elevation 4,300 ft. (1,310 m).

RANGE. This species was discovered in the course of this investigation. It is known only from the type locality.

HABITAT AND HABITS. Eleven of the twelve known specimens were taken beneath pieces of wood in a clearing that was being prepared for the cultivation of quinine. The other individual was found under a log in the undisturbed subtropical zone cloud forest surrounding the clearing. The native forest at the type locality is a mixed hardwood growth that receives over 6 m of rain yearly.

SYSTEMATICS. This species has unique specializations and has been placed in a monotypic genus. Its possible relationships are discussed by Wake and Elias (1983).

Dendrotriton cuchumatanus (Lynch and Wake, 1975)

Figure 5

Chiropterotriton cuchumatanus Lynch and Wake, 1975:6.
Dendrotriton cuchumatanus: Wake and Elias, 1983.

TYPE LOCALITY. On highway 9N, 8.5 km (by road) SW San Juan Ixcoy, Depto. Huehuetenango, Guatemala, elevation 2,860 m.

RANGE. This species is known only from the type locality. Appropriate habitat is present elsewhere in the area, and this species may range more widely than is presently known.

HABITAT AND HABITS. This species has been taken under moss and bark on large fallen trees. The type locality is a patch of great buttressed rain forest oaks on the sub-

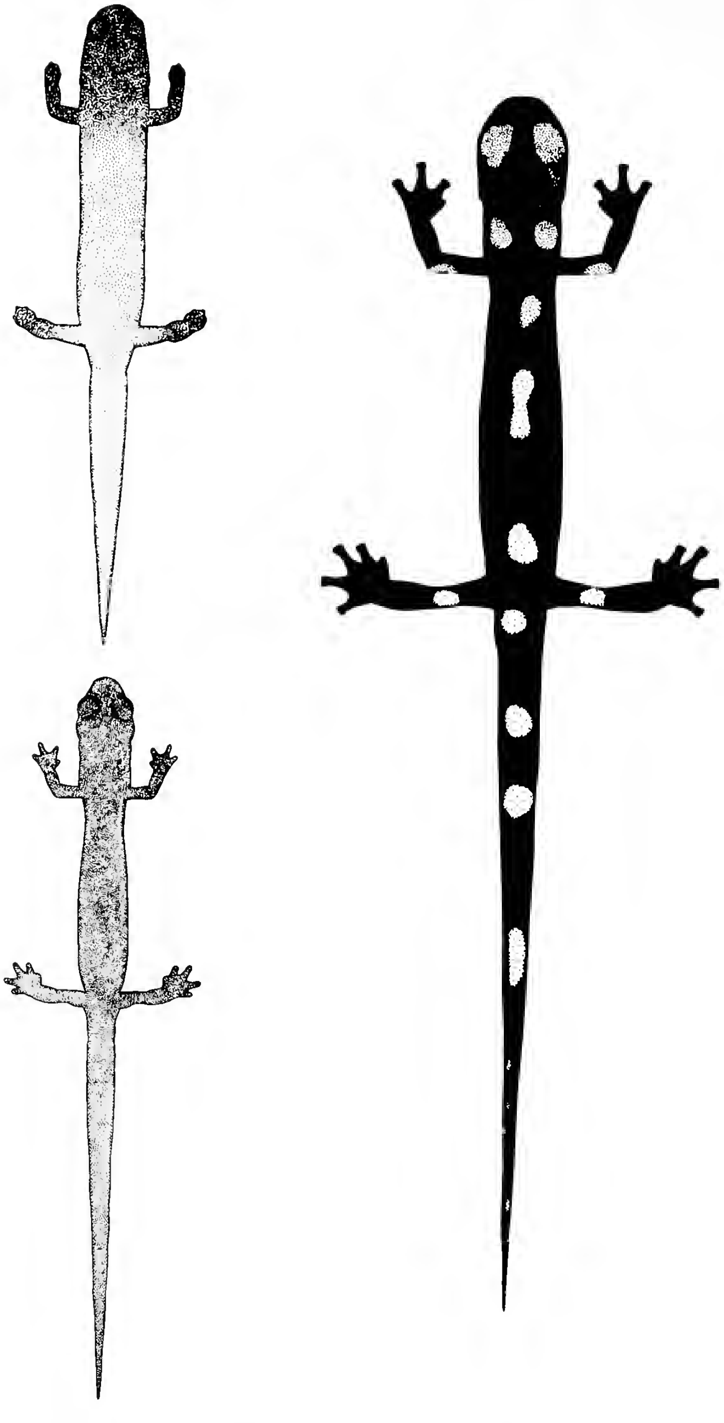

Figure 9. *Bradytriton silus, Pseudoeurycea rex,* and *Nyctanolis pernix,* life size. UPPER LEFT: *Bradytriton silus,* head, legs, and feet slate grey, trunk and tail brick red-brown. LOWER LEFT: *Pseudoeurycea rex* (Cuchumatan specimen), dark brown overall (in some Cuchumatan specimens and in most Cuilco animals, there is light speckling, especially laterally). RIGHT: *Nyctanolis pernix,* background color black, spots on eyelids and nape crimson, those on elbows and knees orange, trunk and tail spots yellow.

tropical-temperate zone border. This area receives a great but undetermined amount of precipitation both in the form of rain and as dense, cold fog.

SYSTEMATICS. The genus *Dendrotriton* has been reviewed by Lynch and Wake (1975). Their results suggest close relationship between *D. cuchumatanus, D. bromeliacea,* and

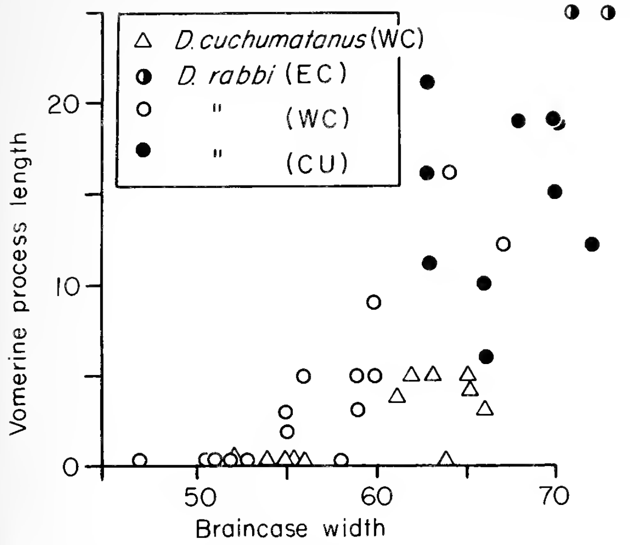

Figure 10. Relationship between length of the preorbital process of the vomer and braincase width in *Dendrotriton rabbi* and *D. cuchumatanus* (in micrometer units). WC = Western Cuchumatanes; EC = Eastern Cuchumatanes; CU = Cuilco.

D. megarhinus (the latter two are inhabitants of the Pacific Uplands), based upon shared configurations of the vomer and the nostril.

Dendrotriton rabbi (Lynch and Wake, 1975)

Figure 5

Chiropterotriton rabbi Lynch and Wake, 1975:2.
Dendrotriton rabbi: Wake and Elias, 1983.

TYPE LOCALITY. 9.5 km W, 8.5 km S (by air) La Democracia, Depto. Huehuetenango, Guatemala, elevation 2,100 to 2,500 m.

RANGE. This species, described and hitherto known only from a spur of the Montañas de Cuilco, is here reported both from the main massif of the Cuilco and from two localities in the Cordillera de los Cuchumatanes.

HABITAT AND HABITS. *Dendrotriton rabbi* occur at the subtropical-temperate border. In the Cuilco, they have most frequently been found in bromeliads but only under bark on logs and stumps in the Cuchumatanes, perhaps because bromeliads are absent from the appropriate elevations. The species occurs from 2,100 to 2,700 m.

SYSTEMATICS. The newly discovered populations have been referred to *D. rabbi* on the basis of a small nostril diameter and the presence of a preorbital process on the vomer in adults (as distinct from *D. cuchumatanus, D. bromeliacea,* and *D. megarhinus*) and because some specimens from each population have ossified septomaxillary bones (absent in *D. xolocalcae*) (for discussion, see Lynch and Wake, 1975, 1978).

Lynch and Wake (1975) examined the ontogeny of the nostril in all of the species of *Dendrotriton* and discovered that all juveniles have similar, relatively large nostrils. They found that patterns of relative growth determined the adult condition; species that as adults have small nostrils experience either no growth or actual shrinkage in the absolute size of the nostril through ontogeny, while large nostriled forms experience nostril growth.

I have examined ontogenetic variation in the presence or absence of the preorbital process of the vomer. The process is large and tooth-bearing in small nostriled species but, if present, is a nub in species with large nostrils. As with nostril size, vomerine process length is initially equal in the large nostriled *D. cuchumatanus* and small nostriled *D. rabbi.* Differential growth produces the difference in the adult condition in the two species (Fig. 10). In this case, interspecific differences are compounded by a differential in maximum adult size. These data further indicate that the newly discovered Cuchumatan populations clearly fall with the nominate *D. rabbi.* With the new localities reported here, *D. rabbi* is known to occur within 250 vertical m and about 25 km of *D. cuchumatanus* in the Cuchumatanes. The two species have been taken in similar habitats without intervening ecological barriers, and the proximity of the two suggests that the first case of sympatry in the genus may yet be found.

Nyctanolis pernix Elias and Wake, 1983

Figure 9

Nyctanolis pernix Elias and Wake, 1983:2.

TYPE LOCALITY. Finca Chiblac, about 10 km NE Santa Cruz Barillas, Depto. Huehuetenango, 1,370 m (4,500 ft.) elevation.

RANGE. This species has been taken at the type locality, just across the Mexican border in Chiapas and in the western end of the Sierra de las Minas near Purulhá, Baja Verapaz (J. Campbell, pers. comm.).

HABITAT AND HABITS. The type series was found under moss and bark during the day and on stumps and logs on wet nights. The type locality is a region of quinine cultivation in the subtropical zone, just above the cloud line. The forest receives over 6 m of rain annually. The Mexican specimen was taken in the mouth of a cave in the cloud forest.

SYSTEMATICS. This species was discovered during the course of this investigation and appears to have no close relatives. The relationships of this monotypic genus were discussed by Elias and Wake (1983).

Pseudoeurycea rex (Dunn, 1921)

Figure 9

Oedipus rex Dunn, 1921:143.
Pseudoeurycea rex: Taylor, 1944:209.

TYPE LOCALITY. Sierra Santa Elena (near Tecpam), Guatemala, elevation 9,500 ft. (2,900 m).

RANGE. *P. rex* is known from the Cuchumatanes and from several regions on the Pacific Uplands. The species is here recorded for the first time from the Montañas de Cuilco.

HABITAT AND HABITS. This form occurs from 2,750 m elevation to over 4,000 m at the top of the highest mountains in its range and occurs in the temperate zone forest and above the treeline in open bunchgrass communities. They live under and within logs, under bark, moss, grass clumps, and stones and were found active in the open on wet nights. *P. rex* is often abundant, reaching densities higher than those of any other Guatemalan salamander.

SYSTEMATICS. The Guatemalan members of the genus *Pseudoeurycea* are four or five similar brown to black-colored species. Species-level differences in foot webbing and color pattern have proven difficult to document and tend to be exceeded by intrapopulational variation. No careful quantitative work on variation in this assemblage has been published, and my allocation of the Cuilco and Cuchumatan populations is based upon their elevational distribution and their general morphological similarities to known populations of *P. rex*.

DISCUSSION

SPECIES GROUPS IN *BOLITOGLOSSA* BETA

Since Wake and Lynch (1976) last outlined species groups in the genus *Bolitoglossa*, examination of new material from the Cuchumatanes, the Cuilco, the Pacific Uplands, and the Sierra de las Minas has blurred certain distinctions and clarified others among the species found in Nuclear Central America (abbreviated NCA and including the entire landmass between the Isthmus of Tehuantepec and the Nicaraguan Depression). Implicit in some of the comparisons made in the preceding species accounts, and crucial to the discussion sections to come, is a revision of the species groups for Guatemalan *Bolitoglossa*.

Wake and Dresner (1967) found that a group of derived structural characters involved in tail autotomy was shared by certain species of *Bolitoglossa*. The derived group, referred to by Wake and Lynch (1976) as "*Bolitoglossa* beta," includes all Mexican and NCA species except the *B. mexicana* group, as well as two forms from the Talamancan highlands further south. Included are the following species: *B. alvaradoi, B. arboroscandens, B. cuchumatana, B. dofleini, B. dunni, B. engelhardti, B. flavimembris, B. franklini, B. hartwegi, B. helmrichi, B. lincolni, B. macrinii, B. melania, B. morio, B. occidentalis, B. riletti, B. rostrata, B. rufescens, B. schmidti, B. stuarti, B. veracrucis, B. yucatana,* and at least one undescribed species (Wake and Lynch, 1982).

Species groups within *Bolitoglossa* beta were first recognized informally. Taylor (1941), in his description of *B. occidentalis*, noted the affinity between his new species and *B. rufescens*. Stuart (1943a) noted that *B. dofleini* and *B. yucatana* were close relatives. He also suggested that *B. cuchumatana, B. dunni, B. engelhardti* and *B. helmrichi* formed a close group in terms of both morphology and ecology, and in a later paper (1952) he named them the *B. dunni* species group. In the description of *B. lincolni* Stuart (1943a) reported the new species to be most closely affiliated with *B. franklini* on morphological grounds, and later (Stuart, 1952) included them with the then newly described *B. nigroflavescens* in a *B. franklini* species group. Recently Wake and Lynch (1982) reduced *B. nigroflavescens* to the status of a subspecies within *B. franklini*. Stuart (1952) erected the *B. morio* group to contain *B. morio* and *B. omniumsanctorum*, but Wake and Elias (1983) synonymized the two.

By 1952, therefore, five species assemblages had been recognized within *Bolitoglossa* beta, leaving unassigned only the following six of the nineteen species then known: *B. flavimembris, B. macrinii, B. riletti, B. rostrata, B. schmidti* and *B. veracrucis* (see Table 3). Wake and Brame (1969) named two new species, *B. hartwegi* and *B. stuarti*, and demonstrated their close morphological similarities to one another and to *B. veracrucis*. In addition they reorganized Stuart's (1943a, 1952) three species groups into two new ones, the *B. rostrata* and *B. helmrichi* groups (Table 3). These two groups were large and heterogeneous as compared to those described above. The *B. rostrata* group included Stuart's (1952) *B. morio* and *B. franklini* groups, *B. dunni* and *B. engelhardti* from his *B. dunni* group, the previously unassigned *B. macrinii, B. riletti* and *B. rostrata*, and the recently described species *B. resplendens* and *B. brevipes*. Their *B. helmrichi* group included *B. cuchumatana* and *B. helmrichi* from Stuart's (1952) *B. dunni* group, the previously unassigned *B. flavimembris* and *B. veracrucis*, and the new species *B. hartwegi* and *B. stuarti*.

Wake and Lynch (1976) assembled the first complete listing of *Bolitoglossa* species groups. They tentatively assigned every species to some group and recognized a total of six species groups within *Bolitoglossa* beta. The *B. dofleini* group was erected to include *B. dofleini, B. yucatana* and the poorly known *B. schmidti*. The *B. rufescens* group was recognized as containing *B. occidentalis* and *B. rufescens*. The two Talamancan species from southern Central America, *B. alvaradoi* and *B. arboroscandens*, were placed together in a *B. alvaradoi* group, and the two species from north of the Isthmus of Tehuantepec, *B. macrinii* and *B. riletti*, were put in a *B. macrinii* group. The two large groups, *B. rostrata* and *B. helmrichi*, of Wake and Brame (1969), were retained with their original membership but for the switching of *B. morio* from one to the other and the inadvertent omission of *B. omniumsanctorum* altogether (see Table 3).

The recognition of polyphyletic groups (groups united by characters not shared by their most recent common ancestor) is a severe obstacle to phylogenetic reconstruction. Ensuring that only nonpolyphyletic (= paraphyletic and monophyletic) species groups are recognized is a first step towards an understanding of the phylogenetic history of *Bolitoglossa* beta. To eliminate possibly polyphyletic groups I have recognized only tight clusters of phenotypically similar species. Morphological similarity between species group members is demonstration of nonpolyphyletic origin of the group insofar as such similarities are homologous (acquired by descent from a similarly endowed common ancestor).

The *B. rostrata* and *B. helmrichi* groups of Wake and Lynch (1976) are large, heterogeneous and united by no specific characters. To compose tighter units more comparable to other species groups in *Bolitoglossa* beta I have subdivided and reorganized these two groups.

The *B. rostrata* group contains a series of species that has been recognized as a phenetic cluster by many authors (Stuart,

Table 3. The species groups of *Bolitoglossa* beta as defined by different authors. Species not assigned to a group until after 1952 (both newly described and described but previously unaffiliated species) are indicated by an asterisk where they first appear.

Early classifications		Wake and Brame, 1969		Wake and Lynch, 1976		Elias, 1983	
	Stuart, 1952	*helmrichi* group	**hartwegi*	*helmrichi* group	*hartwegi*	*veracrucis* group	*hartwegi*
			**stuarti*		*stuarti*		*stuarti*
			**veracrucis*		*veracrucis*		*veracrucis*
dunni group	*cuchumatana*		*cuchumatana*		*cuchumatana*	*dunni* group	*cuchumatana*
	helmrichi		*helmrichi*		*helmrichi*		*helmrichi*
			flavimembris		*morio*		
					flavimembris		
	dunni	*rostrata* group	*dunni*	*rostrata* group	*dunni*		*dunni*
	engelhardti		*engelhardti*		*engelhardti*		*engelhardti*
			**rostrata*		*rostrata*		*rostrata*
morio group	*morio*		*morio*			*morio* group	*morio*
	omniumsanctorum		*omniumsanctorum*				*flavimembris*
			**resplendens*		*resplendens*		
franklini group	*franklini*		*franklini*		*franklini*	*franklini* group	*franklini*
	lincolni		*lincolni*		*lincolni*		*lincolni*
	nigroflavescens		*nigroflavescens*		*nigroflavescens*		**melania*
			brevipes		*brevipes*		
			**macrinii*	*macrinii* group	*macrinii*	*macrinii* group	*macrinii*
			**riletti*		*riletti*		*riletti*
	Dunn, 1926						
	dofleini			*dofleini* group	*dofleini*	*dofleini* group	*dofleini*
	yucatana				*yucatana*		*yucatana*
					**schmidti*		*schmidti*
	Taylor, 1941						
				alvaradoi group	**alvaradoi*	*alvaradoi* group	*alvaradoi*
					**arboroscandens*		*arboroscandens*
	occidentalis	*rufescens* group	*occidentalis*	*rufescens* group	*occidentalis*	*rufescens* group	*occidentalis*
	rufescens		*rufescens*		*rufescens*		*rufescens*

1943a, 1952, as his *B. franklini* group; McCoy and Walker, 1966, Wake and Brame, 1969, and Wake and Lynch, 1976, as the *B. lincolni* subgroup of their *B. rostrata* group; Wake, Yang, and Papenfuss, 1980, and Wake and Lynch, 1982, as the *B. franklini* species group). This assemblage includes *B. franklini, B. lincolni, B. melania,* and one undescribed Chiapan form (Wake and Lynch, 1982, who also include *B. resplendens*). These species are characterized by large adult size, stout bodies and tails, and a black ground color broken dorsally only by a sharply bounded swath, spotting, or reticulation in some lighter color; red in some species to yellow or grey-green in others (see *B. lincolni,* Fig. 3). *B. melania* is solid black. These species all have toetips free of webbing and subdigital pads. They are distributed allopatrically except for an area of elevational parapatry with occasional hybridization between the high elevation *B. lincolni* and lower elevation *B. franklini* on the Pacific Uplands (Wake, Yang, and Papenfuss, 1980).

The remainder of the *B. rostrata* group of Wake and Lynch (1976), including *B. dunni, B. engelhardti* and *B. rostrata,* fits with *B. cuchumatana* and *B. helmrichi* of their *B. helmrichi* group to form an assemblage characterized by blunt rounded toetips, fully developed subdigital pads, and a dark brown ground color, frequently marked with a lighter brown dorsal swath or paired shoulder stripes (see *B. rostrata* in Fig. 3 for typical color pattern and compare *B. rostrata* and *B. cuchumatana* [inset] feet as examples of variation in foot morphology within the group). Stuart (1943a, 1952) recognized this assemblage as his *B. dunni* group but hesitated to include *B. rostrata* because of its different ecology. Relying on morphological similarities, I recognize this assemblage, including *B. rostrata,* as a new *B. dunni* species group. The members of the *B. dunni* group are all either geographically or elevationally (in the case of *B. rostrata* and *B. engelhardti* in the Pacific Uplands) allopatric, except that narrow sympatry is seen between the high elevation *B. rostrata* and the lower *B. cuchumatana* in the Cuchumatanes.

Bolitoglossa hartwegi, B. stuarti, and *B. veracrucis* were recognized by Wake and Brame (1969) to form a compact subgroup within their *B. helmrichi* group. I choose to recognize the similarities of these species by isolating them in a new *B. veracrucis* species group. The three species are united by the combination of fully webbed feet that lack subdigital pads and are differentiated from members of the *B. rufescens* group by posession of a strongly articulated skull with a broad pars dentalis of the premaxilla. The *B. veracrucis* group has the broadest elevational range of any group of NCA salamanders (see elevational distribution section below), and no two species occur sympatrically.

The two remaining species left over from Wake and Lynch's (1976) *B. helmrichi* group are *B. flavimembris* and *B. morio. B. morio* is slightly larger than *B. flavimembris,* but the two share a stout body and tail and a unicolor dorsum (see *B. morio* in Fig. 3). That *B. flavimembris* is not affiliated with the *B. dunni* group is indicated both by its coloration and build and by its rather pointed toetips and poorly developed subdigital pads (see Wake and Lynch, 1976, fig. 22). New evidence that *B. morio* and *B. flavimembris* are relatives comes from the discovery of populations of intermediate morphology in the Pacific Uplands of Guatemala near the Mexican border (D.B. Wake, pers. comm.). Given these indications of relationship, and the absence of other affiliations, I group *B. flavimembris* and *B. morio* together in a new *B. morio* species group.

Aside from the changes proposed above I follow the species group assignments of Wake and Lynch (1976); the full history of species groups among the species of *Bolitoglossa* beta including my revisions is presented in tabular form in Table 3.

PATTERNS OF DISTRIBUTION AND DIFFERENTIATION

Faunal Connections Between the Mexican Plateau, NCA, and the Talamancas

Wake and Lynch (1976) found that the three most mountainous areas of Middle America are especially high in salamander species diversity; these are the Caribbean escarpment of the Mexican Plateau, the mountains of NCA, and the Talamancan highlands of Costa Rica and Panama. That there has been faunal contact between these centers of diversity is demonstrated by the distribution of some genera on more than one of the three upland areas. For example, the NCA fauna includes some genera that range to the Mexican Plateau (*Pseudoeurycea*), others that range to the Talamancas (*Oedipina* and *Nototriton*), still others that occur on all three upland areas (*Bolitoglossa*), as well as genera endemic to NCA (*Bradytriton, Dendrotriton,* and *Nyctanolis*). Each genus has a clear center of intrageneric diversity on one of the three upland regions (except *Bolitoglossa,* in which the alpha and beta subgeneric groups center on two different uplands (Wake and Lynch, 1976)). This pattern suggests that most intrageneric evolution proceeded on single upland areas at a time when the three major uplands were isolated from one another.

If we go one step further back, however, and consider the origins of the genera themselves, we find that genera with distributions centered on the same upland area (i.e., *Bradytriton, Dendrotriton, Nyctanolis,* and the beta complex of *Bolitoglossa* in NCA) do not usually form a clearcut monophyletic group (Wake and Elias, 1983). This implies a complex history of ancient faunal contact between the three great upland regions of Middle America.

Faunal Connections Among the Mountain Ranges of NCA

Within NCA, the uplands form discrete islands of habitat for high elevation salamander species. Between these uplands lie warmer, drier, rain-shadowed valleys that are generally uninhabited by salamanders. Around the coastward periphery of these mountains are warm, humid lowlands that support a restricted plethodontid fauna. Most of the salamanders occurring in NCA are montane (including *Bradytriton, Dendrotriton, Nototriton, Nyctanolis,* and *Pseudoeurycea*). A single genus, *Oedipina,* is restricted to the lowlands. Only *Bolitoglossa* occurs at all elevations, and even this genus is split

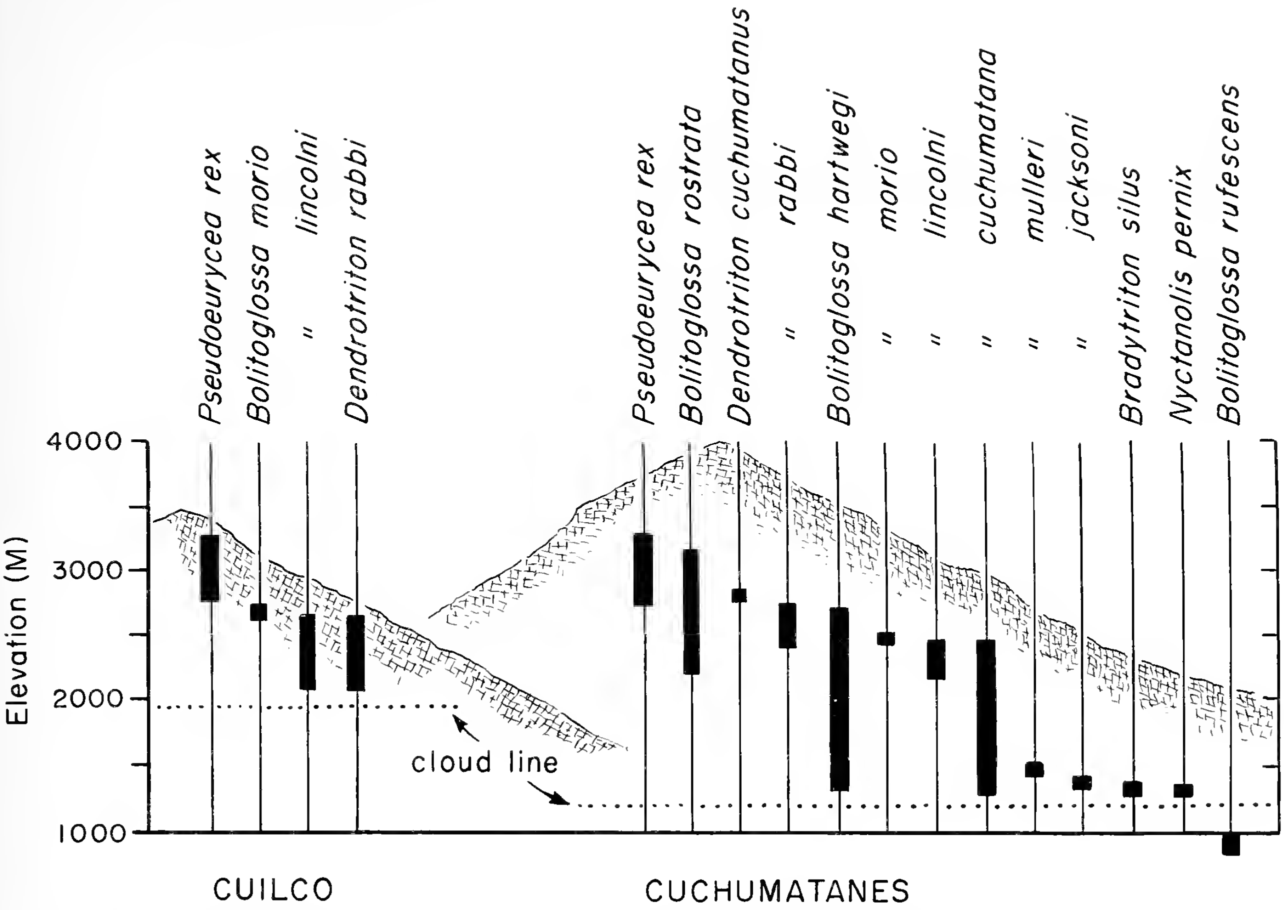

Figure 11. Elevational distribution of salamander species on the Montañas de Cuilco and the Cordillera de los Cuchumatanes (all collections combined).

into upland (*B. helmrichi, B. morio, B. franklini*) and lowland (*B. mexicana, B. dofleini, B. rufescens*) species assemblages (the *B. veracrucis* group is exceptional in its broad elevational range and will be discussed separately below). The upland and lowland faunas intermingle narrowly in the low cloud forest at about 1,000 m elevation, but the upland groups are subject to special biogeographic limitations, which give their current patterns of differentiation particular historical interest.

Comparison of patterns of upland diversity obtaining in the Cuchumatanes relative to the Pacific Uplands raises interesting contrasts. There are fifteen upland salamander species known from the Pacific Uplands (Wake and Lynch, 1976, 1982) and only nine (excluding *B. hartwegi* of the *B. veracrucis* group) from the Cuchumatanes, but the supraspecific diversity is greater in the Cuchumatanes. The nine Cuchumatan species belong to five genera, and the four *Bolitoglossa* fall into three species groups. In the Pacific Uplands, however, the fifteen species are in three genera, and all seven *Bolitoglossa* are in the same three species groups that occur in the Cuchumatanes. No genus or species group in the Pacific Uplands is not also represented in the Cuchumatanes, but two genera present in the Cuchumatanes are absent in the Pacific Uplands. The two areas have four species in common: *Bolitoglossa lincolni* (here including *B. resplendens*), *B. morio, B. rostrata,* and *Pseudoeurycea rex.*

The fact that salamander diversity is so deep in the Cuchumatanes may reflect that region's ancient history as a land-positive area (Rosen, 1978).

The shallowness of salamander diversity on the Pacific Uplands may reflect the topography of that area: the highlands are composed of many abutting cinder cones. Small climatic fluctuations should have caused alternate fragmentation and reunion of the geographic ranges of highland salamander species. When a species' range is subdivided and then reunified after a period in this way, a complex of introgressions, parapatries and sympatries might be expected to result as partially differentiated sister populations are thrown back into contact after a period of allopatry on neighboring cinder cones. Just these sorts of interactions are found among the Pacific Uplands salamanders (Wake and Lynch, 1976; Wake, Yang, and Papenfuss, 1980; Wake and Lynch, 1982).

ELEVATIONAL DISTRIBUTION

Schmidt (1936) documented the elevational ranges of salamander species along a transect down the coastal escarpment of the Pacific Uplands. He found that species there inhabited narrow, sharply bounded elevational ranges and that a given species typically inhabited similar elevations at different transect sites along the Pacific escarpment.

Wake and Lynch (1976) performed a detailed analysis of elevational distribution along a transect near the volcano first studied by Schmidt. They corroborated Schmidt's results and filled them out with detailed studies of elevational boundary zones and possible interspecific competition.

Composite transects (grouping all collections) for the Cuchumatanes and Cuilco (Fig. 11) compared to the transect results of Wake and Lynch (1976) for Volcan Tajumulco in the Pacific Uplands indicate that related populations (either conspecifics or members of related species) show similar elevational ranges wherever they occur. Many of the related populations that have significant variation in elevational distribution between transects appear to vary in response to geographic variation in the elevation of the cloud line.

The results for the Cuchumatanes and Cuilco reinforce the generalization that salamander populations in NCA inhabit narrow elevational belts, and recent information for all uplands in NCA indicates that with one exception no single species or group of related species (meaning species groups in *Bolitoglossa* and entire genera in other cases) occurs over an elevational range as broad as 1,300 m. The exception is *Bolitoglossa hartwegi* (with a 1,500-m elevational range) and the *Bolitoglossa veracrucis* species group with a combined elevational range of over 2,800 m. As Wake and Brame (1969) have pointed out, and as these results reiterate, this exceptional group may have played a key role in the invasion of the lowlands by *Bolitoglossa* beta and must have unique physiological attributes, which, if studied, might expand our understanding of the history of salamanders throughout Middle America.

SPECIMENS EXAMINED

Salamanders are known from the following localities in the Cordillera de Los Cuchumatanes, Depto. Huehuetenango, and the Sierra de Cuilco, Depto. Quiché, Guatemala.

Bolitoglossa cuchumatana. CUCHUMATANES. Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 1,300–1,500 m, 3 km S of buildings, MVZ 134524–72, 134574–79, 134582–88, LACM 135482–85; El Porvenir, 134603–16; Finca Chiblac, 149306–14; 1.5 km S of buildings, 134591–602; San Isidro; 134617–22; El Rayo, 134623–25. On ridge ca. 4 km (airline) NW Santa Cruz Barillas, el. 2,000 m, MVZ 149315.

CUILCO. 6.7 mi. (rd.) S Nebaj on Rta. Depto. 3, el. 2,500 m, MVZ 160993–1005. On ridge 2.5 km W, 2 km N (airline), San Miguel Uspantán, el. 2,200–2,500 m, MVZ 149301–05. Oak forest about 2 km (airline) N Nebaj, el. 1,900 m, UMMZ 89110 (holotype), 89111–13.

Bolitoglossa hartwegi. CUCHUMATANES. Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 1,300–1,500 m, MVZ 134629, 134631–33, LACM 135481; 3 km S of buildings, MVZ 149324. 3 km (airline) NNW San Mateo Ixtatán, el. 2,750 m, MVZ 160355–59.

CUILCO. On ridge 2.5 km W, 2 km (airline) N San Miguel Uspantán, el. 2,200–2,500 m, MVZ 149325.

Bolitoglossa jacksoni. CUCHUMATANES. Finca Chiblac, ca. 12 km (airline) NE Santa Cruz Barillas, el. 1,400 m, MVZ 134634 (holotype).

Bolitoglossa lincolni. CUCHUMATANES. Just N San Juan Ixcoy, UMMZ 123275–76. Ca. 9 mi. (rd.) SW El Reposo, summit between El Reposo and Oja Blanca, el. 2,200–2,300 m, MVZ 161791, 119011. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 149359–64; 9.5 km W, 8.5 km (airline) S, La Democracia, el. 2,100–2,500 m, MVZ 103834–38; 10 km W, 143681–87. Paraiso Hoja Blanca Cumbre, UMMZ 129149–50.

CUILCO. Monte at Salquil Grande, el. 2,450 m, UMMZ 89107 (holotype), 89108–09. On ridge NW San Miguel Uspantán, el. 2,200–2,500 m, 2.5 km N Uspantán, MVZ 149365–69; 3.5 km (air) NNW, 160833–39.

Bolitoglossa morio. CUCHUMATANES. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 149335–43. Todos Santos, el. 2,500 m, UMMZ 102285–86 (holotype and paratype of *Oedipus omniumsanctorum*).

Bolitoglossa mulleri. CUCHUMATANES. Town of Santa Cruz Barillas, el. 1,500 m, MVZ 131691–93, 149327–31, 161102. Finca la Florida ca. 2 mi. (rd.) NE Santa Cruz Barillas, el. 1,500 m, MVZ 149326.

Bolitoglossa rostrata. CUCHUMATANES. Ca. 37–40 km (rd.) N Huehuetenango, el. 2,860 m, MVZ 113418–540. Vicinity Capzín, Rta. Nac. 9N, 50–60 km (rd.) N Huehuetenango, el. 2,800–3,200 m, 52.7 km N, MVZ 114722–65; ca. 50 km N, km post 139, 115494–524, 117039. 2–8 km N, W, and S (airline) San Mateo Ixtatán, el. 2,700–3,200 m; 2 km WSW, MVZ 150940–160299; 6 km WSW, 160300–333; 5 km SSW, 160334–49; 7 km SSW, 160350–51; 3 km NNW, 160353, 160360; 4 km NW, 163928–31, 163973; 2 km W, 171198–202; 4 km SW, 171220–41; 4 km N, 171242; 4 km W, 171173–97; 4 km NW, 171112–43; 5 km SW, 171215; 5 km S, 171203–14; 6 km W, 171163–72; 8 km W, 171144–62. Paquix-Todos Santos road, 4–7 km SE Todos Santos, MVZ 149198–206, 108616–30, 108631–72. 13.6 mi. (rd.) N Santa Eulalia along Rta. Nac. 9N, MVZ 149228. 5.1 mi. (rd.) N Santa Eulalia along Rta. Nac. 9N, MVZ 108673–95, 109296. Cumbre between Ixtiapoc and Villa Linda, el. 2,800–3,400 m, UMMZ 120007–08. Cumbre between Yaiquich and San Mateo Ixtatán, el. 3,000 m, UMMZ 120009. Todos Santos, el. 9,000–10,000 ft., UMMZ 120465–66, 120487. Mina Villa Linda, UMMZ 130073. 9 km (rd.) SW San Juan Ixcoy, el. 2,900 m, UMMZ 120011. Rta. Nac. 9N, 7.4 mi. (rd.) SW San Juan Ixcoy, MVZ 108696–728. Rta. Nac. 9N, 10.6 mi. (rd.) SW San Juan Ixcoy, MVZ 108729–32. 8 km W San Mateo Ixtatán, el. 3,100 m, MVZ 171148–62. 3 km NNW San Mateo Ixtatán, el. 8,700 ft., MVZ 150940–1000, 160201–91, 160353, 160360; 4 km NW, 2,750 m, 171112–43. 2 km WSW San Mateo Ixtatán, el. 8,850 ft., MVZ 160292–

99; 2 km W, 2,750 m, 171198–202. 6 km WSW San Mateo Ixtatán, el. 9,150–9,450 ft., MVZ 160330–33, 160352, 160354; 6 km W, 171163–72. 5 km SSW San Mateo Ixtatán, el. 8,650–9,150 ft., MVZ 160343–49; 4 km SW, 2,835–2,965 m, 171220–41; 4 km W, 2,900 m, 171173–97; 5 km SW, 2,965–3,045 m, 171215–19; 5 km S, 3,150 m, 171203–14. 7 km SSW San Mateo Ixtatán, el. 9,650 ft., MVZ 160350–51. 4 km NW San Mateo Ixtatán, el. 2,750 m, MVZ 163928–31, 163973; 4 km N, 2,650 m, 171242.

CUILCO. Above Salquil Grande, el. 3,000 m, UMMZ 89116–18. 6.7 mi. (rd.) S Nebaj by Rta. Depto. 3, el. 2,500 m, MVZ 160992. On ridge 2.5 km W, 2 km (airline) N San Miguel Uspantán, el. 2,260–2,640 m, MVZ 149229–300.

Bolitoglossa rufescens. CUCHUMATANES. Vicinity Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 950–1,100 m, MVZ 134626–28.

Bolitoglossa rufescens. CUCHUMATANES. Vicinity Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 950–1,100 m, MVZ 134626–28.

Bolitoglossa stuarti (tentative identification). CUCHUMATANES. 15 km (airline) W La Democracia, el. 1,850 m, UMMZ 126781.

Bradytriton silus. CUCHUMATANES. Finca Chiblac, 15 km NE Barillas, el. 4,300 ft. (1,310 m), MVZ 131586, 131587 (holotype), 131589–94, 134635–37, 134638, 173063–64; LACM 134566.

Dendrotriton cuchumatanus. CUCHUMATANES. Along Rta. Nac. 9N, 8.5 km (rd.) SW San Juan Ixcoy, el. 2,860 m, MVZ 113002 (holotype), 113003–05, 113007–19, 113021–22; LACM 105296–97.

Dendrotriton rabbi. CUCHUMATANES. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 105298–300, 149702–05, 149139. 2 km (airline) WSW San Mateo Ixtatán, el. 8,850 ft., MVZ 160437. 3 km (airline) NNW San Mateo Ixtatán, el. 2,750 m, 160422–36. Cloud forest above summit of road between El Reposo and Oja Blanca ca. 9 mi. by rd., SW El Reposo, el. 2,200–2,300 m, MVZ 109297–301.

CUILCO. 9.5 km W, 8.5 km S (airline), La Democracia, Montañas de Cuilco, el. 2,100–2,500 m, MVZ 114766–96, 143920–26, 103839 (holotype), 103840–78, LACM 105298–300. On ridge 2.5 km W, 2 km (airline) N, San Miguel Uspantán, el. 2,400 m, MVZ 160895–96.

Nyctanolis pernix. CUCHUMATANES. Finca Chiblac, 10 km (air) NE Barillas, el. 1,370 m (4,500 ft.), MVZ 131583–85, 134639–40, 134641 (holotype), 134642–44, 149370–73; MCZ 100154.

Pseudoeurycea rex. CUCHUMATANES. Vicinity El Retiro and Peña Blanca peak, el. 2,800–3,300 m, MVZ 149404–33, 149464–520, 149522–58, 149693–700. Vicinity Capzín, Rta. Nac. 9N, 50–60 km (rd.) N Huehuetenango, el. 2,900–3,300 m, MVZ 160973–82, 134211–401. 2–8 km N, W, and S (airline) San Mateo Ixtatán, el. 2,750–3,200 m; 5 km, MVZ 171243–52; 7 km SSW, 160410–19; 6 km WSW, 160409; 4 km NW, 167796–803. Between Cumbre Yaiquich and San Mateo Ixtatán, 3,000 m, UMMZ 120067. 10 km (rd.) SW San Juan Ixcoy, el. 3,300 m, UMMZ 120068.

CUILCO. Above Salquil Grande, el. 3,000 m, UMMZ 89114–15.

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LITERATURE CITED

Boulenger, G.A. 1882. Cat. Batrach. Grad. British Museum, London. 127 pp., 9 plates.

Brocchi, P. 1883. Étude des batraciens de l'Amérique Centrale. Mission Scientifique au Mexique et dans l'Amérique Centrale 3(2):1–122, 21 plates.

Cope, E.D. 1868. Sixth contribution to the herpetology of tropical America. Proc. Acad. Natur. Sci. Philadelphia 1868:305–313.

———. 1869. A review of the species of the Plethodontidae and Desmognathidae. Proc. Acad. Natur. Sci. Philadelphia 21:93–118.

Duellman, W.E. 1963. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. Univ. Kansas Publ. Mus. Natur. Hist. 15(5):205–249.

Dunn, E.R. 1921. Two new Central American salamanders. Proc. Biol. Soc. Washington 34:143–145.

———. 1924. New salamanders of the genus *Oedipus* with a synoptical key. Field Mus. Natur. Hist. Zool. Ser. 12: 95–100.

———. 1926. The salamanders of the family Plethodontidae. Smith College, Northampton, Mass., viii + 441 pp.

Elias, P., and D.B. Wake. 1983. *Nyctanolis pernix,* a new genus and species of plethodontid salamander from northwestern Guatemala and Chiapas, Mexico. Pages 1–12 *in* A. G. J. Rhodin and K. Miyata (eds.), Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams. Mus. Comp. Zool., Cambridge, Mass.

Hanken, J., J.F. Lynch, and D.B. Wake. 1980. Salamander invasion of the tropics. Natur. Hist. 89(12):46–53.

Lynch, J.F., and D.B. Wake. 1975. Systematics of the *Chiropterotriton bromeliacea* group (Amphibia: Caudata), with description of two new species from Guatemala. Los Angeles Co. Natur. Hist. Mus., Contrib. Sci. 265: 1–45.

———. 1978. A new species of *Chiropterotriton* (Amphibia: Caudata) from Baja Verapaz, Guatemala, with comments on relationships among Central American members of the genus. Los Angeles Co. Natur. Hist. Mus., Contrib. Sci. 294:1–22.

McCoy, C.J., and C.F. Walker. 1966. A new salamander of the genus *Bolitoglossa* from Chiapas. Occ. Papers Mus. Zool. Univ. Mich. 649:1–11.

Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27:159–188.

Schmidt, K.P. 1933. New reptiles and amphibians from Honduras. Zool. Ser. Field Mus. Nat. Hist. 322:15–22.

———. 1936. Guatemalan salamanders of the genus *Oedipus.* Zool. Ser. Field Mus. 20:135–166.

Smith, H.M. 1945. Herpetological collecting in banana fields of Mexico. Ward's Natur. Sci. Bull. 1:1–7.

Smith, W.H. 1877. The tailed amphibians. Thesis, Michigan Univ.

Stuart, L.C. 1943a. Taxonomic and geographic comments on Guatemalan salamanders of the genus *Oedipus.* Misc. Publ. Mus. Zool. Univ. Mich. 56:1–33.

———. 1943b. Comments on the herpetofauna of the Sierra de los Cuchumatanes of Guatemala. Occ. Papers Mus. Zool. Univ. Mich. 471:1–29.

———. 1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Mich. 69:1–109.

———. 1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contrib. Lab. Vert. Biol. Univ. Mich. 45:1–77.

———. 1952. Some new amphibians from Guatemala. Proc. Biol. Soc. Washington 65:1–12.

Taylor, E.H. 1941. New amphibians from the Hobart M. Smith Mexican Collections. Univ. Kansas Sci. Bull. 28: 141–167.

———. 1944. The genera of plethodont salamanders in Mexico, Pt. 1. Univ. Kans. Sci. Bull. 30:189–232.

Taylor, E.H., and H.M. Smith. 1945. Summary of the collections of amphibians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proc. U.S. Natl. Mus. 95:521–613.

Wake, D.B., and A.H. Brame, Jr. 1963. The status of the plethodontid salamander genera *Bolitoglossa* and *Magnadigita.* Copeia 1963:382–387.

———. 1969. Systematics and evolution of neotropical salamanders of the *Bolitoglossa helmrichi* group. Natur. Hist. Mus. Los Angeles County, Contrib. Sci. 175:1–40.

Wake, D.B., and I.G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. J. Morph. 122:265–306.

Wake, D.B., and P. Elias. 1983. New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). Natur. Hist. Mus. Los Angeles County, Contrib. Sci. 345:1–19.

Wake, D.B., and J.F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Bull. Natur. Hist. Mus. Los Angeles Co. 25:1–65.

———. 1982. Evolutionary relationships among Central American salamanders of the *Bolitoglossa franklini* group, with a description of a new species from Guatemala. Herpetologica 38:257–272.

Wake, D.B., S.Y. Yang, and T.J. Papenfuss. 1980. Natural hybridization and its evolutionary implications in Guatemalan plethodontid salamanders of the genus *Bolitoglossa.* Herpetologica 36:335–345.

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INSTRUCTIONS FOR AUTHORS

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CONTRIBUTIONS IN SCIENCE

SYSTEMATICS OF XANTUSIID LIZARDS OF THE GENUS *LEPIDOPHYMA* IN NORTHEASTERN MEXICO

Robert L. Bezy

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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SYSTEMATICS OF XANTUSIID LIZARDS OF THE GENUS *LEPIDOPHYMA* IN NORTHEASTERN MEXICO

Robert L. Bezy[1]

ABSTRACT. Discriminant analyses of variation among 30 scale characters indicate that the 21 populations of *Lepidophyma* from northeastern Mexico form six morphological groups. Two of 27 population samples from southern Mexico approach the northern groups in discriminant space. When viewed in terms of univariate differences and geographic distribution, the northern population groups constitute four unique morphological entities that are considered to represent species units. The most distinctive is *Lepidophyma gaigeae* occurring in limestone habitats in the Sierra Madre Oriental of Hidalgo and Querétaro. *Lepidophyma occulor* is known from four localities in the semi-arid Jalpan region of Querétaro and San Luis Potosí, and the cavernicolous *L. micropholis* is confined to the Sierra del Abra of Tamaulipas and San Luis Potosí. The wide-ranging *L. sylvaticum* includes four moderately divergent population groups: northern Madrean (Tamaulipas to San Luis Potosí), southern Madrean (San Luis Potosí to Hidalgo), Veracruzan, and western (Mesa Central of San Luis Potosí to Nuevo León).

The karyotypes of *L. gaigeae* and *L. occulor* are unique within the genus, while most *L. sylvaticum* are chromosomally identical to *L. micropholis.* A heteromorphism in microchromosomes was observed in six females of one population of *L. sylvaticum,* and could represent either ZW sex chromosomes or allodiploidy. This same population plus one in Querétaro have statistically significantly skewed sex ratios that may be associated with hybridization.

RESUMEN. Los análisis discriminatorios de variación entre 30 caracteres de las escamas, indican que las 21 poblaciones de *Lepidophyma* del noreste de México forman seis grupos morfológicos. Dos de los muestreos de la población del sur de México se aproximan a los grupos del norte en espacio discriminatorio. Cuando se examinan en términos de diferencias univariadas y de distribución geográfica, los grupos de la población del norte constituyen cuatro entidades morfológicas únicas que se considera representan unidades de especie. La más distintiva es *Lepidophyma gaigeae* que vive en habitats de piedra caliza en la Sierra Madre Oriental de Hidalgo y Querétaro. *Lepidophyma occulor* se conoce de cuatro localidades de la región semiárida de Jalpan de Querétaro y San Luis Potosí, y el cavernícola *L. micropholis* se encuentra confinado a la Sierra del Abra de Tamaulipas y San Luis Potosí. *L. sylvaticum* de amplia distribución en y cerea de la Sierra Madre Oriental incluye cuatro grupos poblacionales moderadamente divergentes: norte (Tamaulipas a San Luis Potosí), sur (San Luis Potosí a Hidalgo), Veracruz, y occidental (Mesa Central de San Luis Potosí a Nuevo León).

Los cariotipos de *L. gaigeae* y *L. occulor* son únicos dentro del género mientras que la mayoría de *L. sylvaticum* son cromosómicamente idénticos a *L. micropholis.* Se observó heteromorfismo de microcromosomas en seis hembras de una población de *L. sylvaticum* y podría representar ya sea cromosomas sexuales ZW o alodiploidía. Esta misma población, más una en Querétaro han torcido estadísticaniente en forma significativa las proporciones en los sexos que pudieran ser asociadas con hibridización.

INTRODUCTION

Lizards of the xantusiid genus *Lepidophyma* range from Panama to Nuevo León, Mexico, living principally in wet tropical lowland forests in the south, but becoming increasingly restricted to montane and/or rimose habitats in the semi-arid regions to the north. In the rugged ranges of the Sierra Madre Oriental, and in the canyons and valleys along both of its flanks, are a morphologically diverse array of *Lepidophyma* populations. While most of these populations remain taxonomically unallocated, four have been named, and two of these names have been alternatively associated with species occurring to the south (e.g., Smith, 1942; Walker, 1955).

In this paper, the problems of discordant morphological variation, geographic isolation, and small sample sizes of the populations of *Lepidophyma* in northeastern Mexico are handled by treating each locality as a separate sample, and employing multivariate analyses of variation to identify groups of morphologically similar populations. Additional multivariate comparisons with populations to the south, and analyses of univariate differences among all population groups are used to diagnose morphological species. Names are then assigned to the units on the basis of included type or topotypic material, the species of *Lepidophyma* recognized in northeastern Mexico are summarized in brief accounts, including comments on chromosomal variation and skewed sex ratios in certain populations, and a key is presented.

MATERIALS AND METHODS

A total of 152 specimens of *Lepidophyma* from Mexico north of 19°N latitude were used in the analyses. This includes all material studied from the area, except that referable to *L. gaigeae.* One sample (N = 20) of the over 500 known specimens of the species was used as a reference population. In addition, 31 population samples (N = 188) from southern and western Mexico were utilized in the comparative analyses. The selection of 19°N latitude as the southern limit of the study area is based on a distributional hiatus for the genus in the transvolcanic region (ca. 19–20°N), and on preliminary observations suggesting that the populations occurring to the north of this distributional gap share a number of unique morphological similarities.

The localities of the specimens were determined on available maps, and geographic samples were constituted with all specimens from a given locality (or in a few instances by pooling adjacent localities separated by less than 20 km) to form a total of 21 population samples of *Lepidophyma* from northern Mexico (Fig. 1). The specimens and localities are listed in specimens examined, below.

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[1] Section of Herpetology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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The analyses use a total of 30 scale characters, 20 meristics, and 10 ratios of the relative size or proportions of individual scales. No significant sexual dimorphism, ontogenetic variation, or correlation was detected among the 30 characters. The characters were selected largely on the basis of their purported diagnostic strength in the genus (Bezy, 1973; Bezy et al., 1982; Mosauer, 1936; Smith, 1942, 1973; Smith and Alvarez del Toro, 1977; Taylor, 1939; Walker, 1955; Werler, 1957; Werler and Shannon, 1957).

Scale terminology follows Savage (1963). The characters are defined below.

1.	FPT	Femoral pores (total both sides).
2.	LTR	Lateral rows of tubercles (axilla to groin).
3.	DBPVR	Dorsals between paravertebral rows of tubercles.
4.	IWD1	Dorsal interwhorls in first caudal segment.
5.	IWV1	Ventral interwhorls in first caudal segment.
6.	PTMP	Pretympanics (total both sides) separating postocular from second postorbital supralabial.
7.	DBPVT	Distance between large paravertebral tubercles within-row, expressed in number of middorsal scales.
8.	GC1IL	Gulars contacting first pair of infralabials.
9.	GUL	Gulars (fold to second infralabials).
10.	PVTL	Large tubercles in paravertebral row (axilla to groin).
11.	VL	Ventrals (gular to vent; includes preanals).
12.	4TL	Fourth toe lamellae (ventral).
13.	4TLD	Fourth toe lamellae divided (i.e., with ca. midventral sutures).
14.	DOR	Dorsals occiput to rump (above vent).
15.	DAPVR	Dorsals in row immediately above paravertebral row (axilla to groin).
16.	PVR	Total scales in paravertebral row (axilla to groin).
17.	PVS	Scales in paravertebral row (a–g) smaller than 1.5 dorsals.
18.	PVT1	Scales in paravertebral row (a–g) larger than 1.5 dorsals.
19.	PVT2	Scales in paravertebral row (a–g) larger than 2.0 dorsals.
20.	PVT3	Scales in paravertebral row (a–g) larger than 3.0 dorsals.
21.	RPOL	Length of postocular/length of orbit.
22.	RPAW	Width of posterolateral preanal/width of posteromedial preanal.
23.	RPFML	Prefrontal: length along midline/length along lateral border.
24.	RPFL1	Prefrontal: length of mid-line suture/length along lateral border.
25.	RMW	Width of median (prefrontal)/anterior width of interparietal.
26.	RNL	Length of nasal/length of postparietal.
27.	RML	Length of median (prefrontal)/length of frontal.
28.	RAPPSL	Length (total both sides) of all anomalous sutures on postparietals/length of postparietals.
29.	RPNH	Height of postnasal/height of anterior loreal.
30.	RSLH	Height of second postorbital supralabial/height of first postorbital supralabial.

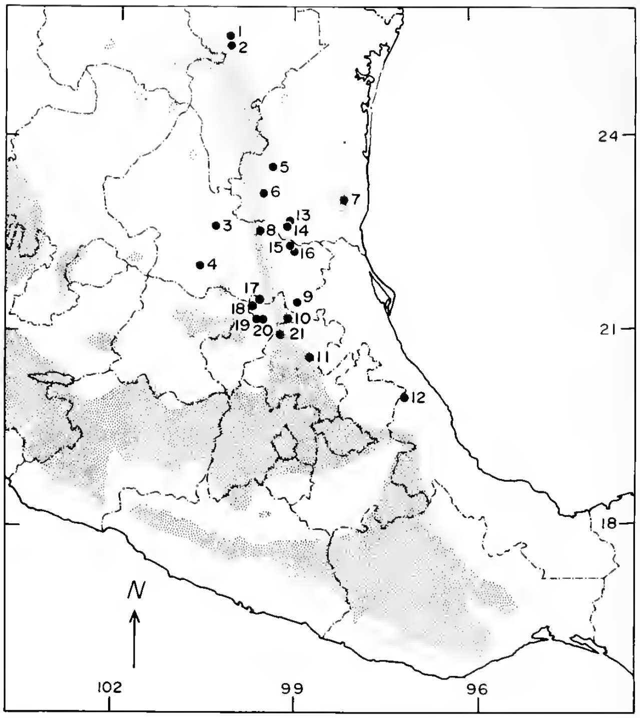

Figure 1. Location of the 21 population samples of *Lepidophyma* in Mexico north of 19°N. Stippled area indicates approximate distribution of pine-oak woodland (after Leopold, 1959). Population numbers are those used throughout the paper (see Specimens Examined for localities).

Variation in the 30 characters was analyzed univariately with BMDP1D for simple data description, and multivariately with BMDP7M for stepwise discriminant analysis (Dixon, 1981). In all discriminant analyses the *a priori* groups were individual population samples rather than population groups or species.

RESULTS AND DISCUSSION

In the following sections the results of discriminant analyses of populations of *Lepidophyma* from northern Mexico are used to identify northern population groups, which in turn are compared with populations from southern Mexico. The northern population groups are then viewed relative to their univariate differences and geographic relationships to arrive at the definition of unique morphological units. Finally, names are allocated to these units (morphospecies) on the basis of included topotypic and/or type material, and each species is briefly summarized.

NORTHERN MEXICO POPULATIONS

The initial discriminant analysis utilized 30 characters and 18 of the 21 populations from northeastern Mexico (Fig. 1,

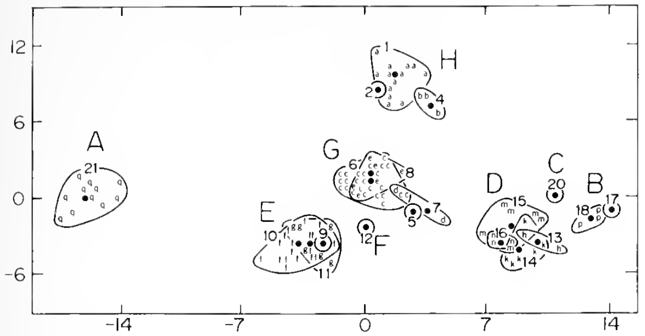

Figure 2. Nineteen population samples of *Lepidophyma* from northeastern Mexico plotted on the first two canonical variables for 25 characters. Population centroids are indicated by dots, and the number of the sample is placed along the line enclosing all included specimens (lower case letters). Upper case letters indicate population groups identified by the analysis.

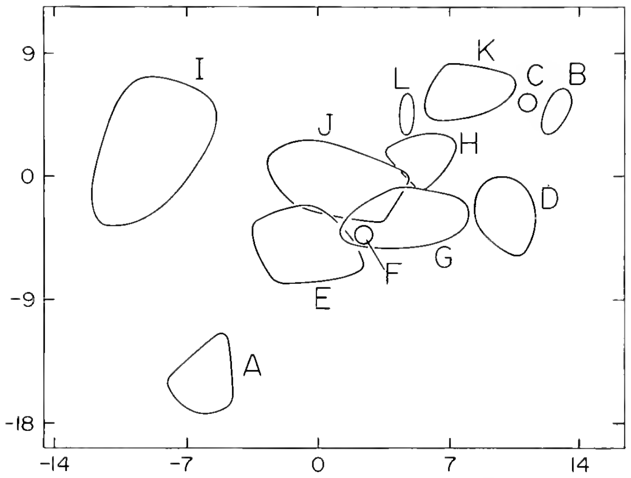

Figure 3. Twelve population groups of *Lepidophyma* from Mexico plotted on the first two canonical variables for 30 characters. Lines enclose all individuals comprising each of the eight northern (A–G) and four southern (I–L) population groups.

Table 1). In samples 3, 5, and 19 there are no individuals on which all of the characters could be scored. The analysis resulted in high resolution of the populations in that 99 percent (127/128) of the individuals were "correctly" assigned by the posterior classification to the locality sample of which they were a member (one specimen of sample 7 was misassigned to 6). A second analysis was performed excluding five characters (IWD1, IWV1, RPFML, RPFL1, RML) in order to allow inclusion of sample 5 (Fig. 2). Samples 3 and 19 were not included in any of the multivariate analyses due to the limitations of the data available from them. While both analyses produced similar results, the reduction in characters of the second lowered the accuracy of the posterior classification (96%; 126/131).

From the second analysis, eight population groups were identified on the basis of overlap or juxtaposition of the included samples and the distance between groups in discriminant space (Fig. 2). The first canonical variable accounts for 57 percent of the variation, is most heavily loaded with LTR, PVS, PVR, DOR, and GUL (in order of decreasing weight), and places group A at one end, and B, C, and D at the other, with E, F, G, and H occupying intermediate positions. The second coordinate has heavy loadings for PVS, PVR, PVT1, LTR, and FPT, accounts for 21 percent of the variation, and effectively separates groups E, G, and H from one another.

The sample comprising group A (21) is highly isolated in discriminant space from all other populations, suggesting it is not a member of the same morphological complex. Group D is a discrete cluster of four overlapping populations (13–16) that is approximately equidistant from B (17, 18) and C (20). The three populations of group E (9–11) form a moderately tight cluster that is only weakly separated from the loosely associated populations of G (5–8) and the one specimen (12) comprising the intermediate group F. The three populations of group H (1, 2, 4) are well separated from their nearest discriminant neighbor, group G.

COMPARISONS WITH SOUTHERN GROUPS

Twenty-seven samples from southern Mexico were compared with the 18 northern populations to identify those that might be closest morphologically to northern groups. The initial discriminant anlaysis utilized 30 characters and a total of 288 specimens arrayed in 45 populations (Fig. 3), and produced high resolution of the populations in that the accuracy of the posterior classification was 98 percent. The first canonical variable is most heavily loaded with PVS, DBPVT, LTR, GUL, and PVR, and expresses 43 percent of the total dispersion; the second expresses 21 percent and is dominated by LTR, PVS, PVTL, FPT, and RPAW. The graph (Fig. 3) was used primarily to identify those southern population groups that are multivariately most similar to the northern ones and which are further resolved in subsequent analyses containing fewer populations.

All but one (F) of the eight northern groups identified in the previous analysis remain separated from each other, although they are approached or overlapped by three southern groups (J, K, L) (Fig. 3). Northern groups B, C, and D were well separated from both southern and northern populations and thus are not included in the subsequent analyses. Southern group I is also strongly separated from all populations, and its nearest discriminant neighbor is another southern group (J). Consequently, it was also excluded from further analysis. In the following analyses, northern groups E through H are compared in greater detail first with K and L, and then with J.

The 10 populations of northern groups E, F, G, and H were analyzed together with the four populations of southern groups K and L (Fig. 4). The posterior classification was 98 percent (121/123) accurate, one specimen of sample 11 being misassigned to 10 (both group E) and one of sample 43 to 44 (both group K). The first canonical variable accounts for 60 percent of the total dispersion, is heavily loaded with

Table 1. Variation among 30 scale characters for 21 population samples of *Lepidophyma* from northern Mexico. Sample size is (*in parentheses*) under each of the population numbers (POP). In each cell the upper number is the mean; the middle, the standard error; and the lower, the range. See text for character abbreviations and locality data.

POP	FPT	LTR	DBPVR	IWD1	IWV1	PTMP	DBPVT	GC1IL	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
1	31.3	18.1	3.17	3.0	2.1	2.1	2.83	.3	45.0	15.9	36.1	25.3	8.1	161.2	83.2	44.8
(*15*)	.37	.59	.093	0	.09	.07	.080	.13	.59	.21	.15	.33	.56	1.88	.99	1.13
	29–34	15–22	2.5–4.0	3	2–3	2–3	2.5–3.5	0–1	42–49	15–17	35–37	24–29	4–12	150–174	77–91	39–53
2	29.0	19.0	2.50	3.0	2.0	3.0	2.50	1.0	46.0	17.0	35.0	26.0	7.0	164.0	83.0	43.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	29	19	2.5	3	2	3	2.5	1	46	17	35	26	7	164	83	43
3	29.0	—	3.50	2.0	2.0	2.0	3.00	1.0	46.0	—	—	20.0	5.0	—	—	—
(*1*)	0	—	0	0	0	0	0	0	0	—	—	0	0	—	—	—
	29	—	3.5	2	2	2	3.0	1	46	—	—	20	5	—	—	—
4	27.0	17.0	3.38	2.5	1.5	2.3	3.00	.3	45.0	16.0	35.3	23.0	6.3	172.5	91.0	47.0
(*4*)	.41	0	.125	.58	.29	.25	0	.25	.71	.41	.25	.41	.25	3.43	1.47	1.08
	26–28	17	3.0–3.5	2–3	1–2	2–3	3.0	0–1	43–46	15–17	35–36	22–24	6–7	163–178	87–94	44–49
5	28.0	31.0	5.00	—	—	1.0	4.50	3.0	56.0	15.0	38.0	31.0	15.0	207.0	98.0	63.0
(*1*)	0	0	0	—	—	0	0	0	0	0	0	0	0	0	0	0
	28	31	5.0	—	—	1	4.5	3	56	15	38	31	15	207	98	63
6	27.8	29.3	3.89	3.2	1.8	2.0	3.08	.5	48.3	16.8	35.8	26.3	14.6	182.1	93.5	51.0
(*32*)	.45	.40	.122	.52	.11	.15	.106	.11	.49	.35	.23	.33	.53	1.96	1.26	.87
	24–35	24–34	3.0–5.0	2–4	0–3	0–4	1.0–4.0	0–2	43–55	15–23	34–39	23–30	9–23	166–217	83–112	42–62
7	28.0	29.0	4.83	3.3	2.0	2.0	3.50	.3	51.0	16.7	35.3	25.3	13.3	206.3	107.0	57.0
(*4*)	1.53	1.00	.167	.58	0	0	.289	.25	1.78	.33	.88	.67	.88	5.36	5.51	5.57
	26–31	27–30	4.5–5.0	3–4	2	2	3.0–4.0	0–1	48–55	17–18	34–37	24–26	12–15	196–214	96–113	46–64
8	26.2	27.8	4.08	3.5	2.5	2.2	3.08	1.0	45.5	18.0	36.0	27.7	14.2	191.3	97.8	53.8
(*6*)	.40	1.14	.201	.55	.22	.31	.201	0	1.09	1.83	.37	.56	.98	2.91	2.12	3.28
	25–27	25–31	3.5–5.0	3–4	2–3	1–3	2.5–4.0	1	43–50	15–27	35–37	26–30	11–18	180–199	91–104	42–64
9	26.0	36.0	4.00	3.0	2.0	2.0	2.50	0	42.0	27.0	37.0	24.0	14.0	191.0	89.0	56.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	26	36	4.0	3	2	2	2.5	0	42	27	37	24	14	191	89	56
10	26.1	33.7	4.64	3.1	1.9	1.6	1.71	.6	44.0	24.9	34.8	25.5	17.7	180.1	91.0	52.2
(*22*)	.31	.44	.082	.47	.06	.15	.146	.11	.42	1.47	.24	.14	.52	1.33	1.25	1.18
	24–30	31–38	4.0–5.0	2–4	1–2	0–2	1.0–3.0	0–1	41–49	15–39	33–37	24–27	13–23	165–188	78–99	40–66
11	25.2	34.2	4.25	4.0	2.2	2.2	3.25	1.1	47.8	19.0	36.6	25.7	18.8	184.6	95.5	61.4
(*10*)	.55	.51	.112	.67	.20	.13	.186	.18	.83	1.09	.16	.45	.57	2.57	1.86	1.63
	23–28	32–36	3.5–4.5	3–5	1–3	2–3	2.5–4.0	0–2	45–54	15–25	36–37	23–28	16–21	167–192	88–104	56–73
12	31.0	35.0	5.00	4.0	2.0	3.0	4.00	0	47.0	17.0	36.0	28.0	18.0	205.0	103.0	53.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	31	35	5.0	4	2	3	4.0	0	47	17	36	28	18	205	103	53
13	32.7	29.3	5.67	5.0	3.0	.7	4.67	.3	62.0	16.0	36.3	25.3	12.3	243.3	126.7	70.3
(*3*)	1.45	1.20	.167	0	0	.67	.333	.33	3.21	.58	.33	.88	1.20	4.41	7.26	4.81
	30–35	27–31	5.5–6.0	5	3	0–2	4.0–5.0	0–1	57–68	15–17	36–37	24–27	10–14	235–250	115–140	61–77
14	32.6	30.6	6.27	4.7	2.5	1.2	4.68	.4	62.4	16.2	35.9	26.5	13.9	244.2	122.5	73.4
(*11*)	.62	.59	.124	.47	.16	.25	.122	.16	.88	.23	.21	.43	.64	1.50	2.14	2.00
	29–36	28–35	6.0–7.0	4–5	2–3	0–2	4.0–5.0	0–1	58–68	15–17	35–37	24–29	11–17	235–251	112–134	65–85
15	29.5	29.2	4.92	3.7	1.8	1.8	5.00	.5	56.8	15.8	36.3	26.0	13.2	237.5	128.0	62.5
(*6*)	.56	.40	.239	.52	.17	.17	0	.34	.70	.31	.21	.45	.65	2.43	2.36	2.14
	28–31	28–31	4.0–5.5	3–4	1–2	1–2	5.0	0–2	55–60	15–17	36–37	25–28	11–15	231–245	119–135	52–66
16	29.8	30.2	4.80	4.0	2.2	2.0	4.90	.8	58.6	15.6	36.0	27.0	16.8	239.4	120.4	60.8
(*5*)	.80	.49	.123	0	.20	0	.100	.20	.81	.40	.32	.71	.66	1.40	2.42	2.43
	28–32	29–31	4.5–5.0	4	2–3	2	4.5–5.0	0–1	56–61	15–17	35–37	25–29	15–19	236–244	112–127	56–70
17	19.0	22.5	5.00	3.5	2.0	2.0	4.00	0	67.0	17.0	37.5	25.0	6.0	228.5	113.0	54.0
(*2*)	1.00	1.50	0	.71	0	0	0	0	4.00	0	.50	0	0	4.50	1.00	1.00
	18–20	21–24	5.0	3–4	2	2	4.0	0	63–71	17	37–38	25	6	224–233	112–114	53–55
18	19.0	21.3	4.67	3.0	1.7	2.0	4.00	0	61.0	15.7	35.3	24.7	7.3	239.3	118.3	60.7
(*3*)	1.15	.67	.441	0	.33	0	0	0	.58	.67	.33	.33	.88	1.33	1.86	4.63
	17–21	20–22	4.0–5.5	3	1–2	2	4.0	0	60–62	15–17	35–36	24–25	6–9	238–242	116–122	53–69
19	19.5	24.0	5.00	4.0	2.0	2.0	4.50	—	66.0	17.0	36.5	24.0	8.5	—	—	—
(*2*)	.50	0	0	0	0	0	.500	—	1.00	1.00	.50	0	.50	—	—	—
	19–20	24	5.0	4	2	2	4.0–5.0	—	65–67	16–18	36–37	24	8–9	—	—	—
20	19.5	21.5	3.00	3.0	2.0	2.5	4.00	0	60.0	15.5	35.5	22.0	4.5	216.5	101.0	53.5
(*2*)	1.50	1.50	0	0	0	.50	0	0	1.00	.50	.50	0	1.50	3.50	1.00	4.50
	18–21	20–23	3.0	3	2	2–3	4.0	0	59–61	15–16	35–36	22	3–6	213–220	100–102	49–58
21	33.5	46.5	4.02	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.38	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–5.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58

Table 1. Continued.

POP	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
1	13.9	30.0	20.2	15.7	.229	.603	.459	.382	.117	.136	.100	0	.704	1.079
(*15*)	.98	.55	.81	.21	.0249	.0311	.0409	.0475	.0514	.0086	.0491	0	.0118	.0476
	7–20	26–34	15–28	15–17	.15–.56	.39–.82	.11–.70	.11–.65	0–.56	.09–.20	0–.63	0	.65–.81	.91–1.61
2	15.0	28.0	17.0	16.0	.247	.788	.456	.456	0	.121	0	0	.754	.890
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	15	28	17	16	.25	.79	.46	.46	0	.12	0	0	.75	.89
3	—	—	—	—	.124	—	.401	.351	0	.309	0	0	.723	1.245
(*1*)	—	—	—	—	0	—	0	0	0	0	0	0	0	0
	—	—	—	—	.12	—	.40	.35	0	.31	0	0	.72	1.25
4	15.0	32.0	26.5	16.3	.181	.706	.485	.485	0	.238	0	.221	.907	1.099
(*4*)	1.47	1.08	.87	.48	.0184	.0289	.0321	.0321	0	.0151	0	.2214	.1605	.0560
	12–19	29–34	24–28	15–17	.14–.23	.64–.77	.42–.54	.42–.54	0	.22–.28	0	0–.89	.73–1.39	.98–1.21
5	43.0	20.0	15.0	14.0	.241	.400	—	—	0	.072	—	0	.742	1.156
(*1*)	0	0	0	0	0	0	—	—	0	0	—	0	0	0
	43	20	15	14	.24	.40	—	—	0	.07	—	0	.74	1.16
6	22.1	28.9	21.4	12.0	.181	.539	.564	.357	.272	.171	.375	.007	.781	1.172
(*32*)	1.25	.72	.84	.59	.0075	.0132	.0222	.0362	.0612	.0082	.0865	.0042	.0236	.0218
	12–37	20–35	15–34	4–18	.11–.27	.41–.69	.38–.84	0–.71	0–.84	.11–.29	0–1.26	0–.11	.66–1.40	.86–1.41
7	26.3	30.7	21.3	15.3	.158	.593	.623	.522	0	.133	0	0	.783	1.279
(*4*)	6.23	.67	2.85	.33	.0006	.0382	.0177	.0203	0	.0318	0	0	.0121	.0246
	14–34	30–32	18–27	15–16	.16	.53–.66	.60–.66	.48–.54	0	.08–.19	0	0	.76–.80	1.23–1.32
8	27.5	26.3	19.3	14.0	.181	.545	.513	.344	.213	.164	.319	.46	.727	1.113
(*6*)	4.43	1.65	2.01	1.03	.0145	.0354	.0504	.0800	.1265	.0130	.2134	.3021	.0282	.0359
	12–38	19–30	16–29	9–16	.13–.23	.40–.66	.36–.68	0–.52	0–.77	.13–.22	0–1.32	0–1.65	.64–.81	1.01–1.23
9	24.0	32.0	27.0	0	.154	.300	.754	.422	.623	.132	.682	0	.787	1.253
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	24	32	27	0	.15	.30	.75	.42	.62	.13	.68	0	.79	1.25
10	21.0	31.2	24.0	2.5	.188	.497	.540	.455	.141	.167	.109	.017	.856	1.180
(*22*)	1.67	.94	1.02	.73	.0140	.0190	.0218	.0259	.0585	.0110	.0483	.0173	.0283	.0338
	7–42	22–37	17–33	0–13	.07–.32	.31–.68	.35–.82	.14–.65	0–.95	.09–.27	0–.85	0–.38	.71–1.37	.95–1.55
11	31.5	29.9	19.1	2.9	.176	.589	.475	.480	.045	.172	.022	.140	.803	1.141
(*10*)	1.89	1.04	.99	.75	.0119	.0364	.0322	.0433	.0284	.0160	.0137	.1102	.0209	.0369
	21–40	26–35	16–25	0–6	.10–.22	.39–.75	.27–.69	.27–.81	0–.28	.12–.28	0–.13	0–1.12	.71–.91	.84–1.25
12	20.0	33.0	22.0	9.0	.200	.466	1.071	.283	.729	.106	.739	0	.750	1.141
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	20	33	22	9	.20	.47	1.07	.28	.73	.11	.74	0	.75	1.14
13	42.0	28.3	23.3	15.0	.146	.498	.562	.611	0	.188	0	0	.744	1.168
(*3*)	5.13	2.85	3.84	1.15	.0042	.1159	.0405	.0654	0	.0051	0	0	.0342	.1171
	35–52	25–34	19–31	13–17	.14–.15	.27–.63	.49–.63	.49–.71	0	.18–.19	0	0	.70–.81	.94–1.32
14	42.6	30.7	23.5	15.6	.168	.570	.579	.579	0	.129	0	0	.745	1.176
(*11*)	2.38	.76	1.26	.34	.0062	.0313	.0321	.0321	0	.0027	0	0	.0276	.0701
	32–56	26–34	17–29	14–18	.14–.20	.35–.74	.46–.76	.46–.76	0	.11–.15	0	0	.66–.95	.95–1.76
15	26.7	35.8	30.3	17.7	.140	.728	.528	.528	0	.181	0	0	.754	1.111
(*6*)	2.20	1.22	1.23	.67	.0085	.0584	.0198	.0198	0	.0129	0	0	.0184	.0427
	17–32	33–40	26–35	16–20	.12–.18	.46–.85	.48–.62	.48–.62	0	.14–.22	0	0	.70–.83	.96–1.21
16	29.8	31.0	28.2	16.2	.189	.500	.544	.544	0	.129	0	0	.743	1.114
(*5*)	2.63	.45	.80	.58	.0177	.0185	.0468	.0468	0	.0123	0	0	.0236	.0259
	25–40	30–32	26–30	15–18	.14–.24	.44–.54	.42–.68	.42–.68	0	.10–.15	0	0	.69–.81	1.02–1.17
17	26.5	27.5	31.5	19.5	.151	.537	.670	.670	0	.136	0	0	.677	.954
(*2*)	5.50	4.50	1.50	1.50	.0217	.0020	.0049	.0049	0	.0232	0	0	.0636	.0087
	21–32	23–32	30–33	18–21	.13–.17	.54	.67	.67	0	.11–.16	0	0	.61–.74	.95–.96
18	30.3	30.3	30.3	20.7	.181	.566	.747	.747	0	.156	0	.037	.775	.819
(*3*)	4.91	.33	.33	1.45	.0206	.0496	.0247	.0247	0	.0102	0	.0370	.0039	.0343
	22–39	30–31	30–31	18–23	.15–.22	.55–.66	.70–.77	.70–.78	0	.14–.18	0	0–.11	.77–.78	.76–.88
19	—	—	—	—	.178	—	—	—	—	—	—	—	—	—
(*2*)	—	—	—	—	.0018	—	—	—	—	—	—	—	—	—
	—	—	—	—	.18	—	—	—	—	—	—	—	—	—
20	22.0	31.5	30.0	16.0	.145	.629	.709	.709	0	.090	0	0	.776	.805
(*2*)	4.00	.50	0	0	.0251	.0592	.0443	.0443	0	.0059	0	0	.0281	.0216
	18–26	31–32	30	16	.12–.17	.57–.69	.67–.75	.67–.75	0	.08–.10	0	0	.75–.81	.78–.83
21	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.137	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–.62	.15–.26	0–.84	0–.59	.68–.80	.59–.86

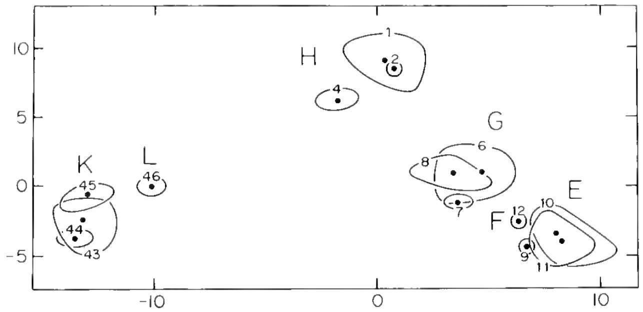

Figure 4. Fourteen samples of *Lepidophyma* of two southern (K and L) and four northern (E–H) population groups plotted on the first two canonical variables for 30 characters. Dots are centroids; sample numbers are along lines enclosing all included specimens.

4TLD, LTR, PVS, PVR, and RMW; the second explains 16 percent of the variation and is most weighted with PVS, PVR, PVT1, FPT, and PVT2. Southern groups K and L are strongly separated from H, their nearest discriminant neighbor among northern groups. However, one population of group H (4) is separated from the other two populations of the group in the direction of group L. The relationships of population 4 are discussed further on p. 7.

The 17 populations of group J were analyzed together with northern groups E through H (Fig. 5). The accuracy of the posterior classification was 98 percent (128/131), two specimens of sample 11 being misclassified as 10 (both group E). The first variable accounts for 42 percent of the total dispersion and is influenced most by PVS, PVR, PVT1, FPT, and LTR; the second expresses 26 percent and has heavy loadings for PVS, PVT1, PVR, LTR, and DAPVR. The five groups are separated from one another, although one population of group J (27) is separated from the remainder of the group and is placed intermediate between J and E and F, and two individuals of sample 37 (group J) approach group G.

GROUP ANALYSES

The multivariate relationships of the 46 populations described above are here considered in respect to univariate similarities or differences between population groups (Table 2) and to geographic distributions (Fig. 6) in order to arrive at the definition of morphologically diagnosable units of *Lepidophyma* occurring in northern Mexico. It is anticipated that the resultant units should consist of groups of populations that are overlapping or juxtaposed in discriminant space, that can be diagnosed by one or more univariate characters, that are not linked to other groups by univariately, multivariately, and geographically intermediate populations, and that thus represent morphospecies. For a genus such as *Lepidophyma,* in which sympatry is rare, discordant variation common, and populations often disjunct and represented by small sample sizes, such morphologically defined units are initial species hypotheses to be tested by securing additional samples and information (e.g., allozyme data).

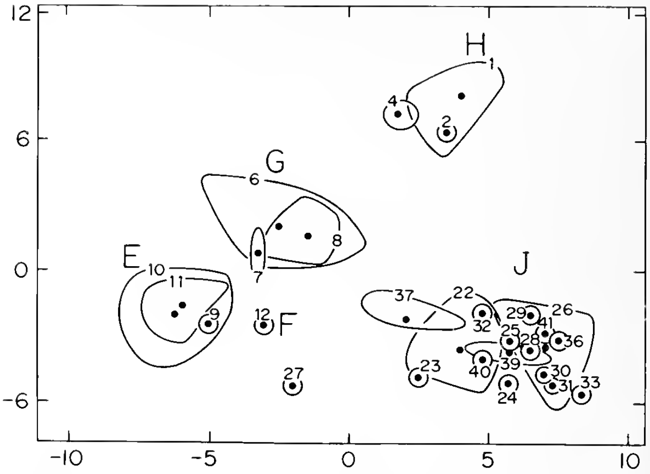

Figure 5. Twenty-seven samples of *Lepidophyma* of one southern (J) and four northern (E–H) population groups plotted on the first two canonical variables for 30 characters. Presentation as in Fig. 4.

Groups E, F, and G are positioned nearest each other in the four discriminant analyses (Figs. 2–5) and they overlap in all individual characters (Table 2). The three appear to represent a single species unit EFG distributed along the Sierra Madre Oriental from southern Tamaulipas to Veracruz (Fig. 6).

The nearest geographic and discriminant neighbor of group H among northern populations is group G (Figs. 2 and 6), from which it differs (=no overlap in range of variation) in LTR (Table 2). The decision as to whether H should be considered specifically distinct from EFG is complicated by

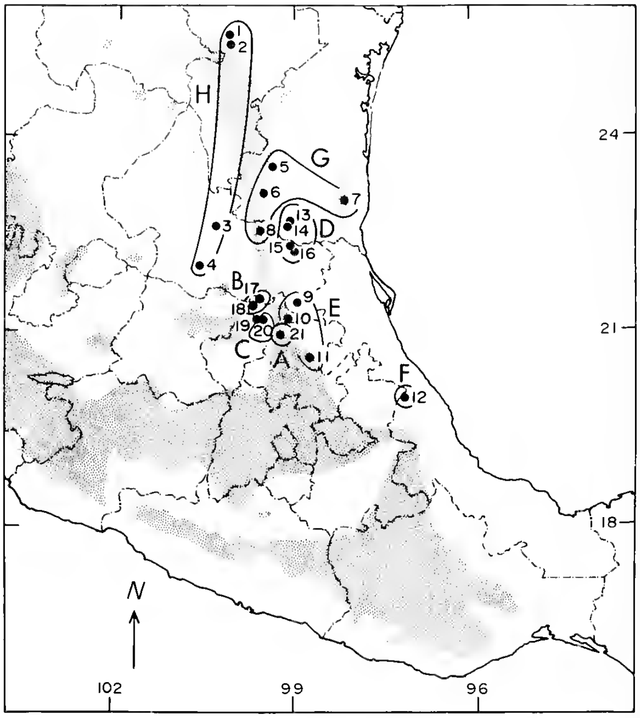

Figure 6. Distribution of eight population groups of *Lepidophyma* in northeastern Mexico. Lines enclose the samples (numbers) included in the groups (letters).

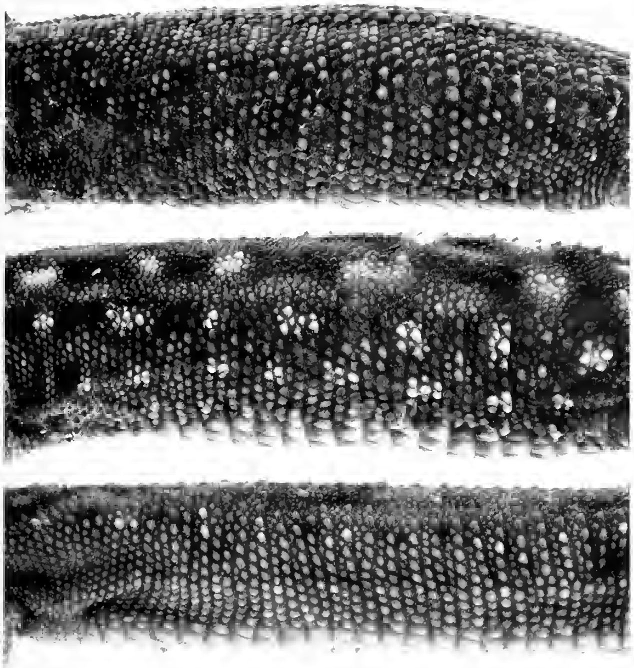

Figure 7. Lateral body surface of specimens of *Lepidophyma* of groups A (*upper*, sample 21, AMNH 13879) and E (*middle*, sample 11, LACM 106742; and *lower*, sample 10, LACM 109771).

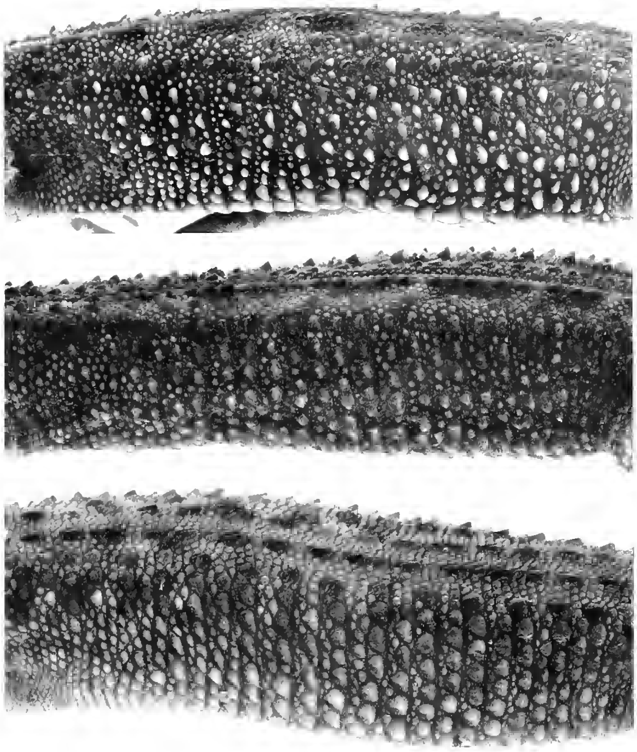

Figure 8. Lateral body surface of specimens of *Lepidophyma* of groups G (*upper*, sample 6, UMMZ 102980; *middle*, sample 8, LACM 131145) and H (*lower*, sample 2, EAL 4644).

the presence of intermediate states, observed in the lateral tubercle rows, that are not expressed in the LTR counts. In some specimens, the low number of lateral tubercle rows that characterizes group H results from a slight reduction of some of the rows in terms of the distance they extend above the ventrals and the relative size of the tubercles which compose them (Figs. 7–8). While uniform criteria were employed throughout the study to determine which rows to include in the counts, for some of the specimens in groups G and H the decision was difficult and repeatability of the counts was low. The difference in LTR between H and EFG is thus less discrete than suggested by the counts and is bridged by intermediate morphological states. While additional specimens and information (e.g., allozyme data) are needed to fully evaluate this situation, it seems best not to place emphasis on the differences in LTR number, and to recognize a single species unit composed of groups E, F, G, and H.

In one of the analyses, population 4 is slightly separated from the other two populations of group H (1, 2) in the direction of southern group L from coastal Michoacán (Fig. 4). For a number of characters (e.g., LTR, IWD1, GUL, 4TL, and 4TLD), the mean for population 4 is intermediate between L and the Nuevo León populations (1, 2) (Tables 1 and 2). Nevertheless, population 4 differs from L in four characters (FPT, PTMP, 4TLD, DOR), and from the Nuevo León populations (1, 2) in one (FPT). Evaluation of these differences is hampered by the small sample sizes of population 4 (N = 4) and group L (N = 3). To estimate the range of variation of 4 and L that would be expected with larger sample sizes, three standard deviations of population 1 (N = 15) were added to and subtracted from the means of each of the characters to encompass 99.7 percent of the population (Simpson, Roe, and Lewontin, 1960:139). The estimated range of population 4 overlaps the observed range of population 1 in all characters, but is separated from the estimated range of group L in FPT (23–31 vs. 13–21) and PTMP (1.5–3.0 vs. 3.2–4.8). While additional material is necessary to fully evaluate the relationships of population 4, the information at hand suggests that it should be considered a member of group EFGH. Further collecting along the western flank of the Sierra Madre Oriental seems likely to produce material linking the Sierra Alvarez population (4) geographically and morphologically with the Nuevo León populations (1, 2) (Fig. 6).

Two populations of southern group J (27, 37) approach EFGH in discriminant space (Fig. 5). The two groups differ

Table 2. Variation among 30 scale characters for eight population groups of *Lepidophyma* in northern Mexico. Presentation as in Table 1.

Group	FPT	LTR	DBPVR	1WD1	1WV1	PTMP	DBPVT	GC11L	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
A	33.5	46.5	4.03	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.09	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–5.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58
B	19.0	21.8	4.80	3.2	1.8	2.0	4.00	0	63.4	16.2	36.2	24.8	7.0	235.0	116.2	58.0
(*5*)	.71	.66	.255	.20	.20	0	0	0	1.96	.49	.58	.25	.71	3.10	1.69	3.03
	17–21	20–24	4.0–5.5	3–4	1–2	2	4.0	0	60–71	15–17	35–38	24–25	6–9	224–242	112–122	53–69
C	19.5	21.5	3.00	3.0	2.0	2.5	4.00	0	60.0	15.5	35.5	22.0	4.5	216.5	101.0	53.5
(*2*)	1.50	1.50	0	0	0	.50	0	0	1.00	.50	.50	0	1.50	3.50	1.00	4.50
	18–21	20–23	3.0	3	2	2–3	4.0	0	59–61	15–16	35–36	22	3–6	213–220	100–102	49–58
D	31.3	30.0	5.58	4.4	2.3	1.5	4.80	.5	60.2	16.0	36.1	26.4	14.1	241.5	123.9	67.9
(*25*)	.47	.33	.157	.13	.11	.16	.071	.12	.73	.16	.13	.28	.46	1.15	1.48	1.64
	28–36	27–35	4.0–7.0	3–5	1–3	0–2	4.0–5.0	0–2	55–68	15–17	35–37	24–29	10–19	231–251	112–140	52–85
E	25.8	33.9	4.50	3.4	2.0	1.8	2.20	.7	45.1	23.1	35.4	25.5	17.9	181.8	92.4	55.1
(*33*)	.27	.33	.072	.11	.07	.12	.167	.10	.49	1.13	.23	.17	.41	1.24	1.06	1.18
	23–30	31–38	3.5–5.0	2–5	1–3	0–3	1.0–4.0	0–2	41–54	15–39	33–37	23–28	13–23	165–192	78–104	40–73
F	31.0	35.0	5.00	4.0	2.0	3.0	4.00	0	47.0	17.0	36.0	28.0	18.0	205.0	103.0	53.0
(*1*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	31	35	5.0	4	2	3	4.0	0	47	17	36	28	18	205	103	53
G	27.6	29.1	4.01	3.0	1.9	2.0	3.15	.6	48.3	17.0	35.9	26.5	14.5	185.7	95.2	52.1
(*43*)	.37	.36	.107	.08	0	.12	.093	.11	.50	.37	.19	.30	.43	1.95	1.19	.94
	24–35	24–34	3.0–5.0	2–4	0–3	0–4	1.0–4.5	0–3	43–56	15–27	34–39	23–31	9–23	166–217	83–113	42–64
H	30.4	17.9	3.18	2.9	2.0	2.2	2.85	.3	45.1	16.0	35.9	24.9	7.7	163.6	85.5	45.2
(*20*)	.49	.45	.083	.06	.10	.08	.064	.11	.46	.18	.15	.33	.45	1.84	1.00	.89
	26–34	15–22	2.5–4.0	2–3	1–3	2–3	2.5–3.5	0–1	42–49	15–17	35–38	22–29	4–12	150–178	77–94	39–53

Table 3. Variation among 30 scale characters for nine species of *Lepidophyma* from Mexico. Presentation as in Table 1.

Species	FPT	LTR	DBPVR	1WD1	1WV1	PTMP	DBPVT	GC11L	GUL	PVTL	VL	4TL	4TLD	DOR	DAPVR	PVR
gaigeae	33.5	46.5	4.03	2.2	2.0	3.8	2.54	.5	36.4	11.3	34.3	26.3	11.1	133.5	64.2	51.2
(*20*)	.28	.54	.057	.09	0	.24	.098	.11	.41	.73	.19	.32	.46	1.09	.69	1.08
	32–37	43–50	3.5–4.0	2–3	2	2–6	2.0–3.0	0–1	33–39	6–18	33–36	25–30	7–16	126–142	59–68	44–58
occulor	19.2	22.2	4.44	3.3	1.9	2.1	4.11	0	63.2	16.2	36.1	23.9	6.8	229.7	111.9	56.7
(*9*)	.46	.55	.306	.17	.11	.11	.111	0	1.28	.36	.35	.44	.70	4.09	3.04	2.46
	17–21	20–24	3.0–5.5	3–4	1–2	2–3	4.0–5.0	0	59–71	15–18	35–38	22–25	3–9	213–242	100–122	49–69
micropholis	31.3	30.0	5.58	4.4	2.3	1.5	4.80	.5	60.2	16.0	36.1	26.4	14.1	241.5	123.9	67.9
(*25*)	.47	.33	.157	.13	.11	.16	.071	.12	.73	.16	.13	.28	.46	1.15	1.48	1.64
	28–36	27–35	4.0–7.0	3–5	1–3	0–2	4.0–5.0	0–2	55–68	15–17	35–37	24–29	10–19	231–251	112–140	52–85
sylvaticum	27.6	28.5	4.01	3.2	2.0	2.0	2.78	.6	46.6	18.9	35.7	25.8	14.2	180.0	92.3	51.7
(*98*)	.27	.64	.074	.06	.05	.07	.083	.06	.33	.52	.12	.18	.46	1.36	.77	.70
	23–35	15–38	2.5–5.0	2–5	0–3	0–4	1.0–4.5	0–3	41–56	15–39	33–39	20–31	4–23	150–217	77–113	39–73
tuxtlae	24.6	34.1	4.09	3.7	2.3	5.5	.29	1.6	42.6	39.3	39.6	25.8	16.3	172.0	79.6	45.0
(*81*)	.22	.20	.053	.06	.06	.11	.032	.09	.28	.43	.14	.16	.22	.97	.70	.43
	20–29	30–40	3.0–5.0	3–5	0–3	4–9	0–.9	0–4	37–49	30–47	37–42	23–28	13–20	150–190	69–98	37–55
pajapanensis	33.3	40.5	4.21	3.4	1.8	7.5	.14	.1	38.9	43.8	36.6	28.3	13.8	164.3	69.6	44.0
(*19*)	.35	.40	.088	.12	.10	.31	.037	.07	.53	1.02	.17	.24	.50	1.59	1.22	.84
	30–36	37–43	4.0–5.0	3–4	1–2	6–10	0–.5	0–1	35–43	39–51	35–38	26–30	10–17	152–175	59–82	37–49
flavimaculatum	33.7	28.5	4.45	3.8	2.1	6.8	2.99	.9	47.3	18.6	36.6	27.3	14.7	197.7	90.1	54.3
(*49*)	.56	.26	.084	.08	.05	.20	.119	.09	.41	.41	.13	.25	.34	1.64	1.17	1.00
	27–41	25–32	3.0–5.5	3–5	1–3	4–11	.5–4.0	0–2	40–55	15–27	34–38	23–31	10–22	173–221	75–118	43–69
smithii	23.1	17.5	4.21	3.0	2.1	2.7	3.18	.7	52.4	16.8	35.8	25.2	5.3	194.0	94.2	48.7
(*36*)	.56	.16	.102	.05	.08	.14	.067	.13	.39	.36	.18	.24	.33	1.43	1.15	.73
	18–29	15–19	3.0–5.5	2–4	1–3	2–4	2.0–4.0	0–3	46–57	14–25	33–38	22–28	2–9	178–214	81–110	37–61
tarascae	17.0	16.7	2.67	2.7	2.0	4.0	2.50	.7	42.3	16.0	34.3	22.7	1.7	146.7	75.0	44.3
(*3*)	.58	.33	.333	.33	0	0	0	.33	.67	0	.33	.33	.33	1.67	1.00	1.20
	16–18	16–17	2.0–3.0	2–3	2	4	2.5	0–1	41–43	16	34–35	22–23	1–2	145–150	74–77	42–46

Table 2. Continued.

Group	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
A	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.127	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–.62	.15–.26	0–.84	0–.59	.68–.80	.59–.86
B	28.8	29.2	30.8	20.2	.169	.555	.716	.716	0	.148	0	.022	.736	.873
(*5*)	3.34	1.59	.58	.97	.0151	.0281	.0233	.0233	0	.0104	0	.0222	.0314	.0381
	21–39	23–32	30–33	18–23	.13–.22	.50–.66	.67–.78	.67–.78	0	.11–.18	0	0–.11	.61–.78	.76–.96
C	22.0	31.5	30.0	16.0	.145	.629	.709	.709	0	.090	0	0	.776	.805
(*2*)	4.00	.50	0	0	.0251	.0838	.0443	.0443	0	.0059	0	0	.0281	.0216
	18–26	31–32	30	16	.12–.17	.57–.69	.67–.75	.67–.75	0	.08–.10	0	0	.75–.81	.78–.83
D	36.2	31.7	26.0	16.2	.163	.585	.557	.563	0	.147	0	0	.747	1.146
(*25*)	1.99	.72	.96	.32	.0060	.0592	.0175	.0187	0	.0067	0	0	.0133	.0334
	17–56	25–40	17–35	13–20	.12–.24	.27–.85	.42–.76	.42–.76	0	.10–.22	0	0	.66–.95	.94–1.76
E	24.3	30.8	22.6	2.5	.183	.519	.527	.462	.127	.167	.100	.054	.838	1.170
(*33*)	1.50	.70	.84	.53	.0100	.0283	.0193	.0214	.0432	.0088	.0376	.0356	.0202	.0252
	7–42	22–37	16–33	0–13	.07–.32	.30–.75	.27–.82	.19–.81	0–.94	.09–.28	0–.85	0–1.12	.71–1.37	.84–1.55
F	20.0	33.0	22.0	9	.200	.466	1.071	.283	.729	.106	.739	0	.750	1.141
(*1*)	0	0	0	0	0	.0193	0	0	0	0	0	0	0	0
	20	33	22	9.0	.20	.46	1.07	.28	.73	.11	.74	0	.75	1.14
G	23.7	28.4	2.09	12.6	.180	.540	.560	.368	.237	.165	.338	.072	.772	1.171
(*43*)	1.30	.65	.73	.50	.0062	0	.0190	.0309	.0508	.0073	.0746	.0473	.0185	.0181
	12–43	19–35	15–34	4–18	.11–.27	.40–.69	.36–.81	0–.71	0–.84	.07–.29	0–1.32	0–1.65	.64–1.40	.86–1.41
H	14.2	30.3	21.3	15.9	.220	.633	.464	.406	.088	.156	.074	.044	.749	1.073
(*20*)	.78	.50	.87	.18	.0194	.0120	.0311	.0370	.0399	.0121	.0373	.0443	.0368	.0377
	7–20	26–34	15–28	15–17	.14–.56	.39–.82	.11–.70	.11–.65	0–.56	.09–.28	0–.63	0–.89	.65–1.39	.89–1.61

Table 3. Continued.

Species	PVS	PVT1	PVT2	PVT3	RPOL	RPAW	RPFML	RPFL1	RMW	RNL	RML	RAPPSL	RPNH	RSLH
gaigeae	36.5	14.6	3.9	0	.208	.407	.491	.405	.094	.199	.127	.052	.744	.745
(*20*)	1.97	1.05	.74	0	.0056	.0168	.0264	.0367	.0400	.0076	.0587	.0323	.0087	.0155
	22–50	8–22	0–11	0	.15–.26	.27–.54	.28–.71	0–.63	0–1.49	.15–.26	0–.84	0–.59	.68–.80	.59–.86
occulor	26.9	29.9	30.6	19.0	.166	.576	.714	.714	0	.131	0	.016	.748	.854
(*9*)	2.76	1.18	.43	1.02	.0099	.0271	.0188	.0188	0	.0129	0	.0159	.0237	.0295
	18–39	23–32	30–33	16–23	.12–.22	.50–.69	.66–.78	.67–.77	0	.08–.18	0	0–.11	.61–.81	.76–.96
micropholis	36.2	31.7	26.0	16.2	.163	.585	.557	.563	0	.147	0	0	.747	1.146
(*25*)	1.99	.72	.95	.32	.0060	.0283	.0175	.0187	0	.0067	0	0	.0133	.0334
	17–56	25–40	17–35	13–20	.12–.24	.27–.85	.42–.76	.42–.76	0	.09–.22	0	0	.66–.95	.94–1.76
sylvaticum	21.9	29.7	21.0	9.8	.190	.551	.532	.408	.171	.165	.200	.059	.790	1.152
(*98*)	.88	.40	.47	.62	.0062	.0109	.0141	.0172	.0287	.0052	.0373	.0253	.0133	.0144
	7–43	19–37	15–34	0–18	.07–.56	.30–.82	.11–1.07	0–.81	0–.95	.07–.31	0–1.32	0–1.65	.64–1.40	.84–1.61
tuxtlae	5.1	39.9	32.2	1.7	.224	.830	.734	.042	1.024	.108	1.216	.027	.734	.547
(*81*)	.47	.37	.63	.33	.0047	.0128	.0092	.0126	.0243	.0049	.0539	.0159	.0054	.0106
	0–18	31–49	11–42	0–15	.11–.33	.59–1.12	.48–.89	0–.57	0–1.31	.04–.29	0–3.15	0–.99	.63–.83	.32–.77
pajapanensis	2.8	41.2	26.6	.1	.222	.540	.803	.157	1.087	.163	1.656	.002	.764	.485
(*19*)	.56	1.02	1.33	.06	.0081	.0189	.0131	.0246	.0264	.0113	.1192	.0015	.0116	.0349
	0–8	34–49	15–40	0–1	.13–.28	.38–.69	.70–.90	0–.31	.85–1.29	.10–.28	1.00–2.65	0–.03	.69–.86	.32–.88
flavimaculatum	20.1	34.2	25.3	13.7	.204	.411	.699	.175	.834	.145	.978	.061	.736	.557
(*49*)	1.17	.65	.71	.76	.0089	.0199	.0126	.0128	.0447	.0075	.0687	.0356	.0063	.0154
	6–44	24–43	17–35	1–24	.11–.39	.19–.69	.52–.88	0–.73	0–1.31	.07–.28	0–2.43	0–1.66	.58–.83	.36–.89
smithii	17.0	31.1	26.9	16.3	.181	.723	.713	.349	.608	.137	.783	.099	.794	.904
(*36*)	.75	.45	.60	.41	.0065	.0459	.0141	.0414	.0681	.0052	.1050	.0398	.0093	.0106
	8–29	25–39	18–32	13–27	.11–.28	.43–1.35	.54–.89	0–.79	0–1.07	.08–.24	0–2.62	0–1.04	.66–.92	.61–1.22
tarascae	13.7	30.7	25.0	16.0	.299	.591	.361	.361	0	.154	0	0	.982	.756
(*3*)	1.33	.33	1.53	0	.0717	.0923	.0664	.0664	0	.0130	0	0	.0227	.0417
	11–15	30–31	23–28	16	.19–.44	.41–.71	.29–.49	.29–.49	0	.14–.18	0	0	.94–1.02	.69–.83

in PTMP (0–3 in 95/97 EFGH and 4–11 in all J) and RSLH (0.84–1.60 in all EFGH and 0.36–0.79 in 49/50 J) (Table 2). The two specimens of EFGH with a PTMP of 4 are from a population (6) at the northern end of the range (Fig. 1), and the specimen of J with RSLH of 0.89 is from a population in Tabasco (37), that is separated from the southernmost sample (12) of EFGH by 350 km and by intervening populations that are clearly assigned to J. Thus the populations of EFGH and J that are most similar in morphology are not geographically intermediate, and the multivariate and univariate differences between the two population groups are sufficiently constant that they are judged to represent units that are likely reproductively isolated.

Group D is multivariately closest to G (Fig. 2). The four populations of D are from the Sierra del Abra of Tamaulipas and San Luis Potosí (Fig. 6), and differ in DOR from all populations of group EFGH including those in the Sierra Madre Oriental to the west and Sierra Tamaulipas to the east (Table 2). While two of the three specimens from the Sierra Tamaulipas (sample 7, group G) approach group D in discriminant space, they are not geographically intermediate (Fig. 6) and do not bridge the gap between the two in DOR (Table 2). It is concluded that group D should be considered specifically distinct from EFGH.

Groups B and C are closest to D in discriminant space, but differ in FPT (18–21 vs. 28–36) and LTR (20–24 vs. 27–35). Evaluation of these differences is hampered by small sample sizes of B (N = 4) and C (N = 2). As an estimate of the range of variation that would be expected with larger samples, three standard deviations of D were added to and subtracted from the means of B and C. The estimated ranges of B and C overlap each other for all characters but differ from the observed range of D for FPT (12–27 vs. 28–36) and LTR (17–26 vs. 27–35). The populations of B and C are located in the Jalpan Valley of Querétaro and San Luis Potosí (Fig. 6), and their combined ranges of variation differ in six characters from the populations of E occurring in the Sierra Madre Oriental, 22 km to the east. While larger sample sizes are necessary to fully evaluate the differences between groups B and C, their multivariate juxtaposition and the small univariate differences between them indicate they are probably members of the same species. On the other hand the number and magnitude of the univariate differences between BC and its nearest geographic (E) and discriminant (D) neighbors are such that they are not likely to be bridged by larger samples. Group BC is considered specifically distinct from D and EFGH.

Group A is strongly separated in discriminant space from the populations of all other groups (Figs. 2–3). It is morphologically and geographically closest to group E (Fig. 6), but differs in 6 of the 30 characters (Table 2). The univariate and multivariate differences between A and other population groups clearly qualify it as a distinct morphospecies.

While the combined problems of small sample sizes, disjunct distributions, and discordant variation confound some of the decisions, four unique morphological units of *Lepidophyma* are recognizable in northeastern Mexico: A, BC, D, and EFGH.

ALLOCATION OF NAMES

Several of the groups identified in the discriminant analyses include lizards that are either types or are from or near the type locality of named taxa: Group A: Population 21: *L. gaigeae* Mosauer, 1936; B: 20: *L. smithii occulor* Smith, 1942; D: 14: *L. micropholis* Walker, 1955; E: 11: *L. sylvaticum* Taylor, 1939; G: 6: *L. flavimaculatum tenebrarum* Walker, 1955; I: 51: *L. tuxtlae* Werler and Shannon, 1957, 41: *L. pajapanensis* Werler, 1957, 48: *L. sawini* Smith, 1973, 47: *L. alvarezi* Smith, 1973; J: 28: *L. flavimaculatum* A. Duméril *in* Duméril and Duméril, 1851; K: 44: *L. smithii* Bocourt, 1876; L: 46: *L. tarascae* Bezy, Webb, and Alvarez, 1982.

The oldest available names for the species units recognized in northern Mexico (Fig. 9) from the foregoing discussions are: A, *L. gaigeae*; BC, *L. occulor*; D, *L. micropholis*; and EFGH, *L. sylvaticum*. These are summarized below.

The systematic relationships among populations of *Lepidophyma* in southern Mexico currently are under study (Bezy, in prep.); the southern population groups used in this paper are considered to represent the following species: I = *L. pajapanensis* (Veracruz) and *L. tuxtlae* (Veracruz, Oaxaca, Chiapas); J = *L. flavimaculatum* (Atlantic versant east of the Isthmus of Tehuantepec in Oaxaca, Veracruz, Tabasco, Chiapas, Quintana Roo); K = *L. smithii* (Pacific versant of Guerrero, Oaxaca, Chiapas); and L = *L. tarascae* (coastal Michoacán).

SPECIES ACCOUNTS

Lepidophyma gaigeae Mosauer

Group A; Figures 7, 10

Lepidophyma gaigeae Mosauer, 1936:3. Holotype: MCZ 42145: Durango, State of Hidalgo, Mexico.
Gaigeia gaigeae: Smith, 1939:24.

DIAGNOSTIC CHARACTERS. Differs from other members of the genus except *L. radula* in having 43–50 subequal scales (rather than 15–42 discrete rows of enlarged tubercles) along the side of the body (axilla to groin) (Figs. 7–8) and fewer dorsal scales (126–142 vs. 145–251) (Table 3). It differs from *L. radula* and *L. dontomasi* in having two (rather than one) caudal interwhorls complete ventrally.

DISTRIBUTION. The species is known from Hidalgo (near the type locality) and Querétaro (between El Lobo and Jalpan; Dixon et al., 1972), where it occurs in limestone crevices primarily in pine-oak woodland (Fig. 9).

REMARKS. The high degree of separation of *L. gaigeae* from other populations in the discriminant analyses is consistent with its proposed separate generic (Smith, 1942) or subgeneric (Smith, 1973) status. Geographic variation and relationships of this form to *L. dontomasi* and *L. radula* are currently under study (Bezy, in prep.).

KARYOTYPE. *Lepidophyma gaigeae* has a diploid chromosome number of 38 with nine pairs of macrochromosomes and 10 pairs of microchromosomes. The karyotype is unique in the genus, but closest to those of *L. flavimaculatum, L. pajapanensis,* and *L. tuxtlae* (Bezy, 1972).

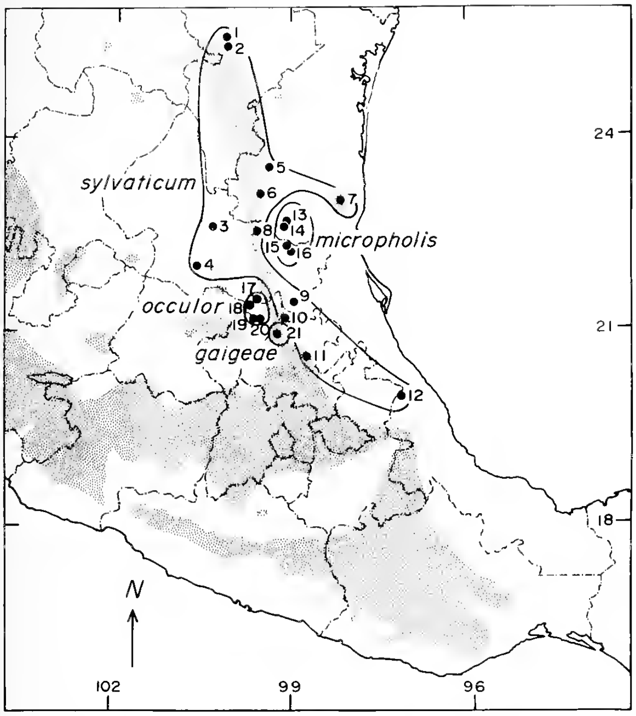

Figure 9. Distribution of the four species of *Lepidophyma* recognized in northeastern Mexico (north of 19°N). Lines enclose the samples included in each species.

Lepidophyma occulor Smith

Group BC; Figure 10

Lepidophyma smithii occulor Smith, 1942:378. Holotype: USNM 47133: Jalpan, Querétaro.
Lepidophyma flavimaculatum occulor: Walker, 1955:5.
Lepidophyma occulor: Bezy, 1972:15.

DIAGNOSTIC CHARACTERS. Differs from all other species of *Lepidophyma* except *L. micropholis* in having more gulars (59–71 vs. 33–57), and from *L. micropholis* in having fewer femoral pores (17–21 vs. 28–36), fewer lateral tubercle rows (20–24 vs. 27–35), and fewer divided fourth toe lamellae (3–9 vs. 10–19) (Table 3).

DISTRIBUTION. *Lepidophyma occulor* is known from four localities in the Jalpan Valley of Querétaro and San Luis Potosí (Fig. 9), where it has been found beneath stones in arid tropical scrub (Dixon et al., 1972).

REMARKS. The species alternatively has been considered a subspecies of either *L. smithii* (Smith, 1942) or *L. flavimaculatum* (Walker, 1955) from both of which it is well separated multivariately (Fig. 3), differing from the former in lateral tubercle rows and gulars and from the latter in femoral pores, lateral tubercle rows, pretympanics, gulars, and divided fourth toe lamellae. It is multivariately closest to *L. micropholis* from which it differs in femoral pores, lateral tubercle rows, and divided fourth toe lamellae (Table 3).

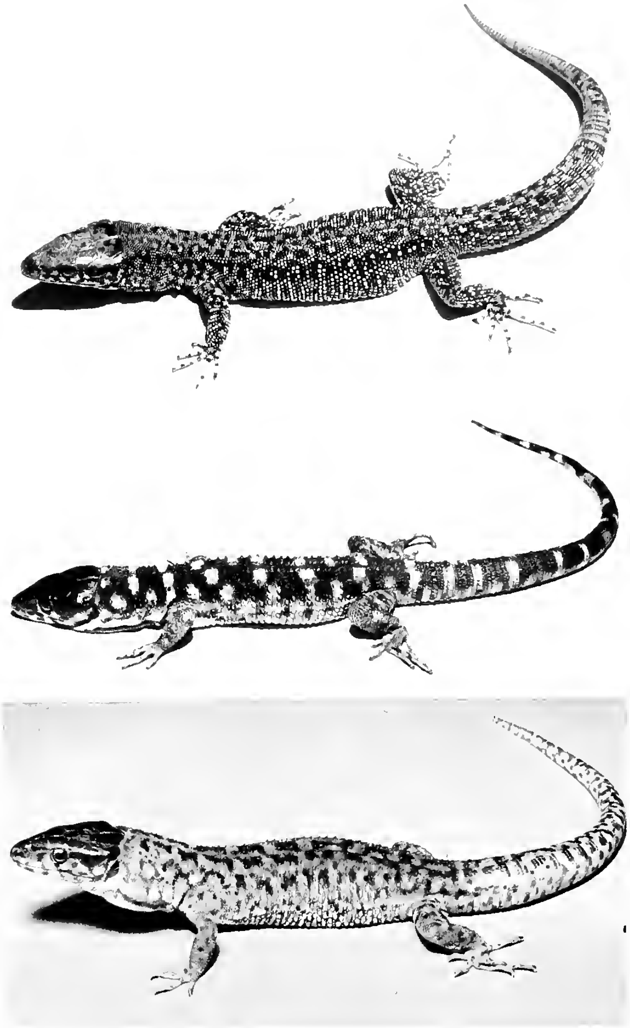

Figure 10. Living individuals of *Lepidophyma gaigeae* (*upper,* LACM 127170), *L. occulor* (*middle,* sample 18, TCWC 35605), and *L. micropholis* (*lower,* sample 16, TCWC 60767).

KARYOTYPE. *Lepidophyma occulor* has a diploid chromosome number of 36, with the lowest number of microchromosomes (18) known in the family Xantusiidae (Bezy, 1972).

Lepidophyma micropholis Walker

Group D; Figure 10

Lepidophyma micropholis Walker, 1955:6. Holotype: UMMZ 101298: cave at El Pachon, about 5 miles NNE of Antigua Morelos, Tamaulipas.

DIAGNOSTIC CHARACTERS. Differs from all other species in the genus (except *L. occulor*) in having more dorsal

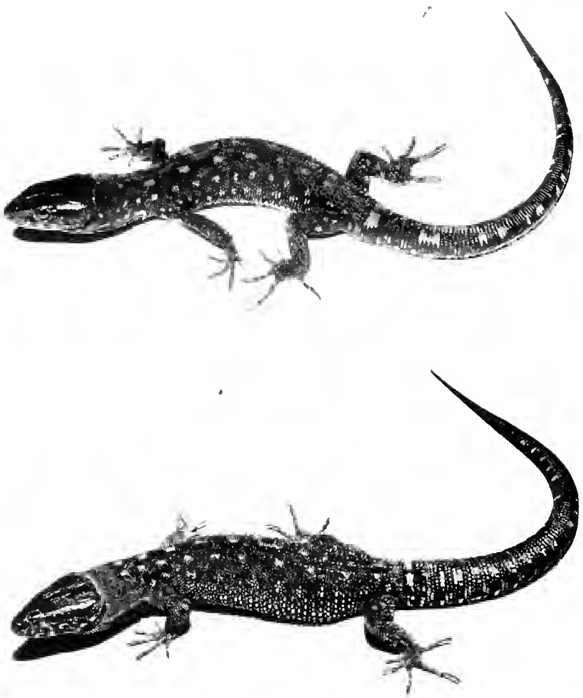

Figure 11. Living individuals of southern Madrean (*upper*, sample 11, LACM 106752) and northern Madrean (*lower*, sample 8, LACM 131146) population groups of *Lepidophyma sylvaticum*.

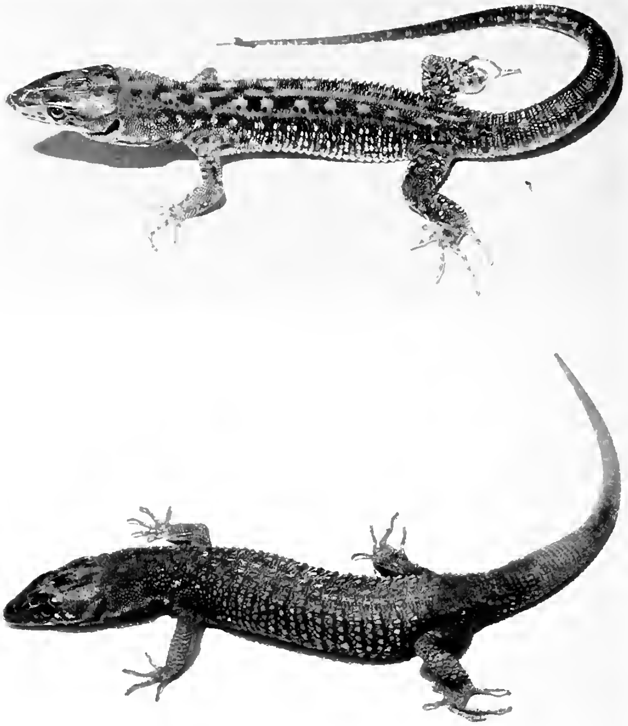

Figure 12. Living individuals of northern Madrean (*upper*, sample 6, LACM 106752) and western (*lower*, sample 1, LACM 106781) population groups of *Lepidophyma sylvaticum*.

scales (231–251 vs. 126–222) and from *L. occulor* in having more lateral tubercle rows (27–35 vs. 20–24) (Table 3).

DISTRIBUTION. *Lepidophyma micropholis* occurs in southern Tamaulipas and northern San Luis Potosí at four localities situated along the Sierra del Abra (Fig. 9). This caverniferous, low-lying range constitutes the easternmost front of the Sierra Madre Oriental in the highly dissected region between the Rio Guayalejo and the Rio Tamuin (Mitchell et al., 1977). The lizards have been found primarily in limestone caves (El Pachon and Quintero) and fissures.

REMARKS. This extensively cavernicolous species is closest in scalation to *L. occulor* and *L. sylvaticum*, and future work may demonstrate the existence of morphologically and biochemically intermediate populations, similar to those occurring between the epigean and troglodytic *Astyanax mexicanus* of the Sierra del Abra (Avise and Selander, 1972; Mitchell et al., 1977).

KARYOTYPE. *Lepidophyma micropholis* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes (Bezy, 1972).

Lepidophyma sylvaticum Taylor

Group EFGH; Figures 7–8, 11–12

Lepidophyma sylvatica Taylor, 1939:131. Holotype: FMNH 100102: 7 mi. north of Zacaultipan, Hidalgo.

Gaigeia sylvatica: Smith, 1942:380.

Lepidophyma sylvaticum: Walker, 1955:9.

Lepidophyma flavimaculatum tenebrarum Walker, 1955:1. NEW SYNONYMY. Holotype: UMMZ 101374: ±5 miles NW (by road) of Gomez Farias in the Sierra Madre Oriental at "Rancho del Cielo."

DIAGNOSTIC CHARACTERS. Differs from *L. gaigeae* and *L. occulor* in numbers of gulars (41–56 vs. 33–39 and 59–71, respectively), from *L. micropholis* in numbers of dorsals (150–217 vs. 231–251), from *L. tarascae* in numbers of femoral pores (23–35 vs. 16–18), from *L. smithii* in having a parietal foramen, from *L. flavimaculatum* in numbers of pretympanics (0–3 vs. 4–11, 99%) and ratio of supralabial height (0.84–1.61 vs. 0.36–0.79, 99%), from *L. tuxtlae* in ratio of supralabial height (0.84–1.61 vs. 0.32–0.77), and from *L. pajapanensis* in numbers of pretympanics (0–4 vs. 6–10) (Table 3).

DISTRIBUTION. The 12 populations occur from Veracruz to Nuevo León along the Sierra Madre Oriental and adjacent Mesa Central and Sierra Tamaulipas (Fig. 9).

REMARKS. The four population groups included in *L. sylvaticum* are moderately divergent from one another and further work may indicate that one or more of them should be given separate taxonomic recognition (i.e., subspecies).

The northern Madrean group (G) includes four populations in southern Tamaulipas and northern San Luis Potosí, three from along the main axis of the Sierra Madre Oriental and

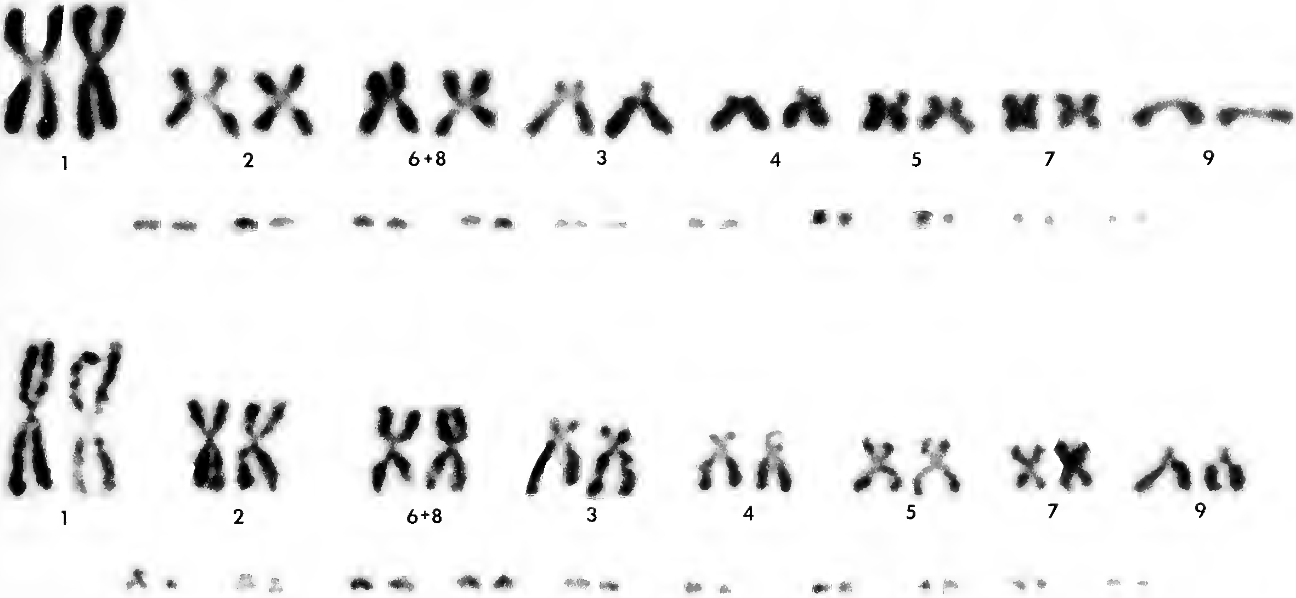

Figure 13. Karyotypes of *Lepidophyma sylvaticum* (sample 6; *upper*, LACM 106758, ♂; *lower*, LACM 106763, ♀).

one in the Sierra Tamaulipas. They differ from the three populations (group E) of southern San Luis Potosí, Querétaro, and Hidalgo in lateral tubercle rows (34/39 northern Madrean with 31 or less, 30/33 southern Madrean with 32 or more) (Table 2). The hiatus between the ranges of the two corresponds roughly to the Rio Panuco gap in the Sierra Madre Oriental. Should further work demonstrate a need to accord them separate nomenclatural status, *L. sylvaticum* Taylor, 1939 is applicable to the southern group, and *L. f. tenebrarum* Walker, 1955 is available for the northern group.

The southernmost specimen (group F) assigned to *L. sylvaticum* is from ca. 170 km SE of the type locality and occurs at the northern base of the Cordillera Volcanica in central Veracruz (Fig. 6). It has similarities to both southern and northern Madrean *L. sylvaticum*, being closest to the former in lateral tubercle rows and femoral pores, and to the latter in dorsals. No other *Lepidophyma* are known from the Cordillera Volcanica. The nearest populations to the south are *L. tuxtlae* and *L. pajapanensis* of the Tuxtlas region (which differ from *L. sylvaticum* in numbers of large paravertebrals, pretympanics, and dorsals, and in ratio of supralabial height), and *L. flavimaculatum* of the northern Isthmus of Tehuantepec (which differ in pretympanics, lateral tubercle rows, and ratio of supralabial height) (Tables 2–3).

The western group of *L. sylvaticum* (H, Figs. 6, 8, 12) includes one population in the Sierra Alvarez on the Mesa Central of southeastern San Luis Potosí and two in canyons around the northern base of the Sierra Madre Oriental below the Cumbres de Monterey of Nuevo León. A fourth locality (sample 3) is represented by a fragmentary specimen, but the limited data obtainable from it suggests it is a member of the western group. The group differs from all other *L. sylvaticum* in lateral tubercle rows, and from southern Madrean samples of *L. sylvaticum* in numbers of fourth toe lamellae and numbers of paravertebrals larger than three dorsal scales (Table 2).

KARYOTYPE. Chromosomal information was obtained from 16 specimens (6♂, 9♀, 1 juv.) of *L. sylvaticum*: three from sample 11, one from 10, eight from 6, and four from 1. A total of 271 metaphase spreads were studied.

In all four populations the karyotype was found to consist of a diploid number of 36 with 16 macrochromosomes and 20 microchromosomes (Fig. 13). There are five metacentric to submetacentric (Nos. 1, 2, 2A, 5, 7), two subtelocentric (3, 4), and one acrocentric (9) pairs of macrochromosomes (pair numbering after Bezy, 1972). No secondary constrictions were observed. The cells of six specimens (5♀, 1 juv.) of sample 6 were found consistently to have a pair of heteromorphic chromosomes involving the largest pair of microchromosomes, with a metacentric member, ca. 1.5 times the size of the next largest micro (Fig. 13).

The karyotype of *L. sylvaticum* appears identical in all respects (except the heteromorphism) to that of *L. micropholis* (Bezy, 1972). It differs from that of *L. flavimaculatum, L. tuxtlae,* and *L. pajapanensis* in having one less pair of macrochromosomes (the large metacentric 2A presumably was formed from centric fusions involving pairs 6 and 7), a pair 3 that lacks terminal satellites, and a submetacentric rather than subtelocentric pair 7; from that of *L. smithii* in that pair 2A is more metacentric (rather than submetacentric), pair 3 lacks satellites, and the smallest macro pair is acrocentric rather than subtelocentric; and from that of *L. occulor* in having one more pair of macrochromosomes, one less pair of microchromosomes, and an acrocentric (rather than submetacentric) pair 9.

Lepidophyma sylvaticum thus differs karyotypically from the species that are closest to it in scalation (*L. flavimaculatum, L. smithii,* and *L. occulor*) except *L. micropholis*. Such chromosomal differences in themselves would not be expected to present reproductive barriers, and some cases of extraordinary geographic variation in karyotypes have been documented in species of other lizard families (e.g., Hall and Selander, 1973; Sites, 1983). However, among lizards chromosomal divergence most often is associated with differentiation at or above the species level. The karyotypic identity of *L. micropholis* and *L. sylvaticum* serves to underscore the morphologic and biogeographic relationships which suggest that the former may be a troglodytic derivative of the latter, and that future work might demonstrate a morphologic and genetic continuum between the two.

The microchromosomal heteromorphism found in the females of sample 6 was not detected in samples 1, 10, and 11. It occurs in all females (five; plus one juvenile) of sample 6, but is absent in the two females of sample 1 and in all males studied (two each from samples 1, 6, and 11, and one from 10). It may constitute a sex chromosomal heteromorphism (ZW) present in population 6, absent in population 1, and of unknown occurrence in populations 10 and 11 (no preparations from females available). On the other hand, it may represent a heterozygous condition where unsampled homozygous individuals (for the large macrochromosome) occur in the population, or in adjacent populations. Until additional material is obtained, all that can be said is that it is a heteromorphic condition which has been found only in females of population 6, and not detected in any other population in the family.

SEX RATIO. Two samples of *L. sylvaticum* have sex ratios (♀/♂ + ♀) that differ significantly (0.05 level, Fisher exact test, Yates correction) from 0.50: sample 6 with 0.89 (25/28) and sample 10 with 0.85 (11/13). The skewed sex ratios of these samples have been discussed earlier in relationship to the unisexual populations of *L. flavimaculatum* occurring in Panama and Costa Rica (Bezy, 1972). Although the sample sizes of populations 6 and 10 of *L. sylvaticum* remain smaller than desirable, both are now sufficiently large to conclude that the sex ratios differ significantly (0.05 level) from those of other *Lepidophyma* populations in eastern Mexico: *L. tuxtlae* (30/59) and *L. gaigeae* (150/260).

In addition to previously discussed factors that may be responsible for the observed skewed sex ratios (Bezy, 1972), temperature-dependent sex determination has now been documented for lizards (Bull, 1980), and comparable effects could be operative in *Lepidophyma*. Theoretical considerations would predict that this may not be the case in that temperature-dependent sex determination is thought to interfere with the evolution of both viviparity (ovoviviparity) and sex chromosomes (Bull, 1980). Viviparity appears to be universal among xantusiids (Blackburn, 1982), and the population (6) of *L. sylvaticum* with the most aberrant sex ratio is the only one in the family with heteromorphism, possibly indicating the presence of sex chromosomes. Experimental data are needed to evaluate the role of environmental factors, particularly temperature, in determining sex ratio in xantusiids.

The aberrant sex ratios and the heteromorphic chromosomes of populations of *L. sylvaticum* could be a consequence of hybridization. Both conditions frequently are found in hybrid populations, the skewed sex ratios perhaps resulting from a disruption in the balance of the sex-determining mechanism or an increased expression of lethals in one of the sexes (Darevsky et al., 1978; White, 1973). The identification of populations homozygous for the large microchromosome and additional data (e.g., allozymes) would be required to establish the existence of and possible participants in such a hybridization.

KEY TO THE SPECIES OF *LEPIDOPHYMA* OF NORTHEASTERN MEXICO

1a. Side of body lacking vertical rows of enlarged keeled tubercles (Fig. 7), but with 43–50 subequal scales (axilla to groin); less than 145 dorsal scales (occiput to rump); tail with two interwhorls complete dorsally and ventrally . . . . *L. gaigeae*

1b. Side of body with enlarged, keeled tubercles arranged in 15–42 vertical rows (A–G) separated by smaller granular scales (Figs. 7–8); 145 or more dorsal scales (O–R); tail usually with more than 2 interwhorls complete dorsally 2

2a. Total femoral pores 21 or less (gulars 59 or more; divided 4th toe lamellae 9 or less; lateral tubercle rows 24 or less) . . . . *L. occulor*

2b. Total femoral pores 23 or more 3

3a. Dorsal scales (O–R) 231 or more (gulars 55 or more; divided 4th toe lamellae 10 or more; lateral tubercle rows 27 or more) . . . . *L. micropholis*

3b. Dorsal scales (O–R) 217 or less (gulars 56 or less; divided 4th toe lamellae 4–23; lateral tubercle rows 15–38) . . . . *L. sylvaticum*

SPECIMENS EXAMINED

The 351 specimens and 52 population samples studied from Mexico are listed below. Sample numbers are in parentheses preceding localities.

L. gaigeae

HIDALGO: (21): La Placita, 8 km S Jacala (UIMNH 26180–86, 26191–99, 26204, 26207–09).

L. micropholis

SAN LUIS POTOSÍ: (15): 6 mi. E Valles (BCB 13837–42); (16): 5.5 mi. S, 1.4 mi. E Valles (TCWC 60621, 60766–67). TAMAULIPAS: (13): Gruta de Quintero, 1.5 mi. S Quintero (AMNH 93409, LACM 66662, SAM 885); (14): cave at El Pachon, ca. 5 mi. (by rd) NNE Antigua Morelos (LACM 106767–68, UAZ 28762, 28767–69, UMMZ 101299, 102886–88); 11.3 mi. S Ciudad Mante, Hwy 85 (TCWC 57256).

L. occulor

QUERÉTARO: (18): 2.5 mi. S Conca, Hda. Conca (TCWC 35605–06, 48499); (19): Jalpan (USNM 47134–35); (20): 1.2 mi. E Landa de Matamoros (TCWC 29691); 1.5 mi. E Landa

(TCWC 33063). SAN LUIS POTOSÍ: (17): Boa Capulin (LSUMZ 2379–80).

L. sylvaticum

HIDALGO: (11): 5.8 mi. (by Hwy 105) S Tianquistengo (LACM 106741–48); 4.0 mi. (by Hwy 105) S Tianquistengo (LACM 106721); 3 mi. S Tianquistengo (UIMNH 26230). NUEVO LEÓN: (1): La Boca (KU 92612–13); ca. 7 km NE Santiago, Presa La Boca (LACM 106781–792); (2): 5 mi. N Las Ajuntas (EAL 4644). QUERÉTARO: (10): El Madroño, 3.5 mi. W (rd) El Lobo [and vic] (LACM 109771, SAM 1104, TCWC 29692–29707, 32291, 33064, 35607, UMMZ 129749). SAN LUIS POTOSÍ: (3): Buenavista (ca. 20 mi. NE Cerritos) (AMNH 64025); (4): Alvarez (58 kilo) (MCZ 24507–08); between San Francisco and Alvarez (MCZ 157826); Valle de los Fantasmos (SDNHM 60482); (8): 27 km (by Mex 80) W El Naranjo (LACM 131145–48); 3.8 mi. (by Hwy 80) NNE Ciudad del Maiz (LACM 131144); 5 mi. NE Ciudad del Maiz (TCWC 35582); (9): Huichihuagan (FMNH 39631). TAMAULIPAS: (5): 8 mi. S, 6 mi. W Victorio, Sierra Madre Oriental (KU 33992); (6): Rancho del Cielo [and vic] (AMNH 107273, LACM 106751–60, 106762–65, LSUMZ 10989, UMMZ 101301, 101375, 102977–81, 109763–67); (7): Sierra de Tamaulipas, Santa Maria (UMMZ 102889–90); 10 mi. W, 2 mi. S Piedra (KU 33993–94). VERACRUZ: (12): 4 km W Tlapacoyan (KU 26909).

L. flavimaculatum

CHIAPAS: (22): Palenque (LACM 65117–19); Ruinas de Palenque (EAL 3030–31, FSM 32915–16, KU 94104–05); San Juanito, Palenque (USNM 111486–87); (23): 4.5 km S Pichucalco (KU 94106); (24): El Estoracan, ca. 50 km N Cintalapa (AMNH 73468); (25): Chiapa, 1 mi. W (TNHC 27517–18); (26): Ocozocoautla Selvas El Ocote (MCZ 54321–22); 16.1 mi. NW Ocozocoautla (LACM 61259); 26 km N Ocozocoautla (UTEP 5367–68); 32 km NW Ocozocoautla, Selva del Ocote (JFC); 25 mi. (by rd to Malpaso) NW Ocozocoautla (UAZ 28764, 28805–07); 12 km N Berriozabal (UTEP 5365–66); (27): ca. 5 km S Solusuchiapa (UAZ 31635); (28): Lago Miramar, near San Quintin (JFC); (29): Lacanja (LACM 114244). OAXACA: (30): 2.8 mi. N Rio Sarabia (UMMZ 115096); (31): 2 km S Tolosita (KU 39676); (32): Rio Mono Blanco, Juchitan (UIMNH 36832); (33): La Gloria (UIMNH 35515); (34): Mogoñe (UIMNH 40811); (35): 50.5 mi. S Acayucan, Hwy 185 (TNHC 25182). QUINTANA ROO: (36): 4.1 km NE Felipe Carrillo Puerto (UMRC 79-252). TABASCO: (37): Teapa (LACM 61260–61, LSUMZ 6878–79, UIMNH 47883, UMMZ 113777); (38): Soledad (UIMNH 47884). VERACRUZ: (39): 20 km E Jesus Carranza (KU 24453); 25 km SE Jesus Carranza (KU 26920–21); 35 km SW Jesus Carranza (KU 26919); (40): Rio de las Playas (USNM 118638).

L. pajapanensis

VERACRUZ; (41): Sontecomapan, Los Tuxtlas [and vic] (TCWC 21365, UAZ 28765, 28808–11, UTAR 3107, 3110, 3116, TCWC 21365); Coyame, 9 mi. (by rd) SE Catemaco (UAZ 28804); Univ. Mex. Biol. Exp. Sta., ca. 33 km ENE Catemaco (TCWC 53351); Colonia de Bastonal, above Quezalapam (TCWC 19133); Laguna Catemaco, nr Cuezalapan (UMMZ 126363–64); 4 mi. SE Tebanca, Los Tuxtlas (TCWC 21364); S slope Volcan San Martin (KU 97290, UMMZ 118220, 126362); (42): 35 km SE Jesus Carranza (KU 26913).

L. smithii

CHIAPAS: (43): La Esperanza (UIMNH 10952–56, 10958–59, 10963, 10965, 10968–69, 10970–71, 10975–79, 10997–98); (44): Tonala (UIMNH 26227–29). GUERRERO: (45): 2 km W Puerto Marquez (CU 9676–79, 9692–93, 9772, LACM 128590, 130027–29).

L. tarascae

MICHOACÁN: (46): near Mexiquillo, Aquila District (ENCB 9221–22, LACM 134226).

L. tuxtlae

CHIAPAS: (47): 25 mi. (by rd to Malpaso) NW Ocozocoautla (UAZ 28780–82). OAXACA: (48): Vista Hermosa (KU 87396–98); 30 mi. (by rd) NE Llano de las Flores (UMMZ 125870); (49): Mts nr La Gloria (UIMNH 37236); (50): Finca San Carlos, Matias Romero Oaxaca (FSM 32918). VERACRUZ: (51): Volcan San Martin (TCWC 22102–03, TNHC 29792–93, UIMNH 80695–99, UMMZ 118219, 121165, 122112, 126360–61); S slope Volcan San Martin Tuxtla (KU 59560); Rancho El Tular, 15 mi. N San Andres Tuxtla (USNM 139731); Rio Tecolapan, 2.4 mi. NNW Tapalapan (UMMZ 115098–99); Salto de Eyipantla (TCWC 19134); Montepio (FSM 32917); Sontecomapan [and vic] (CM 41470, FSM 32914, TCWC 19135, 26717, UAZ 28770–79, UTAR 3101, 3103–04, 3108–09, 3111–13, 3115, 3127); 7.7 mi. NW Sontecomapan (UTAR 3728–30, 3733–34); E of Lago Catemaco, 12.7 mi. from Catemaco by rd (LACM 106795); 18 mi. NNE Catemaco (JCL 67); Univ. Mex. Bio. Exp. Sta., ca. 33 km ENE Catemaco (TCWC 53352–53); between Laguna Catemaco and Volcan Martin (UMMZ 121166); Coyame (UAZ 28763); midway between Coyame and Tebanca (UMMZ 121164); 4 mi. SE Tebanca (TCWC 21366); 5.6 mi. ESE Tebanca (UTAR 3156); Rio Quetzalapan [and vic] (TCWC 19136, 21367–69, UTAR 3133, 3139–40); Colonia de Bastonal (TCWC 19137); Dos Arroyos, 5 mi. E Zapoapan (TCWC 21370–71); (52): 25 km SE Jesus Carranza (KU 26912).

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LITERATURE CITED

Avise, J.C., and R.K. Selander. 1972. Evolutionary genetics of cave-dwelling fishes of the genus *Astyanax*. Evolution 26(1):1–19.

Bezy, R.L. 1972. Karyotypic variation and evolution of the lizards in the family Xantusiidae. Contributions in Science 227:1–29.

———. 1973. A new species of the genus *Lepidophyma* (Reptilia: Xantusiidae) from Guatemala. Contributions in Science 239:1–7.

Bezy, R.L., R.G. Webb, and T. Alvarez. 1982. A new species of the genus *Lepidophyma* (Sauria: Xantusiidae) from Michoacan, Mexico. Herpetologica 38(3):361–366.

Blackburn, D.G. 1982. Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia-Reptilia 3(2/3):185–205.

Bocourt, M. 1876. Note sur quelques reptiles de l'isthme de Tehuantepec (Mexique) donnés par M. Sumichrast au Muséum. Journal de Zoologie, Paris 5:386–411.

Bull, J.J. 1980. Sex determination in reptiles. The Quarterly Review of Biology 55(1):3–21.

Darevsky, I.S., L.A. Kupriyanova, and M.A. Bakradze. 1978. Occasional males and intersexes in parthenogenetic species of Caucasian rock lizards (genus *Lacerta*). Copeia 1978(2):201–207.

Dixon, J.R., C.A. Ketchersid, and C.S. Lieb. 1972. The herpetofauna of Queretaro, Mexico, with remarks on taxonomic problems. Southwestern Naturalist 16(3 & 4):225–237.

Dixon, W.J. [Editor]. 1981. BMDP Statistical software. University of California Press, Berkeley.

Duméril, A.M.C., and A.H.A. Duméril. 1851. Catalogue méthodique de la collection des reptiles. Museum d'Histoire Naturelle de Paris.

Hall, W.P., and R.K. Selander. 1973. Hybridization of karyotypically differentiated populations in the *Sceloporus grammicus* complex (Iguanidae). Evolution 27(2): 226–242.

Leviton, A.E., R. McDiarmid, S.Moody, M. Nickerson, J. Rosado, O. Sokol, and H. Voris. 1980. Museum acronyms—second edition. Herpetological Review 11(4): 93–102.

Leopold, A.S. 1959. Wildlife of Mexico. The game birds and mammals. University of California Press, Berkeley.

Mitchell, R.W., W.H. Russell, and W.R. Elliott. 1977. Mexican eyeless characin fishes, genus *Astyanax*: environment, distribution, and evolution. Special Publications, The Museum, Texas Tech University 12:1–89.

Mosauer, W. 1936. A new xantusiid lizard of the genus *Lepidophyma*. Herpetologica 1(1):3–5 + Plate II.

Savage, J.M. 1963. Studies on the lizard family Xantusiidae IV. The genera. Los Angeles County Museum Contributions in Science 71:1–38.

Simpson, G.G., A. Roe, and R.C. Lewontin. 1960. Quantitative zoology. Revised Edition. Harcourt, Brace, and Co., New York.

Sites, J.W. 1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus*. I. Chromosome polymorphisms. Evolution 37(1):38–53.

Smith, H.M. 1939. Notes on Mexican reptiles and amphibians. Zoological Series of Field Museum of Natural History 24(4):15–35.

———. 1942. Mexican herpetological miscellany. Proceedings of the United States National Museum 92(3153): 349–395.

———. 1973. A tentative rearrangement of the lizards of the genus *Lepidophyma*. Journal of Herpetology 7(2): 109–123.

Smith, H.M., and M. Alvarez del Toro. 1977. A new troglodytic lizard (Reptilia, Lacertilia, Xantusiidae) from Mexico. Journal of Herpetology 11(1):37–40.

Taylor, E.H. 1939. A new species of the lizard genus *Lepidophyma* from Mexico. Copeia 1939(3):131–133.

Walker, C.F. 1955. Two new lizards of the genus *Lepidophyma* from Tamaulipas. Occasional Papers of the Museum of Zoology University of Michigan 564:1–10.

Werler, J.E. 1957. A new lizard of the genus *Lepidophyma* from Volcan San Martin Pajapan, Veracruz. Herpetologica 13(3):223–226.

Werler, J.E., and F.A. Shannon. 1957. A new lizard of the genus *Lepidophyma* from Veracruz, Mexico. Herpetologica 13(2):119–122.

White, M.J.D. 1973. Animal cytology and evolution. Third Edition. Cambridge University Press, London.

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CONTRIBUTIONS IN SCIENCE

MEGAPALEONTOLOGY OF THE EOCENE LLAJAS FORMATION, SIMI VALLEY, CALIFORNIA

Richard L. Squires

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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MEGAPALEONTOLOGY OF THE EOCENE LLAJAS FORMATION, SIMI VALLEY, CALIFORNIA

Richard L. Squires[1]

ABSTRACT. The paleontology and stratigraphic distribution of the megafossils in the late early through early middle Eocene age Llajas Formation, Simi Valley, Los Angeles and Ventura Counties, southern California, are described in detail. One hundred and seven species and subspecies, representing 88 identifiable genera, are recorded for 132 localities. Twenty-six of these species are previously unreported from the Llajas Formation.

Illustrations, synonymies, primary type material information, West Coast molluscan stage ranges, geographic distributions, local occurrences, and remarks are provided for the taxa, which include one large foraminifer, two corals, one brachiopod, one annelid, two scaphopods, 65 gastropods, 29 bivalves, one nautiloid, one sepiid, one brachyuran, one spatangoid, and two sharks. The sepiid can be identified only to the family level. A new species of *Cerithiopsis* and a new species of *Ancistrolepis*? are named. *Crassatella uvasana* and *C. u. semidentata* are shown to be identical.

Most of the megafossils occur in channel-fill deposits in shallow-marine strata but have undergone minimal postmortem transport. The Llajas megafauna lived in warm waters less than 80 m depth.

Mollusks indicative of the lower of the two faunal zones of the West Coast provincial molluscan "Capay Stage" (lower Eocene) are present in the lowermost fossil-bearing beds of the Llajas Formation. The remaining fossil-bearing part of the Llajas contains mollusks indicative of the "Domengine Stage" (upper lower through lower middle Eocene). Age refinement of the Llajas extends the molluscan stage ranges of several molluscan species. The Llajas megafauna is similar to those in late early–early middle Eocene age formations from San Diego, California through southwestern Oregon. These megafaunas were in the same faunal province that extended, at least, from southern California into Washington. Most of the genera were already present on the West Coast by Llajas time and several species were carry-overs from earlier times. A few genera were early Eocene immigrants from the Caribbean and Old World Tethyan regions, and some were early middle Eocene immigrants from the same regions. Several genera originated on the West Coast during the early middle Eocene.

INTRODUCTION

Since the early 1900's, paleontologists have collected megafossils from the late early through early middle age Eocene Llajas Formation in the Simi Valley area, Los Angeles and Ventura Counties, southern California. The fossils are predominantly mollusks and nearly every paleontological museum on the West Coast has a representative collection. To date, however, there has been no comprehensive taxonomic and stratigraphic analysis of the Llajas megafauna. Researchers, therefore, have been hindered in performing detailed comparative studies on the taxonomy, biogeography, and time-correlation of the Llajas megafossils. The objectives of this paper are 1) to tabulate the species and show their distribution within the formation, 2) to provide synonymies and illustrations of the species, 3) to provide taxonomic refinements of certain known taxa and describe two new gastropods, 4) to interpret the paleoenvironment and biogeography of the megafauna, 5) to refine the age assignment and correlation of the Llajas Formation, and 6) to refine the West Coast molluscan stage ranges of the taxa.

The Llajas Formation crops out in the southwestern Santa Susana Mountains and along the south side of Simi Valley (Fig. 1). It disconformably overlies the late Paleocene through earliest Eocene age marine Santa Susana Formation and, except where local faults occur, is unconformably overlain by the early late Eocene through Oligocene age nonmarine Sespe Formation (Figs. 2 and 3).

Outcrops of the Llajas Formation are typically extensively covered. Best exposures are at the 545-m-thick type section in the southwestern Santa Susana Mountains (Fig. 1). In 1981 and 1983b, I reported that the Llajas Formation in the southwestern Santa Susana Mountains consists mostly of a transgressive (retrogradational) sequence of facies that grades vertically from coastal alluvial fan, to shallow marine, to outer shelf and slope with incised channels. The outer shelf and slope facies was subsequently covered by regressive (progradational) shallow-marine facies. The regressive sequence is

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[1] Department of Geological Sciences, California State University, Northridge, California 91330, and Research Associate, Invertebrate Paleontology, Natural History Museum of Los Angeles County.

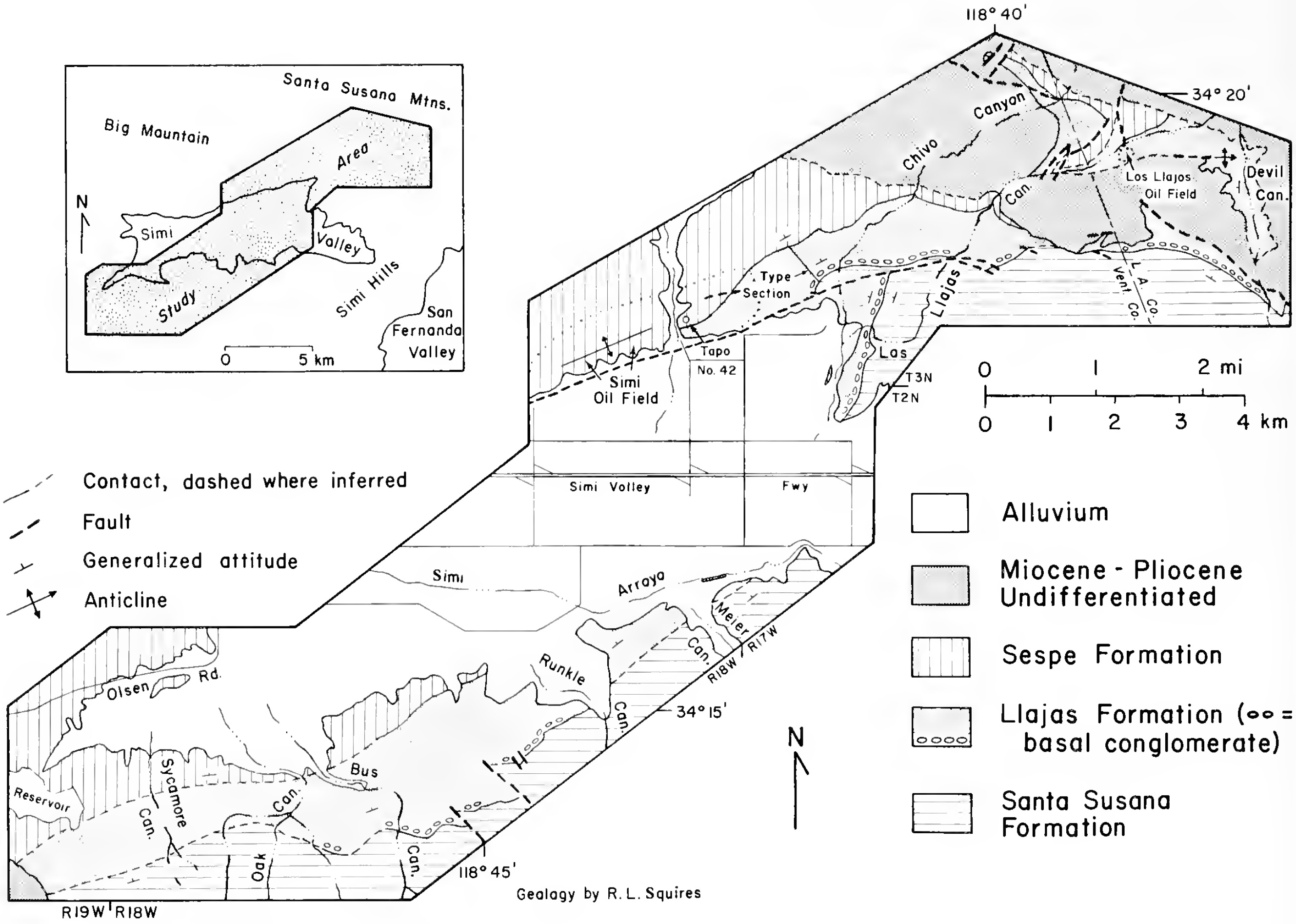

Figure 1. Geologic map showing outcrops of the Llajas Formation in the Simi Valley area, southern California (after Squires, 1983b).

incomplete due to erosional truncation by the Sespe Formation (Fig. 2).

HISTORICAL REVIEW

In the last 70 years, starting with Waring (1914), there have been many investigations dealing with the megafossils of the Llajas Formation. These previous studies have included partial faunal lists (Waring, 1917; Clark, 1926; Hanna, 1927; McMasters, 1932; Cushman and McMasters, 1936; Turner, 1938; Vokes, 1939; Lewis, 1940; Seiden, 1972), descriptions of new taxa (Waring, 1914, 1917; Schenck, 1926; Stewart, 1927, 1930; Clark, 1934, 1942; Merriam and Turner, 1937; Vokes, 1937, 1939; Bentson, 1940; Merriam, 1941; Hertlein and Grant, 1944; Sutherland, 1966; Squires, 1983a), and taxonomic refinements or miscellaneous comments on known species. In this last category, the most notable papers are those of Schenck (1931), Gardner and Bowles (1934), Clark and Vokes (1936), Turner (1938), Vokes (1935, 1939), Merriam (1941), Hanna and Hertlein (1943), Verastegui (1953), Marincovich (1977), Givens (1979), Squires (1979), and Saul (1983).

As the name "Llajas Formation" was not formalized until 1936 by Cushman and McMasters, earlier workers referred to such strata by various names (Fig. 4). Clark and Vokes (1936), Turner (1938), and Vokes (1939) used the terms "Lower Llajas" and "Upper Llajas" but did not define them.

Various aspects of the microfossils of the Llajas Formation have been reported on by McMasters (1932), Cushman and McMasters (1936), Laiming (1940a, 1940b, 1943), Mallory (1959), Schymiczek and Squires (1981), Schymiczek (1983a, 1983b), and Filewicz and Hill (1983).

MEGAFOSSILS

One hundred and seven taxa, more than 90 percent of which are mollusks, were identified from the Llajas Formation. Taxa identified to species and subspecies include 64 gastropods, 28 bivalves, two scaphopods, two solitary corals, and one species each of large foraminifer, brachiopod, annelid, nautiloid, brachyuran, and spatangoid. One gastropod, one bivalve, and two sharks are identified only to genus. A spirulimorph sepiid could only be identified to the family level. All of these taxa are illustrated in Figures 5 through 13. Other

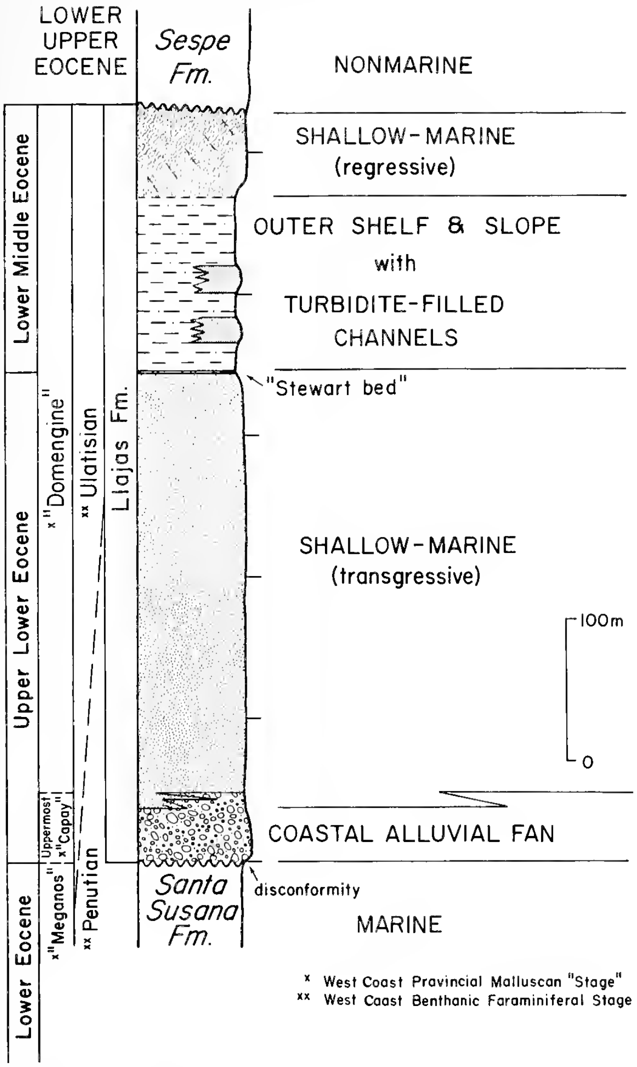

Figure 2. Stratigraphic column of the Llajas Formation, showing depositional environments based on Squires (1981, 1983b).

taxa, too poorly preserved for even generic determination, include a bryozoan, two brachiopods, calcareous worm tubes, two gastropods, a nautiloid, a myliobatoid, and scattered *Teredo*?-bored wood fragments.

The identifications of Llajas species and subspecies studied in this report are based on published figures and descriptions and selected comparisons with type specimens and non-type specimens on deposit at 1) Department of Earth and Space Sciences, University of California at Los Angeles, 2) University of California, Museum of Paleontology, Berkeley, 3) Natural History Museum of Los Angeles County, and 4) California State University, Northridge.

Megafossils were collected at 121 localities in the southwestern Santa Susana Mountains and 11 localities along the south side of the Simi Valley. All of the localities are described in the "Localities" section, and the relative stratigraphic position of each one is shown in Figures 14 through 19.

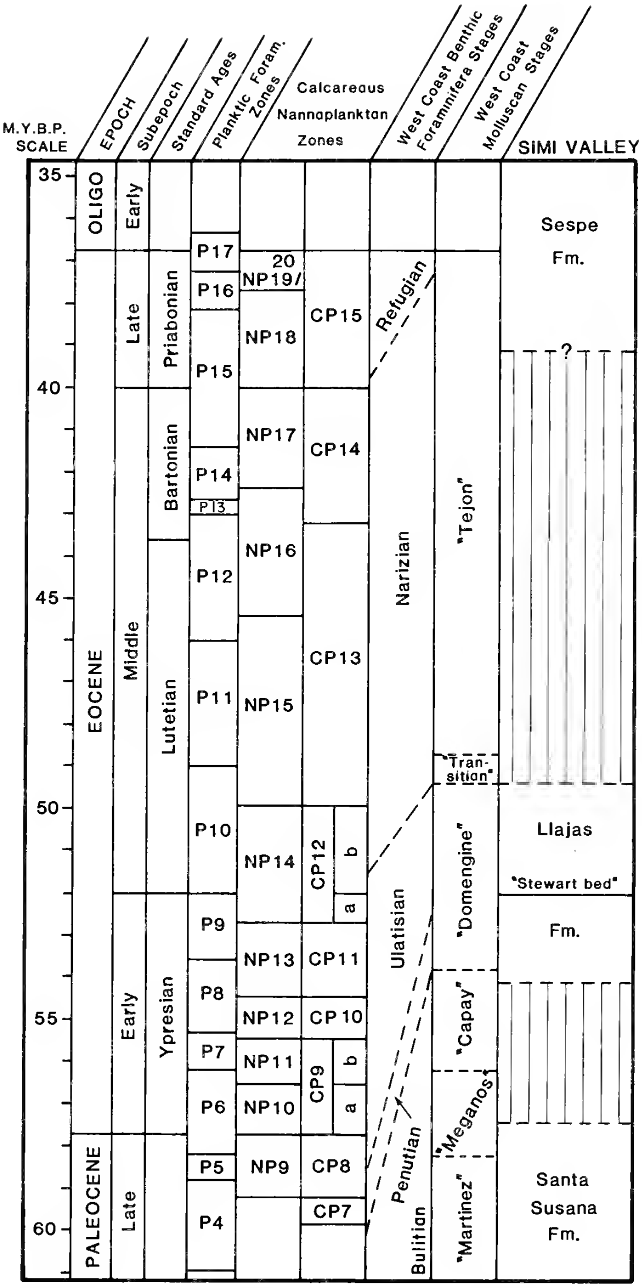

Figure 3. Correlation of the Llajas Formation with Eocene West Coast molluscan stages (after Saul, 1983); millions of years before present (M.Y.B.P.) scale, epochs, subepochs, standard ages, planktic foraminifera zones, and calcareous nannoplankton zones (all after Berggren, Kent, and Flynn, in press); and West Coast benthic foraminifera stages (after Poore, 1980).

Species and subspecies with holotype localities in the Llajas Formation are listed in Table 1. Species not previously reported from the Llajas Formation are listed in Table 2.

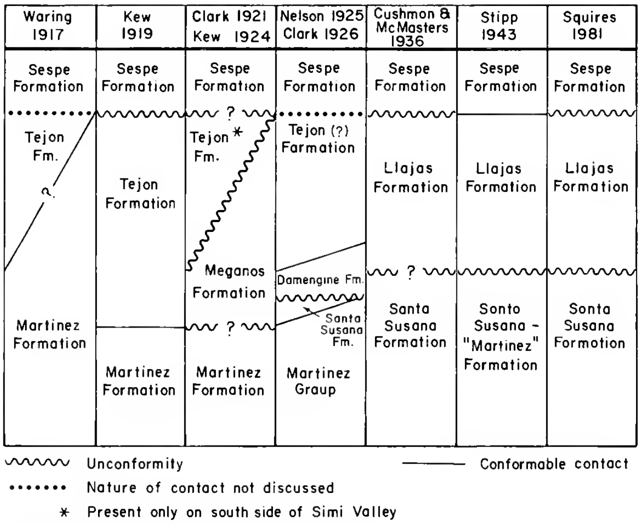

Figure 4. Comparative concepts of Paleogene stratigraphy in the Simi Valley area (after Squires, 1983b).

Some megafossil species previously reported (Waring, 1914, 1917; Clark, 1921:158–159, 1926:114–116; Clark, 1942; Kew, 1924:25, 29; Hanna, 1927:260; Vokes, 1935, 1939:23–26, 30–31; Clark and Vokes, 1936; Turner, 1938:33–37; Bentson, 1940; Ingram, 1940) from the Llajas Formation (or generally equivalent strata) were not found during the present study. There are serious problems in trying to substantiate the records of these species because 1) locality information is either lacking or vague, and/or 2) previously used formation names (i.e., Meganos and Domengine) are not the exact equivalents of the Llajas Formation (Fig. 3). In addition, because these species names usually have only been listed, without illustration or reference to catalogued museum specimens, there is no way to verify the identifications. Some of these so-called "Llajas" species can be shown to be from the underlying late Paleocene through earliest Eocene age Santa Susana Formation. Based on analysis of Zinsmeister's (1974, 1983a) work on the megafauna of the Santa Susana Formation, the following species are from this unit: *Cucullaria morani* [=*Cucullaea*], mentioned by Waring (1914, 1917); *Polinices hornii, Mesalia martinezensis* [=*Turritella*], *Turritella infragranulata,* and *Septifer elegans,* mentioned by Waring (1917). Clark (1942) reported that the type locality of *Chedevillea stewarti* and *Tibia* (*Eotibia*) *llajasensis* is in the lower portion of the Llajas Formation. According to Keen and Bentson (1944:143), this locality (University of California, Museum of Paleontology, Berkeley, locality 7015) plots within Paleocene strata as mapped by Nelson (1925).

The marine strata of the Llajas Formation have been thoroughly bioturbated, but the only identifiable trace fossils are *Ophiomorpha, Thalassinoides,* and *Chrondites*?. The first two ichnogenera are fairly common in the shallow-marine facies, especially in certain beds where this facies interfingers with the coastal alluvial-fan facies. An *Ophiomorpha* burrow in one of these beds is figured by Squires (1981:930, fig. 6C; 1983b, fig. 6E). *Chrondites*? is common in the outer shelf and slope facies.

Table 1. Megafossils with holotype localities in the Llajas Formation.

Brachiopoda
  Eogryphus tolmani Hertlein and Grant, 1944

Gastropoda
  Ancistrolepis? *carolineae* n. sp.
  Architectonica (*Architectonica*) *llajasensis* Sutherland, 1966
  Cerithiopsis llajasensis n. sp.
  Conus caleocius Vokes, 1939
  Cymatium (*Septa*) *janetae* Squires, 1983
  Eocithara mutica californiensis (Vokes, 1937)
  Exilia llajasensis Bentson, 1940
  Fusiturricula (*Crenaturricula*) *crenatospira domenginica* Vokes, 1939
  Galeodea (*Caliagaleodea*) *californica* Clark, 1942
  Galeodea (*Gomphopages*) *susanae* Schenck, 1926
  Lyria andersoni Waring, 1917
  Pachycrommium clarki (Stewart, 1927)
  Ranella katherineae Squires, 1983
  Tectarius ligniticus Vokes, 1939 (see *Benoistia umpquaensis*)
  Turritella andersoni lawsoni secondaria Merriam, 1941
  Turritella andersoni susanae Merriam, 1941
  Turritella meganosensis protumescens Merriam and Turner, 1937
  Turritella uvasana etheringtoni Merriam, 1941 (see *T. u. applinae*)
  Turritella uvasana infera Merriam, 1941

Bivalvia
  Nayadina (*Exputens*) *llajasensis* (Clark, 1934)
  Callocardia (*Nitidavenus*) *tejonensis* (Waring, 1914)
  Pinna lewisi Waring, 1917
  Pinna llajasensis Squires, 1983
  Venericardia (*Pacificor*) *hornii calafia* Stewart, 1930

DEPOSITIONAL ENVIRONMENTS AND STRATIGRAPHIC DISTRIBUTION OF MEGAFOSSILS

Based on sedimentologic and lithologic features of the Llajas Formation, on comparative studies of modern and ancient sedimentary sequences, and ecology of representative genera of mollusks and benthic foraminifers, the following facies have been recognized in the Llajas Formation: coastal alluvial fan, shallow marine, and outer shelf and slope with incised channels. In a vertical sense, most of the formation is transgressive (retrogradational) in that shallower facies are overlain by deeper facies. The uppermost part of the formation, however, represents a regressive (progradational) event in which the outer shelf and slope facies and associated

Table 2. Megafossils previously unreported from the Llajas Formation.

Anthozoa
  ?Trochocyathus striatus (Gabb, 1864)
  Turbinolia dickersoni Nomland, 1916

Annelida
  Rotularia tejonense (Arnold, 1909)

Scaphopoda
  Dentalium (*Laevidentalium*) *calafium* Vokes, 1939
  Dentalium stentor Anderson and Hanna, 1925

Gastropoda
  Ancistrolepis? *carolineae* n. sp.
  Cerithiopsis llajasensis n. sp.
  Cirsotrema sp.
  Laevityphis (*Laevityphis*) *antiquus* (Gabb, 1864)
  Molopophorus cretaceus (Gabb, 1864)
  Nerita cf. *N.* (*Amphinerita*) *eorex* Vokes, 1939
  Neverita (*Neverita*) *globosa* Gabb, 1869
  Olivella mathewsonii Gabb, 1864
  Terebra californica Gabb, 1869

Bivalvia
  Anomia mcgoniglensis Hanna, 1927
  Cardiomya aff. *C. russelli* (Hanna, 1927)
  Corbula (*Caryocorbula*) *dickersoni* Weaver and Palmer, 1922
  Gari aff. *G. eoundulata* Vokes, 1939
  Glycymeris (*Glycymeris*) *rosecanyonensis* Hanna, 1927
  Macoma rosa Hanna, 1927
  Marcia (*Mercimonia*) *bunkeri* (Hanna, 1927)
  Pitar (*Calpitaria*) *uvasanus* (Conrad, 1855)
  Spondylus carlosensis Anderson, 1905
  Teredo? sp.

Vertebrata
  Isurus cf. *I. praecursor* (Leriche, 1906)
  Odontaspis sp.

Table 3. Explanation of reference abbreviations for Tables 4 and 5.

A1	Abbott, 1968a
A2	Abbott, 1974
A&D	Abbott and Dance, 1982
C	Cossmann, 1901
D	Dance, 1976
D&D	Dell and Dance, 1963
E	Eisenberg, 1981
G	Grassé, 1968
Ha	Habe, 1968
H&G	Hertlein and Grant, 1972
K	Keen, 1971
K&C	Keen and Coan, 1974
Ki	Kira, 1965
L	Lindner, 1978
Ma	Marincovich, 1977
Mc	McMillan, 1968
Me	Merriam, 1941
M1	Morris, 1966
M2	Morris, 1975
N1	Nordsieck, 1968
N2	Nordsieck, 1969
O	Olsson, 1961
R	Rios, 1970
S	Schenck, 1936
T	Tebble, 1976
W&D	Weaver and duPont, 1970

turbidite-filled incised channels were covered by shallow-marine facies (Squires, 1981, 1983b) (Fig. 2).

The coastal alluvial-fan facies, equivalent to the basal conglomerate depicted in Figure 1, is unfossiliferous. The zone of interfingering between this facies and the shallow-marine facies contains fairly abundant mollusks. Many of these mollusks are the same species that occur in the stratigraphically higher shallow-marine facies. Some of the mollusks, however, are restricted in their occurrence in the Llajas Formation to this zone of interfingering. These mollusks are *Nerita* cf. *N.* (*Amphinerita*) *eorex, Velates perversus, Turritella meganosensis protumescens, Turritella andersoni,* and *Venericardia* (*Pacificor*) *aragonia joaquinensis.* Unidentifiable ostreid remains also characterize this zone of interfingering. At CSUN locality 542, such remains form an ostreid coquinite. *Turritella meganosensis protumescens* typically occurs as robust, thick-shelled fragments up to 5.5 cm in length. This taxon belongs to the *T. reversa* stock of Merriam (1941). According to Saul (1983), the presence of large members of this stock, as well as the presence of *Venericardia* (*Pacificor*) *aragonia joaquinensis,* in the Llajas Formation indicate nearshore, shallow-water conditions. The presence of ostreid coquinites indicates similar conditions. *Nerita* occurs along shorelines today (Tables 3 and 4), and *Velates,* a closely allied but extinct genus, probably occurred in the same type of environment.

Most of the fossils in the formation occur in the shallow-marine facies proper, which can be divided into a transgressive phase and a regressive phase. The transgressive phase makes up most of the lower part of the formation. It consists of alternating laminated and bioturbated sandstone with scattered fossiliferous beds mostly confined to channels. The laminated sandstone represents storm-influenced stratification and the biogenic reworking is inter-storm activity (Squires, 1981). These deposits probably accumulated where the coastal alluvial-fan rivers emptied into the ocean. The resulting sediment buildup would have been subjected to reworking by waves (Squires, 1983b). The fossils have undergone a small distance of postmortem transport and constitute indigenous death assemblages (Squires, 1981). Many fossils show preservation of delicate features, such as protoconchs, outer lips, and ribs. There is much variability in the taxonomic composition of the fossils in these channel-fill deposits. At many localities, only one or two species of megafossils

Table 4. Recent bathymetry of extant molluscan genera of the Llajas Formation.

Genus (subgenus)	Depth range (m)	*MFR depth (m)	**References
Scaphopoda			
Dentalium	4–2320	7–100	A2,K,K&C,M2,R
Gastropoda			
Ancilla	6–87	21–70	A2,R
Ancistrolepis	40–200	100	K
Architectonica	0–134	2–37	A2,K
Calyptraea	0–70	0–37	A1,M1,M2,K
Cerithiopsis	0–823	24–60	A2,M1
Cirsotrema	33–274	73–137	A2,Ha,Ki
Conus	0–550	9–55	K,M1,R
Cymatium (*Septa*)	0–146	24–60	A2,M1,M2
Cypraea	0–140	9–24	A1,M1,M2,R
Fusinus	0–3616	18–60	A1,A2,K,K&C,Ki,M1,M2
Fusiturricula	56–65	60	R
Galeodea	7–330	8	Mc,N1
Lyria	0–133	2–24	Ha,K,Ki,W&D
Natica (*Naticarius*)	0–280	32–60	Ma,R
Nerita	0–9	0–9	K,M1,M2
Neverita (*Neverita*)	11–2860	658–1281	M
Olivella	0–90	0–27	A1,A2,K,K&C,R
Phalium (*Semicassis*)	18–100	37–55	Ha,Ki
Polinices (*Euspira*)	0–4794	15–200+	Ma,M1
Pseudoliva	0–3	0–3	C,L
Ranella	55–915	110	D&D
Scaphander	20–5200	50–160	A1,A2,K
Sinum	0–170	24–48	K,K&C,Ma,R
Terebra	0–280	4–18	K,M1
Turritella	4–185	26–56	K,K&C,Ki,M1
Xenophora	0–200	20–144	A1,A2,Ha,K,Ki,M2,R
Bivalvia			
Acanthocardia	0–360	5	N2,T
Acila (*Truncacila*)	7–1256	20–100	A1,A2
Anomia	0–550	0–9	A2,K,M1,M2
Brachidontes	0–31	0–24	K,M1,M2,R
Callista (*Costacallista*)	30–214	45–100	A2,R
Cardiomya	4–2400	60–190	K,M1,M2,Ha,R
Corbula (*Caryocorbula*)	0–823	10–27	A2,K
Gari	0–150	10–50	A2,Ha,M1
Glycymeris	0–110	9–60	A1,K,M1,M2
Macoma	0–1545	0–45	A1,K&C,M1,R
Nemocardium	9–640	25–90	A2,Ha,H&G,K,Ki,M1,K&C
Nuculana (*Saccella*)	2–1097	10–80	A2,K
Ostrea	0–91	0–24	H&G,K,M1,M2
Pinna	0–200	0–24	A2,Ha,K,M1,M2
Pitar (*Lamelliconcha*)	0–110	30–80	K,O
Solena	Nearshore		K
Spondylus	3–140	15–50	A1,K,M1,M2,R
Teredo	Bores into wood		A2,M2

* Most frequently reported; ** see Table 3 for abbreviations.

are present. *Turritella andersoni lawsoni* is usually one of these species. At other localities, such as CSUN locality 371, as many as 45 species of megafossils have been found.

The regressive phase of the shallow-marine facies makes up the uppermost part of the formation. It consists of bioturbated silty sandstone with minor occurrences of laminated sandstone and scattered fossiliferous units. These deposits were in slightly deeper waters than those of the transgressive phase and were less affected by storm reworking (Squires, 1983b). Fossils are unabraded, and at CSUN locality 475 articulated *Pinna lewisi* specimens were found. The fossils in the regressive phase are also interpreted to be indigenous death assemblages.

Where the sandstone of the transgressive and regressive phases of the shallow-marine facies grades into muddy siltstone of the outer shelf and slope facies, the sandstone is more silty and more bioturbated, and most of the fossils are confined to a few beds with indistinct contacts due to bioturbation (Squires, 1981).

One such bed, informally known as the "Stewart bed" (Squires, 1979, 1981, 1983b), is the most distinctive fossiliferous unit in the shallow-marine facies. This 1-m-thick layer occurs in the uppermost part of the transgressive phase of the shallow-marine facies in the northern part of the study area and can be traced laterally for about 10 km eastward from the type section of the formation. Fossils in the lower part of the "Stewart bed" show less evidence of postmortem transport than those elsewhere in the shallow-marine facies. Many of the taxa are represented by nearly complete growth series (with only the early juvenile individuals lacking). Articulation of valves is also common. There is a nearly 1:1 ratio of opposite valves of the bivalves *Crassatella uvasana* and *Venericardia* (*Pacificor*) *hornii calafia*. Some specimens of these bivalves, especially *Crassatella*, are articulated but are not in growth position. Specimens of all taxa show preservation of delicate morphologic features. There is random orientation of the faunal remains. Most of the specimens occur in the lower 50 cm of the bed and seem to be somewhat concentrated in indistinct pods. Based on the above features, as well as the lack of sedimentary structures indicative of high energy, it is interpreted that a residual (winnowed) paleocommunity, as defined by Fagerstrom (1964), occurs at many exposures of the lower part of the "Stewart bed" (Squires, 1981).

The uniformity of the lithology throughout the "Stewart bed" suggests uniform depositional and environmental conditions. The megafauna is also fairly uniform throughout the bed. The most abundant faunal elements are carnivorous naticid gastropods (*Eocernina* and *Pachycrommium*), herbivorous gastropods (*Turritella* and *Ectinochilus*), infaunal suspension feeder bivalves (*Crassatella* and *Venericardia*), and carnivorous solitary ahermatypic scleractinian corals (*Trochocyathus*?). This *Eocernina-Turritella-Crassatella-Trochocyathus*? paleocommunity is best developed at and in the vicinity of CSUN locality 374, with 50 species of megafossils present. The shallow-marine "Stewart bed" was deposited near the shelf/slope break based on calcareous nannofossil studies (Filewicz and Hill, 1983) and on the presence of outer shelf and slope deposits directly above it. The presence of abundant large specimens of *Trochocyathus*? in the "Stewart bed," as well as in a few thin beds a few meters above the "Stewart bed" at the type section, is consistent with a shelf/slope break environment for this part of the Llajas. Solitary ahermatypic scleractinian corals tolerate a wide range of temperatures and live at all depths, attaining their best development along margins of the continental shelves (Wells, 1957; Heckel, 1972).

Megafossils which characterize the transgressive phase of the shallow-marine facies are *Pseudophragmina* (*Proporocyclina*) *clarki*, *Cylichnina tantilla*, *Ectinochilus* (*Macilentos*) *macilentus*, *Eocernina hannibali*, *Pachycrommium clarki*, *Turritella andersoni lawsoni*, *Turritella buwaldana*, *Brachiodontes* (*Brachidontes*) *cowlitzensis*, and *Dentalium* (*Laevidentalium*) *calafium*. The only taxon that characterizes the regressive phase of the shallow-marine facies is *Macoma rosa*.

Megafossils which commonly occur in both the transgressive and regressive phases of the shallow-marine facies are *Calyptrea diegoana*, *Phalium* (*Semicassis*) *tuberculiformis*, *Turritella uvasana applinae*, *Corbula* (*Caryocorbula*) *dickersoni*, and *Glycymeris* (*Glycymeris*) *rosecanyonensis*.

Many of the molluscan genera of the shallow-marine facies of the Llajas are extant and most commonly occur today in seas less than 80 m depth (Tables 3 and 4). The discocyclinid foraminifers lived in very shallow water (below tide level to perhaps 100 m) (Vaughan, 1945). Small calcareous benthic foraminifers present in the transgressive and regressive phases of the shallow-marine facies of the formation are indicative of inner to middle neritic conditions (Schymiczek, 1983a, 1983b).

Megafossils are scarce in the outer shelf and slope facies, but foraminifers indicative of bathyal depths are common (Squires, 1981; Schymiczek, 1983a, 1983b). The mollusks that occur in this facies also occur in the shallow-marine facies. Apparently, many of the outer shelf and slope facies mollusks are shallow-marine species that were transported into the deeper water facies. This is especially true for the mollusks at CSUN locality 541. This locality is from the base of a turbidite-filled channel in the outer shelf and slope facies. Some of the fossils occur as fragments.

PALEOCLIMATE

West Coast Eocene megafauna have long been assigned to tropical or subtropical environments (Arnold, 1909; Dickerson, 1917; Smith, 1919; Clark and Vokes, 1936; Berthiaume, 1938; Vokes, 1940; Durham, 1950). Among the Eocene molluscan genera that Durham (1950) listed as particularly characteristic of tropical (20°C or warmer), the following also occur in the Llajas Formation: the gastropods *Ancilla*, *Architectonica*, *Conus*, *Cypraea*, *Ectinochilus* [=*Rimella*], *Eocernina*, *Eocithara* [=*Harpa*], *Ficopsis*, *Paraseraphs* [=*Terebellum*], *Pseudoliva*, *Terebra*, *Turritella*, *Velates*, *Xenophora*; the bivalves *Corbula*, *Pinna*, *Pitar*, *Spondylus*, large *Venericardia*, *Crassatella* [=*Crassatellites*]; and the cephalopod *Aturia*.

Table 5. Recent, marine faunal regions (Ross, 1974:4) of extant molluscan genera of the Llajas Formation.

Genus (subgenus)	Boreal	Warm temperate	Tropical	*References
Scaphopoda				
Dentalium	x	x	M	D,K,R
Gastropoda				
Ancilla			M	A2,D,R
Ancistrolepis	M			A&D,E,Ha,K
Architectonica		x	M	A2,K,M2
Calyptraea	x	x	M	A1,D,K,M1,M2
Cerithiopsis	x	x	M	A2,K,K&C,M1
Cirsotrema		x	M	A2,Ha,Ki,K
Conus	x	x	M	K,M1,R
Cymatium (*Septa*)		x	M	A2,D,E,K,M1,M2
Cypraea		x	M	A1,K,L,M1,R
Fusinus	x	x	M	A1,A2,D,K,Ki,M1,M2
Fusiturricula			M	A&D,R
Galeodea		M	x	D,E,Ha,Mc,N1
Lyria		x	M	A2,Ha,K,Ki,W&D
Natica (*Naticarius*)		x	M	Ma,R
Nerita			M	K,L,M1,M2
Neverita (*Neverita*)	M	x		M
Olivella	x	x	M	A2,D,K,K&C,R
Phalium (*Semicassis*)	x	x	M	E,Ha,Ki,L
Polinices (*Euspira*)	x	x	M	Ma
Pseudoliva			M	C,G,L
Ranella	x	M		D,E
Scaphander	x	M	x	A1,A2,D,K,M2
Sinum		x	M	K,K&C,Ma,R
Terebra		x	M	D,K,M1
Turritella		x	M	K,K&C,Ki,M1,Me
Xenophora		x	M	A1,A2,Ha,K,Ki,M2,R
Bivalvia				
Acanthocardia	x	M		D,E,L,N2,T
Acila (*Truncacila*)	M	M	x	A1,S
Anomia	x	M	x	A2,D,K,L,M1,M2
Brachidontes	x	x	M	D,K,M1,M2,R
Callista (*Costacallista*)		x	M	A2,L,R
Cardiomya	x	x	M	Ha,K,M1,M2,R
Corbula (*Caryocorbula*)		x	M	A2,K
Gari	x	x	M	A2,D,Ha,L,M1
Glycymeris	x	x	M	A1,K,M1,M2
Macoma	M	M	x	A1,D,M1,R
Nemocardium	x	x	M	A2,D,Ha,H&G,K,Ki,M1
Nuculana (*Saccella*)	x	x	M	A2,K
Ostrea	x	x	M	D,H&G,K,M1,M2
Pinna	x	x	M	A2,D,Ha,K,M1,M2
Pitar (*Lamelliconcha*)			M	K,O
Solena			M	K
Spondylus		x	M	D,K,M1,M2
Teredo	x	M	x	A2,M2

x = Present, M = Most frequently reported occurrence. * See Table 3 for abbreviations.

Berthiaume (1938) and Durham (1950) also mentioned that discocyclinid foraminifers are indicative of tropical or subtropical environments. All the recorded species of American Discocyclinidae occur in tropical, subtropical, and south temperate latitudes (Vaughan, 1945).

More recent and independent evidence supports a tropical to subtropical environment interpretation for West Coast Eocene faunas. Mineralogical analyses of kaolinite and quartz-rich, buried-soil profiles in northwest Baja California and southwest California indicate that humid tropical climatic conditions prevailed during Paleocene to mid-Eocene time (Peterson and Abbott, 1979).

Based on oxygen isotope compositions of Tertiary planktic foraminifer tests throughout the world, Savin, Douglas, and Stehli (1975) concluded that ocean temperatures remained warm and relatively constant from Paleocene through middle Eocene time. Kennett (1982) has similarly stated that during the Paleocene and Eocene, world climates were relatively warm and equable with low pole-to-equator temperature gradients. He further stated that a late Paleocene warming trend culminated in a period of peak warming during the early Eocene to early middle Eocene. This interval of time coincides with the age of the Llajas Formation. Such equable conditions ceased in earliest Oligocene time with the appearance of a worldwide cooling trend. This cooling was associated with the development of circum-Antarctic circulation (Kennett et al., 1975; Kennett, 1982; Zinsmeister, 1982).

Although 56 percent of the molluscan genera collected from the shallow-marine facies of the Llajas Formation are extant (Tables 3 and 5), the percentage is not high enough to permit accurate generic comparison studies with modern molluscan faunas like those done by Addicott (1970) for Oligocene, Miocene, and Pliocene molluscan faunas of the West Coast. Generic comparison studies with modern molluscan faunas are also difficult to do with early Tertiary faunas because of the likelihood of significant changes in environmental tolerance in progressively older faunas (Addicott, 1970). Nevertheless, a general comparison with modern molluscan faunas can be made. Most of the extant molluscan genera of the shallow-marine facies of the Llajas most commonly occur today in tropical seas (Tables 3 and 5). It should be noted also that most of these genera can occur in warm-temperate seas as well.

The taxa *Ancilla, Pseudoliva, Nerita, Pitar* (*Lamelliconcha*), and *Solena* are particularly significant as they are confined to tropical waters today. In addition, several of the extinct generic and subgeneric taxa in the Llajas fauna, including *Ectinochilus, Eocernina, Eocithara* [=*Harpa*], *Ficopsis, Gomphopages, Laevityphis, Lyriscapha* [= *Volutocristata*], and *Exputens*, have modern analogues that are also tropical or subtropical in distribution (Clark and Vokes, 1936; Palmer, 1967; Givens, 1974).

The presence of large *Turritella* (i.e., *T. meganosensis protumescens*) in the Llajas is indicative of shallow waters that were warmer than are presently found at this latitude (Saul, 1983).

A small percentage of the Llajas megafauna does have a temperate water aspect to it. *Acanthocardia* and *Ranella* are most commonly found in temperate seas today. *Ancistrolepis*? and *Neverita* (*Neverita*) are strictly cold-water gastropods (Tables 3 and 5). *Acanthocardia* is most abundant in the "Stewart bed," and *Ranella* and *Ancistrolepis*? were found only in this bed. *Neverita* (*Neverita*) was found at about the same horizon as the "Stewart bed." Most likely, their presence in or near the "Stewart bed," which was deposited near the shelf/slope break, was due to "tropical submergence." This phenomenon has been observed in modern mollusks (Ekman, 1953). Many cold-water mollusks that occur in shallow water at higher latitudes have been found to inhabit only deeper water of similar temperature in the tropics.

AGE

The Llajas Formation is late early Eocene through early middle Eocene in age, based on mollusks, benthic foraminifers, and calcareous nannofossils. Assignment to European Standard Ages, various standard plankton zones, and West Coast provincial benthic foraminifer and molluscan stages in shown in Figure 3.

Prior to 1936, early workers using mollusks reported the age of the Llajas Formation as Eocene (Waring, 1914, 1917; Kew, 1919, 1924) or middle Eocene (Clark, 1921, 1926; Cushman and McMasters, 1936).

Clark and Vokes (1936) informally proposed five molluscan provincial Eocene "Stages": namely "Meganos," "Capay," "Domengine," "Transition," and "Tejon." They recognized two faunal zones in their "Capay Stage," and they assigned the Llajas Formation to the upper zone of the "Capay Stage" through the "Transition Stage." Givens (1974) showed that their upper faunal zone of the "Capay" should be considered part of the "Domengine Stage," and he restricted the use of "Capay Stage" to their lower faunal zone of the "Capay Stage." It is in this restricted sense that "Capay Stage" is used herein.

Saul (1983) regarded the "Meganos Stage" as late Paleocene–early Eocene, the restricted "Capay Stage" of Givens (1974) as early Eocene, the "Domengine" as late early through early middle Eocene, and the "Transition" as middle Eocene. These ages are used for this present report (Fig. 3). Weaver et al. (1944) regarded the "Tejon" as late Eocene, and Givens and Kennedy (1979) regarded it as late middle Eocene and/or late Eocene. Such ages are used for this present report (Fig. 3).

Merriam and Turner (1937) reported that in the Llajas Formation the "Capay Stage" is represented by the "basal conglomerate" because of the presence of *Turritella meganosensis protumescens*, a subspecies regarded by them as an index fossil for the "Capay Stage." Based on this present study, this subspecies occurs only where the basal conglomerate (coastal alluvial-fan facies) interfingers with the shallow-marine facies.

Vokes (1939) assigned the lower part of the Llajas Formation to the lower "Capay Stage" based, in part, on the presence of *Galeodea sutterensis*. I was unable to find any *G. sutterensis* in the Llajas. Vokes did not figure his *Galeodea* species from the Llajas Formation, nor did he give any locality information or catalog numbers of the specimen(s). Vokes (1939) assigned the middle part of the Llajas Formation to the upper "Capay Stage" based on the presence of *Galeodea susanae,* which can be documented as a Llajas species (i.e., CSUN locality 371). The "*G. susanae* Zone" of Clark and Vokes (1936) was originally assigned to the upper part of the "Capay Stage," but it was shown to be faunally indistinguishable from the "Domengine Stage" by Givens (1974) and was reassigned to the "Domengine Stage."

Vokes (1939) also used the presence of *Fusiturricula* (*Crenaturricula*) *crenatospira* in the "Lower Llajas" as an indicator of the "Capay Stage." He noted the presence of *F.* (*C.*) *crenatospira domenginica* in the "Upper Llajas" and considered this subspecies confined to the "Domengine Stage." In this present study, *F.* (*C.*) *crenatospira* was found only in the "Stewart bed" (just above the middle of the formation) where it is associated with *F.* (*C.*) *crenatospira domenginica. F.* (*C.*) *crenatospira domenginica,* furthermore, occurs in strata below the "Stewart bed."

Merriam (1941) reported the presence of *Turritella andersoni susanae* and *T. uvasana infera* from the "basal conglomerate" of the Llajas Formation. In this present study, *T. andersoni susanae* is considered equivalent to *T. andersoni.* As with *T. meganosensis protumescens,* these taxa occur in the Llajas Formation only where the coastal alluvial-fan facies interfingers with the shallow-marine facies. *T. andersoni* is a "Capay Stage" index fossil. Although it has not been previously reported from the Llajas Formation, Weaver et al. (1944) assigned the lower part of the Llajas Formation to their "Capay" *Turritella andersoni* Zone. The rest of the Llajas Formation was assigned to the "Domengine" and lower "Transition" "Stages" by Weaver et al. (1944).

Squires (1981, 1983a, 1983b) and Saul (1983) reported the lowermost mollusk-bearing beds of the Llajas Formation to be late early Eocene in age and the rest of the fossil-bearing beds as early middle Eocene in age.

Based on the above discussions, it is concluded that the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine facies is assignable to the *Turritella uvasana infera* fauna of the restricted "Capay Stage" of Givens (1974) which is equivalent to the lower of the two faunal zones of the "Capay Stage" of Clark and Vokes (1936), Vokes (1939), and Weaver et al. (1944). Due to the presence of many "Domengine" molluscan species associated with the "Capay" species where the coastal alluvial-fan facies interfingers with the shallow-marine facies, it is probable that most of the "Capay Stage" is not represented in the Llajas Formation. The part that is present is probably near the "Capay-Domengine" boundary. Saul (1983) put this boundary near the P8–P9 boundary of the "Standard" planktic foraminiferal zonation scheme as used by Berggren, Kent, and Flynn (in press) (Fig. 3). Saul (1983) also noted that most of the "Capay Stage" is probably missing in the Simi Valley area. The uppermost "Capay Stage" part of the Llajas Formation, therefore, probably corresponds to latest early Eocene time.

Fossil-bearing rocks of the Llajas Formation, therefore, cannot be assigned to any molluscan stage older than the *Turritella uvasana infera* fauna of the "Capay," as used in the restricted sense of Givens (1974). As noted by Saul (1983), no mollusks restricted to Clark and Vokes' (1936) older "Meganos Stage" have been recovered from the Llajas Formation. Although *T. uvasana infera* and *T. andersoni susanae* have been reported from the upper 100 m of the Meganos-age Santa Susana Formation, specimens are variants slightly different from those at the type localities low in the Llajas (Merriam, 1941; Saul, 1983). Filewicz and Hill (1983) reported a hiatus of approximately 4 million years between the Llajas Formation and the underlying Santa Susana Formation. In this present study, this hiatus is considered to be more on the order of 3 million years (Fig. 3).

The remaining part of the Llajas Formation is associated with megafossils that have been reported (Vokes, 1939; Merriam, 1941; Verastegui, 1953; Rehder, 1973; Givens, 1974, 1979; Givens and Kennedy, 1979; Saul, 1983) elsewhere on the West Coast only from the "Domengine Stage." These taxa are *Conus caleocius, Eocithara mutica californiensis, Fusinus teglandae, Fusiturricula* (*Crenaturricula*) *crenatospira domenginica, Lyriscapha lajollaensis, Molopophorus cretaceus, Olequahia domenginica, Proximitra*? *cretacea, Pseudoliva lineata, Turritella andersoni lawsoni, Turritella uvasana applinae, Xenophora stocki, Claibornites diegoensis, Pitar* (*Lamelliconcha*) *joaquinensis,* and *Venericardia* (*Pacificor*) *hornii calafia.*

Additional evidence for a "Domengine" age for the Llajas Formation is the overlap or joint occurrence of taxa that have been reported (Givens, 1974; Givens and Kennedy, 1979) elsewhere on the West Coast as having their lowest stratigraphic occurrence in the "Domengine Stage," including *Ficopsis cooperiana, Laevityphis* (*Laevityphis*) *antiquus, Ranellina pilsbryi, Terebra californica, Glycymeris* (*Glycymeris*) *rosecanyonensis,* and *Glyptoactis* (*Glyptoactis*) *domenginica*; with taxa that have been reported (Givens, 1974; Givens and Kennedy, 1979) elsewhere as having their highest stratigraphic occurrence in the "Domengine Stage," including *Architectonica* (*Stellaxis*) *cognata, Ectinochilus* (*Macilentos*) *macilentus, Pseudoperissolax blakei praeblakei, Velates perversus,* and *Nayadina* (*Exputens*) *llajasensis.*

Based on calcareous nannofossils and mollusks in the Llajas Formation, Saul (1983) reported the "Domengine Stage" to be of late early through early middle Eocene age.

Strata assignable to the middle Eocene "Transition Stage" were not recognized in the Llajas Formation in this present study. The unique association of molluscan species that is utilized in recognizing this "stage" (Givens, 1974; Givens and Kennedy, 1979) was not found in the Llajas Formation.

Workers using benthic foraminifers have reported the age of the Llajas Formation as middle Eocene (Cushman and McMasters, 1936) or early to middle Eocene (Laiming, 1940a, 1940b, 1943; Mallory, 1959; Schymiczek, 1983a, 1983b).

Laiming (1940a, 1940b, 1943) assigned the Llajas Formation to the B-3 (upper part), B-2, B-1, and B-1A "Zones" of his tentative benthic foraminiferal zonation scheme. He correlated these "zones" to the upper "Capay" through "Domengine" molluscan "Stages" of Clark and Vokes (1936).

Mallory (1959) reported that the lower Llajas corresponds to his Penutian Stage (lower Eocene, "Capay") and that the bulk of the formation corresponds to his Ulatisian Stage (middle Eocene, "Domengine to Transition"). An updated version of these benthic foraminiferal stages, now known to be time-transgressive, is given in Poore (1980). Schymiczek (1983a, 1983b) assigned the Llajas Formation to the Ulatisian Stage. Givens and Kennedy (1979) have concluded that the "Domengine Stage" is correlative with the Ulatisian (and probably in part Penutian) Stage.

Using the calcareous nannofossil biostratigraphic zones of Okada and Bukry (1980) and the absolute dates assigned to these zones by Berggren, Kent, and Flynn (in press), Filewicz and Hill (1983) reported that most of the shallow-marine (transgressive) facies of the Llajas Formation is of latest early Eocene or earliest middle Eocene age (*Discoaster lodoensis–D. sublodoensis* Zones, CP11–CP12). The uppermost 30 m or so of this facies (*Discoasteroides kuepperi* Subzone, CP12a) and the outer shelf and slope facies are of middle Eocene age (*Rhabosphaera inflata* Subzone, CP12b–CP13, to *Nannotetrina quadrata* Zone, CP13). *Rhabdosphaera inflata* first occurs 4 m above the "Stewart bed." These results are summarized in Figure 3.

According to Filewicz and Hill (1983), the *R. inflata* Subzone plots within the TE2.1 global, eustatic sea-level cycle of Vail, Mitchum, and Thompson (1977), and the sudden shift to upper bathyal waters just above the "Stewart bed" may be in response to both a steady increase in sea level and tectonism.

CORRELATION

Correlations between California and Oregon/Washington can be easily accomplished with molluscan assemblages of middle and early late Eocene age because these mollusks occupied a single faunal province (Armentrout, 1975).

Twenty-two (or 42 percent) of the species listed by Givens and Kennedy (1979) for the "Domengine Stage" Mount Soledad, Ardath Shale, and Scripps Formations of the La Jolla Group near San Diego, California also occur in the Llajas Formation. All three formations yield *Turritella andersoni lawsoni.* In addition, the Ardath Shale yields *T. uvasana applinae* and has planktic foraminifers correlative with P10/11 Zones and calcareous nannofossils correlative with the CP12 Zone (Givens and Kennedy, 1979).

Most of the megafauna of the late early through middle age Eocene Maniobra Formation, Orocopia Mountains, southeastern California is conspecifie with that of the Llajas Formation. The lower part of the formation has calcareous nannofossils indicative of CP9 through CP11. *Turritella andersoni lawsoni* is present in the upper part of the formation (Crowell and Susuki, 1959; Advocate, 1982).

As mentioned earlier, the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine facies of the Llajas Formation can be correlated to the *Turritella uvasana infera* fauna described by Givens (1974). This fauna is from the lowermost part of the Juncal Formation, Pine Mountain area, California. Fifteen (or 40 percent) of the species restricted to the *Turritella uvasana applinae* fauna described by Givens (1974) from the upper half of the Juncal Formation in the same area occur also in the Llajas Formation above the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine facies. This Juncal Formation fauna corresponds to the upper of the two faunal zones of the "Capay Stage" of Clark and Vokes (1936) through the "Domengine Stage" (Givens, 1974, fig. 6).

Twenty-seven (or 69 percent) of the megafossil species listed by Squires (1977) from the "Domengine-Transition" "Stages" unnamed stratigraphic unit E_2, lower Piru Creek area, Transverse Ranges, California, also occur in the Llajas Formation.

In central California, the megafaunas of both the Avenal Sandstone (Stewart, 1946) and the Domengine Formation (Vokes, 1939) are similar to that of the Llajas.

In southwestern Oregon, the megafaunas in the Umpqua and Tyee Formations, as used by Turner (1938), are similar to that in the Llajas Formation. Turner (1938:32) assigned most of the Umpqua Formation megafauna to the "Capay Stage." He locally subdivided the Umpqua into lower and upper portions, and he considered the upper portion of his Glide section as possibly intermediate between the "Capay" and "Domengine" "Stages." He assigned the Tyee megafauna to the "Domengine Stage."

Turner's "lower Umpqua" now corresponds to the Roseburg Formation, and his "upper Umpqua" includes both the Lookingglass and Flournoy Formations (Baldwin, 1974). The base of the Lookingglass Formation is considered by Baldwin to coincide with the division between Turner's "lower" and "upper Umpqua." Based on a study of planktic foraminifers, Miles (1981) assigned the Roseburg Formation to Zone P7–8 of the "Standard" zonation, the Lookingglass Formation to Zone P7–8, and the Flournoy Formation to Zone P10. He assigned the Tyee Formation to an early middle Eocene age.

Miles (1981), in his study of the southwestern Oregon Eocene strata, placed the "Capay-Domengine" boundary near the P9–10 boundary, but Saul (1983) has pointed out that this molluscan stage boundary actually should lie near the P8–9 boundary. Using Miles' (1981) figures 3 and 7 and Saul's (1983) refinement of the "Capay-Domengine" boundary, the Roseburg and Lookingglass Formations can be shown to be equivalent to the "Capay Stage" and the Flournoy Formation to be equivalent to the "Domengine Stage."

Miles (1981, fig. 7) assigned most of the Llajas Formation to early Eocene time, but such an age assignment does not conform to the findings of this present report or to the findings of Filewicz and Hill (1983), Schymiczek (1983a, 1983b), or Saul (1983).

BIOGEOGRAPHY

The widespread aspect of West Coast warm-water Eocene faunas can be demonstrated by the recognition of some of Clark and Vokes' (1936) Eocene "stages" from southern California (latitude 33°N) to as far north as the Gulf of Alaska (latitude 60°N) (Addicott, 1970). About 30 percent of the Llajas molluscan species, for example, ranged from San Diego into Oregon/Washington. Two other species, *Acila* (*Truncacila*) *decisa* and *Nuculana* (*Saccella*) *gabbii*, ranged from southern California to Kamchatka.

Clark and Vokes (1936) used the presence of *Velates perversus*, which occurs in the lower part of the Llajas, as evidence of a seaway connection in the tropical Central American region between the Atlantic Ocean and the waters of the West Coast of North America. *Velates* is predominantly Tethyan in its distribution and has been found in Western Europe, Africa, Asia, Burma, West Pacific, Jamaica, Florida, Panama, and southern and central California (Vokes, 1935; Clark and Vokes, 1936; Palmer, 1967). It was a shallow-water mollusk indicative of tropical and subtropical climate, as are species of the subgenus *Pacificor* of the bivalve *Venericardia* (Palmer, 1967) which also occur in the Llajas.

The discocyclinid foraminifer *Pseudophragmina* (*Proporocyclina*) *clarki* has been found in Florida, Mexico, and Peru, as well as along the West Coast (Cole and Applin, 1964; Blondeau and Brabb, 1983). The presence of this species in the Llajas Formation is additional evidence of the seaway connection mentioned above.

Clark and Vokes (1936) also cited the presence of *Clavilithes* n. sp. A and *Cryptochorda californica* from the Llajas as further evidence of a Central American seaway connection because these species are closely related, respectively, to *Clavilithes scalaris* and *Cryptochorda stromboides* from the Paris Basin Eocene. Other Llajas megafauna species used as evidence for the seaway are *Clavilithes tabulatus*, *Lyria andersoni*, and *Eocithara mutica californiensis*, which are closely related, respectively, to *Clavilithes parisiensis*, *Lyria maga*, and *Eocithara mutica* of the Paris Basin Eocene (Clark and Vokes, 1936; Vokes, 1937). Some other Llajas species which have been noted as similar to ones from the Paris Basin Eocene are *Callocardia* (*Nitidavenus*) *tejonensis* [=*Isocardia*] which resembles *Cytherea nitida* from France (Vokes, 1939) and *Benoistia umpquaensis* which closely resembles *B. brevicula* from France (Givens and Kennedy, 1976).

Gardner and Bowles (1934) commented upon middle Eocene gastropod species from the Chiapas locality, Isthmus of Tehuantepec, southern Mexico (Atlantic side), that are closely related to ones from the Llajas Formation. These species from Chiapas are *Cernina* (*Eocernina*) *chiapasensis*, *Amaurellina malinchae*, *Amaurellina cortezi*, and *Volutocristata chiapasensis*, which are closely related, respectively, to *Eocernina hannibali*, *Tejonia moragai*, *Pachycrommium clarki*, and *Lyriscapha lajollaensis* from the Llajas. Gardner and Bowles (1934) inferred that the two areas were once connected by a seaway.

Givens (1979), in a detailed study of *Lyrischapa*, concluded that this genus, which is present in the shallow-marine (transgressive) facies of the Llajas, probably evolved in the Carribbean region during Paleocene or early Eocene time. It subsequently spread northward during the middle Eocene or it immigrated from the Old World Tethyan biogeographic province. Entrance into the Pacific Coast region of North America was by way of a narrow seaway connection across southern Central America (Costa Rica, Panama) or northwestern South America (Givens, 1979).

According to Zinsmeister (1983a), the first indication of the influx of large numbers of mollusks from the Gulf Coast and the Caribbean into western North America was in the late Paleocene, and this influx of immigrants continued in the early Eocene. "It is not known whether these immigrants came in distinct pulses associated with major tectonic events in Central America or represent a continuous long-term westward migration of Caribbean taxa into the Pacific as a result of a general climatic warming during the Eocene" (Zinsmeister, 1983a:66).

Most of the megafauna genera of the Llajas Formation were already present on the West Coast by Llajas time. In addition, several species of the Llajas megafauna were carryovers from earlier times. The Llajas taxa *Calyptraea diegoana*, *Pseudoperissolax blakei praeblakei*, *Olivella mathewsonii*, *Scaphander* (*Mirascapha*) *costatus*, *Surculites mathewsonii*, *Acila* (*Truncacila*) *decisa*, *Nemocardium linteum*, and *Nuculana* (*Saccella*) *gabbii* have been reported from late Paleocene "Martinez Stage" strata on the West Coast (Nelson, 1925; Weaver, 1953; Smith, 1975; Zinsmeister, 1974, 1983a). The Llajas taxa *Turbinolia dickersoni*, *Polinices* (*Euspira*) *nuciformis*, and *Schizaster diabloensis* have been reported from late Paleocene strata on the West Coast (Clark and Woodford, 1927; Quayle, 1932; Marincovich, 1977). The Llajas taxa *Neverita* (*Neverita*) *globosa*, *Turritella uvasana infera*, and *Brachidontes* (*Brachidontes*) *cowlitzensis* have been reported from late Paleocene–early Eocene "Meganos Stage" strata on the West Coast (Givens, 1974; Saul, 1983).

Several genera immigrated into the West Coast region during Llajas time. Equatorial paleocirculation of surface waters was still largely unrestricted worldwide during Llajas time and until at least 45 million years ago (middle Eocene), even though the Tethyan Seaway was closing up due to compressive tectonic forces (Kennett, 1982). As mentioned earlier, migration from points east of the West Coast was accomplished by means of a narrow seaway across southern Central America or northwestern South America (Woodring, 1966; Givens, 1977, 1979; Zinsmeister, 1983a). Molluscan genera/subgenera present in the Llajas Formation and coeval strata but not in older Tertiary strata of the West Coast will be discussed below. Unless otherwise noted, biogeographic data for these genera were obtained from Wenz (1938–1944), Palmer and Brann (1965–1966), Cox et al. (1969), Palmer (1974), Marincovich (1977), and Moore (1983), as well as from the "Systematics" portion of this present report.

Architectonica (*Stellaxis*), *Paraseraphs*, and *Strepsidura* possibly arrived during the early Eocene (uppermost "Capay" part), most likely from the Caribbean province. *Domenginella* apparently originated on the West Coast at this time, possibly as a northern variant of *Scobinella*, as suggested by Vokes (1939).

Benoistia and *Megistostoma* arrived during the late early–early middle Eocene ("Domengine") on the West Coast from the Tethyan province. *Eocithara* (see Rehder, 1973), *Natica* (*Naticarius*), *Ranella* (see Squires, 1983a), and possibly *Conus*, *Phalium* (*Semicassis*), and *Marcia* (*Mercimonia*) arrived during this time, most likely from the Caribbean region. *Lyriscapha* (see Givens, 1979) may have arrived from either the Caribbean or Tethyan regions. *Cymatium* (*Septa*) (see Squires, 1983a), *Galeodea* (*Caliagaleodea*), *Olequahia, Tejonia, Glyptoactis* (*Glyptoactis*), and possibly *Proximitra*? originated on the West Coast at this time. *Ancistrolepis*? probably arrived during the early middle Eocene from the Pacific Northwest.

In summary, the influx of mollusks into western North America that Zinsmeister (1983a) commented on continued, at least, into the early middle Eocene. As noted by Smith (1975), the megafauna of the Llajas Formation is of mixed origins, having cosmopolitan, Tethyan, Caribbean, and North American elements.

SYSTEMATIC MATERIALS AND METHODS

From 1978 to 1983, an intensive and meticulous search of the Llajas Formation was undertaken by the author in order to amass megafossil specimens that would represent the composition and the stratigraphic distribution of the fauna more accurately than the cursory collections on which previous workers based their reports. About 5000 specimens were obtained from 132 localities, permitting the addition to the known fauna of many rare species that otherwise would not have been found. Numerous return visits were made to several of the richest localities. Several hundred man-hours were spent quarrying CSUN locality 374 ("Stewart bed") and CSUN locality 371. Because specimens with preservation superior to those previously figured were obtained and because many of the holotypes of species erected for Llajas Formation specimens are from localities that are either unknown or only vaguely known, most of the holotypes are not refigured.

Systematic arrangement of the generic and higher taxonomic categories follows that of Cole (1964) for the large foraminifer; Wells (1956) for the scleractinians; Muir-Wood, Elliott, and Hatari (1965) for the brachiopod; Howell (1962) for the annelid tube; Ludbrook (1960) for the scaphopod; Cox et al. (1969) and Vokes (1980) for the bivalves; Miller (1947) for the nautiloid; Jeletzky (1966) for the sepiid; Glaessner (1969) for the brachyuran; Fischer (1966) for the echinoid; and Compagno (1973) for the sharks. The systematic arrangement of Wenz (1938–1944) is followed generally for the gastropods.

Most of the figured specimens are on deposit in the Natural History Museum of Los Angeles County, Invertebrate Paleontology section. Figured specimens borrowed from the paleontology collections of the University of California, Los Angeles, Department of Earth and Space Sciences are on deposit there. Additional unfigured specimens are on deposit in the Department of Geological Sciences Paleontology collection, California State University, Northridge.

The synonymies are selective. Works that include original figures and/or descriptions are listed. References that add pertinent and documentable biostratigraphic information are also included. More complete synonymies of many of the gastropods and bivalves can be found in Stewart (1927, 1930).

Primary type material, molluscan stage range, geographic distribution, local occurrence, and remarks are listed for all the species. Unless otherwise noted, such data are derived from references listed in the synonymies or from new data obtained in the course of this present study. "Primary type material" refers to the holotype, paratype(s), syntypes, lectotype, paralectotype(s), or neotype of the senior subjective synonym of each taxon. In the case of homonyms, the junior homonym "primary type material" is listed, and if the new name "primary type material" is different it is listed also. The molluscan stages are for the West Coast, and they are from Clark and Vokes (1936) and Weaver et al. (1944), with refinements made by Givens (1974) and Saul (1983). The stages are provisional, hence the names are placed in quotation marks. The relative age of each stage and correlation with various biostratigraphic zones are shown in Figure 4. Any taxa stage range extensions that are the result of this present study of the Llajas material are so mentioned under the "Remarks" for each species. Locality information for all the localities mentioned in this report is given in the "Localities" section.

Letter abbreviations used for catalog and/or locality numbers are:

ANSP = Academy of Natural Sciences of Philadelphia
CAS = California Academy of Sciences
CIT = California Institute of Technology
CSUN = California State University, Northridge
MCZ = Museum of Comparative Zoology, Harvard
HS = Herman Schymiczek (CSUN master's thesis field station)
LACMIP = Los Angels County Museum, Invertebrate Paleontology Section
SU = Stanford University (collections now housed at the California Academy of Sciences)
UCMP = University of California Museum of Paleontology (Berkeley)
UCLA = University of California, Los Angeles
UCR = University of California, Riverside
UO = University of Oregon
USGS = United States Geological Survey (Washington, D.C. register)
USNM = United States National Museum of Natural History
UW = University of Washington

SYSTEMATICS

Phylum Protista

Subphylum Sarcodina

Class Rhizopodea

Subclass Granuloreticulosia

Order Foraminiferida

Suborder Rotaliina

Superfamily Orbitoidacea

Family Discocyclinidae Galloway, 1928

Genus *Pseudophragmina* Douvillé, 1923

Type Species. By original designation, *Orthophragmina floridana* Cushman, 1917.

Pseudophragmina (*Proporocyclina*) *clarki* (Cushman, 1920)

Figures 5a–b

Orbitolites sp. A Arnold, 1910:pl. 3, fig. 6.
Orthophragmina clarki Cushman, 1920:41–42, pl. 7, figs. 4–5.
Discocyclina clarki (Cushman). Schenck, 1929:221, figs. 1–2, 5, text fig. 7. Keenan, 1932:pl. 4, figs. 1–2. Vaughan, 1936:255–256, pl. 43, figs. 1–2. Berthiaume, 1938:496, pl. 61, fig. 12. Turner, 1938:7, 12, 21. Stewart, 1946:table 1. Shepard, Lankford, and Milow, 1957:columnar section.
Discocyclina cloptoni Vaughan. Cushman and McMasters, 1936:516, pl. 77, figs. 6–9. [Misidentification *fide* Schymiczek, 1983b:50.] Vaughan, 1945:98–99, pl. 42, fig. 2.
Pseudophragmina (*Proporocyclina*) *clarki* (Cushman). Vaughan, 1945:104, 106. Cole, 1958:419–420, pl. 52, figs. 3–11. Crowell and Susuki, 1959:589. Mallory, 1959:259. Cole and Applin, 1964:47, pl. 9, figs. 1–4. Blondeau and Brabb, 1983:47, pl. 6, fig. 17, and table 5.
Pseudophragmina clarki (Cushman). Schymiczek and Squires, 1981:989. Squires, 1983b:fig. 9i.

Primary Type Material. Holotype and paratype, USNM collections, upper Lodo Formation, northeast side of Domengine Creek near the corner of the SW ¼ of section 29, T 18 S, R 15 E, Domengine Ranch quadrangle, California.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Florida, Mexico, Peru through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 457, 469l, 470b, 472, 473, 477, 479, 487, 491, 504, 511, 522, 527a, 527b, 548.

Remarks. Specimens are essentially confined to the shallow-marine (transgressive) facies. Most occur in several 50-cm-thick beds approximately 100 m above the base of the formation (e.g., localities 457, 469l, 487, 511, 527b). In such beds, the tests are concentrated in small pods. *Turritella andersoni lawsoni* may or may not occur with the tests, but if present it is usually the only associated megafossil or the most abundant megafossil. The tests of *P.* (*P.*) *clarki* are mostly complete, unabraded, and 1.5 to 7 mm in diameter.

The stratigraphic highest occurrence of the specimens in the Llajas Formation is at locality 473, about 14 m above the "Stewart bed" at the type section. The bed that locality 473 occurs in probably represents a shallow-marine (transgressive) facies bed that interfingers with the outer shelf and slope facies.

Phylum Coelenterata

Subphylum Cnidaria

Class Anthozoa

Subclass Zoantharia

Order Scleractinia

Suborder Caryophylliina

Superfamily Caryophylliicae

Family Caryophylliidae Gray, 1847

Subfamily Caryophylliinae Gray, 1847

Genus *Trochocyathus* Milne-Edwards and Haime, 1848

Type Species. By subsequent designation (Milne-Edwards and Haime, 1850b), *Turbinolia mitrata* Goldfuss, 1827.

?*Trochocyathus striatus* (Gabb, 1864)

Figure 5c

Trochosmilia striata Gabb, 1864:207–208, pl. 26, fig. 195.
Trochocyathus striatus (Gabb). Vaughan, 1900:101–102, pl. 7, fig. 24; pl. 8, figs. 1–3. Dickerson, 1913:265. Hanna, 1927:269.

Primary Type Material. UCMP holotype 12256, Division B, near Mt. Diablo, California.

Molluscan Stage Range. "Capay"?; Domengine.

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 438, 444, 445, 447, 451, 458, 459, 471c, 472, 473, 477, 479, 480, 493, 494, 495, 496, 500, 510, 525.

Remarks. ?*Trochocyathus striatus* occurs primarily in the "Stewart bed." At a few localities (e.g., locality 374) there is a partial growth series, with the early juveniles missing. Most specimens in the Llajas Formation are complete, unattached, and unabraded.

Specimens at locality 473 occur in a bed that probably represents a shallow-marine facies bed that interfingers with the outer shelf and slope facies.

The genus and species of the most abundant coral in the Llajas Formation are questioned because of a lack of modern comparative taxonomic work on middle Eocene solitary scleractinian ahermatypic corals. The type of this taxon is largely imbedded in matrix and probably cannot be well enough prepared to make a valid comparison (Durham, 1981, pers. commun.).

Dickerson (1913) reported *T. striatus* from "Capay"-age strata in central California, but he gave no specific locality information nor did he figure the species. For these reasons, the "Capay" age occurrence is uncertain.

Subfamily Turbinoliinae Milne-Edwards and Haime, 1848

Genus *Turbinolia* Lamarck, 1816

Type Species. By subsequent designation (Milne-Edwards and Haime, 1850b), *Turbinolia sulcata* Lamarck, 1816.

Turbinolia dickersoni Nomland, 1916

Figures 5d–e

Turbinolia dickersoni Nomland, 1916:61, pl. 3, figs. 5–8. Palmer, 1923:306, pl. 56, figs. 2, 4. Quayle, 1932:98–99, pl. 6, figs. 1–5.

Primary Type Material. UCMP holotype 12020 (missing since 1932), Cerros Shale Member of the Lodo Formation, UCMP locality 1817.

Molluscan Stage Range. Upper Paleocene through "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 467.

Remarks. Only four specimens were found in the Llajas Formation. This small coral is distinguished from the much larger ?*Trochocyathus striatus* by the presence of a stellate columella. This columella does not project noticeably above the corallum wall.

The type locality of this species is in the lower part of the Cerros Shale Member (late Paleocene age) or the Lodo Formation (Marincovich, 1977:252; Moore, 1983:A88).

Clark (1926:114) reported this species from "Domengine"-age strata in central California, but such a report is uncertain because of his lack of locality data. The presence of this species at CSUN locality 467 does extend, with certainty, its molluscan stage range into the "Domengine Stage."

Phylum Brachiopoda

Class Articulata

Order Terebratulida

Suborder, Superfamily, and Family UNKNOWN

Genus *Eogryphus* Hertlein and Grant, 1944

Type Species. By original designation, *Eogryphus tolmani* Hertlein and Grant, 1944.

Eogryphus tolmani Hertlein and Grant, 1944

Figure 5f

Eogryphus tolmani Hertlein and Grant, 1944:89–90, pl. 5, figs. 1–3, 7; pl. 18, figs. 1, 9–11; text figure 22.

Primary Type Material. UCLA holotype 6203, CAS paratypes 7279–7282; all from upper Llajas Formation, upper Las Llajas Canyon, 3000 feet north and 1500 feet east of the southwest corner of section 23, T 3 N, R 17 W (Hertlein and Grant, 1944:89).

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 438, 468a, 515, 525.

Remarks. Many specimens were found at and near the vicinity of locality 438. Many of the specimens are articulated. Plotted on the topographic map available in 1944, the locality of the type specimens probably plots about 1500 feet (457 m) east of CSUN locality 515 in an area in which slope wash has covered the exposures. The southwest corner of section 23 was unmarked and had to be projected. The locality of the type specimens, however, is in the general vicinity of all the CSUN localities in which specimens of *Eogryphus tolmani* were found.

Smith (1975:470) reported *Eogryphus* cf. *E. tolmani* from the "Martinez Stage" (Paleocene) part of the Lodo Formation, central California.

Phylum Annelida

Class Polychaetia

Order Sedentaria

Family Serpulidae Lamarck, 1818

Genus *Rotularia* Defrance, 1827

Type Species. By original designation, *Serpula spirulaea* Lamarck, 1818.

Rotularia tejonense (Arnold, 1910)

Figure 5g

Spiroglyphus? *tejonensis* Arnold, 1910:51, pl. 4, fig. 18. Dickerson, 1916:pl. 37, figs. 5a–b. Vokes, 1939:162–163, pl. 20, figs. 20–22. Stewart, 1946:pl. 11, fig. 21.

?*Tubulostium tejonense* (Arnold). Keen and Bentson, 1944: 195.

Rotularia tejonense (Arnold). Nilsen, 1973:table 1. Squires, 1977:table 1.

Primary Type Material. USNM holotype 165658, Avenal Formation, USGS locality 4617.

Molluscan Stage Range. "Capay" through "Transition."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 703. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 445, 494, 521, 546.

Remarks. Most specimens were found in the "Stewart bed" encrusting other shells, most notably *Ostrea*.

According to Clark (1921:table 1), *R. tejonense* [=*Spiroglyphus* (?) *tejonensis*] occurs in "Meganos" age strata. Such a report, however, cannot be substantiated at this time because of his lack of locality information and because his rock unit names are not clearly defined.

Phylum Mollusca

Class Scaphopoda

Family Dentaliidae Gray, 1834

Genus *Dentalium* Linné, 1758

Type Species. By subsequent designation (Montfort, 1810), *Dentalium elephantinum* Linné, 1758.

Dentalium stentor Anderson and Hanna, 1925

Figure 5h

Dentalium stentor Anderson and Hanna, 1925:145, pl. 13, fig. 17.

Dentalium stentor? Anderson and Hanna. Squires, 1977:table 1.

Primary Type Material. CAS holotype 819, Tejon Formation, CAS locality 792.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. Simi Valley through southern San Joaquin Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 374, 444, 445, 447, 449, 451, 493, 494, 500, 510.

Remarks. Abundant large, thick-shelled specimens were found locally in the "Stewart bed" (locality 374 and vicinity). Although some specimens are nearly complete (up to 75 mm in height), no apices were found. Due to the absence of apices, the specimens could not be assigned with certainty to any subgenus of *Dentalium.*

Subgenus *Laevidentalium* Cossman, 1888

Type Species. By original designation, *Dentalium incertum* Deshayes, 1825.

Dentalium (*Laevidentalium*) *calafium* Vokes, 1939

Figure 5i

Dentalium (*Laevidentalium*) *calafium* Vokes, 1939:105, pl. 16, figs. 30–31. Squires, 1983b:fig. 9h.

Primary Type Material. UCMP lectotype 15750, Domengine Formation, UCMP locality A-1027; UCMP paralectotype 15751, Domengine Formation?, UCMP locality A-1003.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 455, 466, 467, 484, 491, 499, 500, 507, 508, 510, 529b, 538, 539, 548.

Remarks. Specimens occur in channel-fill deposits in the Llajas Formation. They are small, smooth, and fragmented specimens. The presence of the apical notch on the convex side of the shell serves to distinguish this taxon.

Vokes (1939) designated two syntypes (UCMP 15750 and 15751) but no holotype for his species. In accordance with the International Code of Zoological Nomenclature (1964) article 74, therefore, UCMP 15750 is herein designated as the holotype of *D.* (*L.*) *calafium.*

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Superfamily Neritacea

Family Neritidae Rafinesque, 1815

Subfamily Neritinae Rafinesque, 1815

Genus *Nerita* Linné, 1758

Type Species. By subsequent designation (Montfort, 1810), *Nerita peloronta* Linné, 1758.

Nerita cf. *N.* (*Amphinerita*) *eorex* Vokes, 1939

Figure 6a

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 700, 701.

Remarks. Specimens were found only in the "Capay Stage" portion of the Llajas Formation. A total of 22 specimens was found, and all but two specimens were from locality 700. Due to the presence of well-cemented matrix in the aperture area of each specimen, the labial areas could not be studied. The small specimens have a very low spire, large body whorl, and a smooth shell surface. Apparently, there is no umbilicus, and the outer lip is not dentate.

The specimens most closely resemble *N.* (*A.*) *eorex* Vokes (1939:180–181, pl. 22, figs. 24, 26, 29) from the Domengine Formation, Reef Ridge area, California. Vokes (1939) regarded this species as the only smooth-shelled *Nerita* from the West American Eocene.

Genus *Velates* de Montfort, 1810

Type Species. By original designation, *Velates conoideus* Montfort, 1810 [=*Nerita perversa* Gmelin, 1791].

Velates perversus (Gmelin, 1791)

Figures 6b–c

Nerita perversa Gmelin, 1791:vol. 1, pt. 6, p. 3686.

Velates conoideus Montfort, 1810:355.

Velates perversus (Gmelin). Vokes, 1935:382–383, pl. 25, figs. 1–5; pl. 26, figs. 1–2. Clark and Vokes, 1936:875, pl. 1, figs. 7–8. Givens, 1974:61, pl. 5, figs. 5–6, 13. Givens and Kennedy, 1979:83.

Primary Type Material. No holotype was designated by Gmelin (1791). Gmelin did not have a collection but worked mainly from the literature, according to Smith (1970:459). Gmelin (1791) lists the Chemnitz Cabinet as the source of his *Nerita perversa,* and if the Cabinet is still extant, the lectotype could be designated.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Western Europe, Africa, Asia, Burma, West Pacific, Jamaica, southern and central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 700, 701, 702.

Remarks. Specimens were found only in the "Capay Stage" portion of the Llajas Formation. Except at locality 701, only fragments were found. A very large specimen (diameter 70

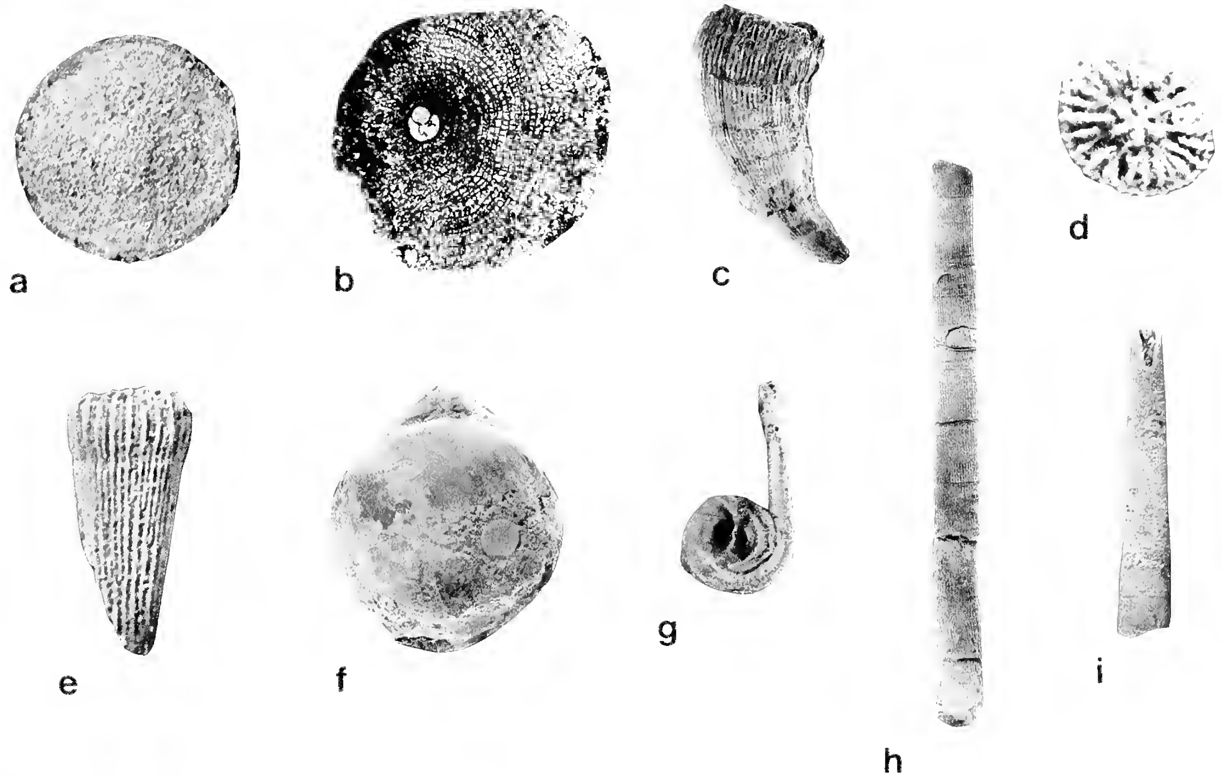

Figure 5. Llajas Formation large benthic foraminifer, solitary corals, brachiopod, calcareous worm tube, and scaphopods. **a and b.** *Pseudophragmina* (*Proporocyclina*) *clarki* (Cushman, 1920). **a**, test exterior, LACMIP hypotype 6500, CSUN loc. 511, ×8. **b**, equatorial section, LACMIP hypotype 6501, HS loc. HS-A-11(4), ×25. **c.** ?*Trochocyathus striatus* (Gabb, 1864), lateral view, LACMIP hypotype 6502, CSUN loc. 374, ×1. **d and e.** *Turbinolia dickersoni* Nomland, 1916, LACMIP hypotype 6503, CSUN loc. 467. **d**, dorsal view, ×7. **e**, lateral view, ×5. **f.** *Eogryphus tolmani* Hertlein and Grant, 1944, dorsal view, LACMIP hypotype 6504, CSUN loc. 438, ×0.75. **g.** *Rotularia tejonense* (Arnold, 1910), LACMIP hypotype 6505, CSUN loc. 444, ×1.5. **h.** *Dentalium stentor* Anderson and Hanna, 1925, partial specimen, side view, LACMIP hypotype 6506, CSUN loc. 444, ×1. **i.** *Dentalium* (*Laevidentalium*) *calafium* Vokes, 1939, partial specimen, apical notch view, LACMIP hypotype 6507, CSUN loc. 373, ×4.5.

cm) was found at locality 701. The best specimens from the Llajas are in the UCMP collection and are from a locality equivalent to CSUN locality 702 (i.e., UCMP locality 7193). UCMP specimen 37435 (Figs. 6b–c) is from this locality. Vokes (1935) figured two hypotypes from this same locality.

The most characteristic feature of this species is the presence of seven or eight small teeth on the inner lip.

Order Mesogastropoda

Superfamily Cerithiacea

Family Turritellidae Woodward, 1851

Genus *Turritella* Lamarck, 1799

Type Species. By monotypy, *Turbo terebra* Linné, 1758.

Turritella meganosensis protumescens Merriam and Turner, 1937

Figure 6d

Turritella meganosensis n. subsp. Clark, 1929:pl. 10, figs. 1–2.

Turritella meganosensis protumescens Merriam and Turner, 1937:104, pl. 6, figs. 8–10. Turner, 1938:85, pl. 22, fig. 15. Merriam, 1941:75–76, pl. 8, figs. 1–2, 5, 6, 8. Weaver, 1943:369–370, pl. 74, figs. 14, 18. Saul, 1983:pl. 2, fig. 1.

Primary Type Material. UCMP holotype 15353, "basal conglomerate" of the Llajas Formation, UCMP locality 7195.

Molluscan Stage Range. "Capay."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 452, 454, 469a, 469b, 469c, 501, 542, 545.

Remarks. According to Merriam and Turner (1937:104), this taxon occurs in the basal conglomerate of the Llajas Formation. This is misleading, as specimens do not occur in the basal conglomerate proper (equivalent to the coastal alluvial-fan facies). They actually are confined to beds that represent shallow-marine facies interfingering with the coastal alluvial-fan facies. At a few of the localities, the thick-shelled, robust *T. meganosensis protumescens* exhibits growth series.

Turritella andersoni Dickerson, 1916

Figure 6e

Turritella andersoni Dickerson, 1916:501–502, pl. 42, figs. 9a–b. Turner, 1938:83, pl. 22, figs. 4–6. Merriam, 1941: 76–77, pl. 9, figs. 1–2; pl. 10, figs. 1, 3–5, 8; pl. 12, figs. 1–3. Givens, 1974:62, pl. 5, figs. 7–10.

Turritella andersoni susanae Merriam, 1941:79, pl. 11, fig. 6. Saul, 1983:pl. 2, fig. 5.

Primary Type Material. UCMP holotype 12131, Domengine Formation, UCMP locality 1817.

Molluscan Stage Range. Upper "Meganos"?, "Capay."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Upper part of Santa Susana Formation?; interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies of the Llajas Formation: CSUN localities 469d, 700.

Remarks. Only a single specimen was found at locality 469d. This specimen (Fig. 6e) consists of only 2½ whorls, but the characteristic noded three primary spiral ribs, the median one situated closer to the anterior than the posterior primary, are present.

Although the holotype (UCMP 15295, UCMP locality A-993) of *T. a. susanae* is from strata equivalent to the interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies, specimens have been reported by Merriam (1941) from the upper part of the underlying Santa Susana Formation. Saul (1983) identified these specimens with *T. andersoni* n. sp. because none has the sculpture of the Llajas specimens. Saul (1983), however, did note that some of the Santa Susana specimens are very close to *T. andersoni* Dickerson, especially from localities near the Llajas–Santa Susana contact.

Turritella andersoni lawsoni Dickerson, 1916

Figures 6f–g

Turritella lawsoni Dickerson, 1916:502, pl. 42, figs. 10a–b. Hanna, 1927:308, pl. 49, fig. 5. Hanna and Hertlein, 1943: fig. 62-15. Stewart, 1946:pl. 11, figs. 27–29.

Turritella andersoni Dickerson, Waring, 1917:pl. 15, fig. 18.

Turritella andersoni lawsoni Dickerson. Vokes, 1939:161. Merriam, 1941:77–78, pl. 9, figs. 3–8; pl. 12, fig. 4. Crowell and Susuki, 1959:pl. 2, fig. 12. Givens, 1974:62–63, pl. 5, figs. 11–12, 14. Givens and Kennedy, 1979:82–83, table 1. Saul, 1983:pl. 2, figs. 10–11. Squires, 1983b:fig. 9e.

Turritella andersoni lawsoni secondaria Merriam, 1941:78–79, pl. 9, fig. 9. Crowell and Susuki, 1959:pl. 2, fig. 11.

Turritella andersoni lawsoni forma *secondaria* Merriam. Saul, 1983:pl. 2, fig. 12.

Primary Type Material. UCMP holotype 12128, Domengine Formation, UCMP locality 2295.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 439, 440, 441, 442, 443, 444, 445, 447, 449, 453, 455, 457, 468b, 469j, 470c, 471a, 471b, 471e, 481, 485, 487, 490, 493, 494, 510, 516, 522, 523, 527a, 529a, 529b, 537, 539, 548, 704.

Remarks. *Turritella andersoni lawsoni* is one of the most abundant megafaunal components in the Llajas Formation. At many localities (e.g., 442 and 471a), it is the only megafossil present. *T. andersoni lawsoni* is restricted in the Llajas Formation to the shallow-marine (transgressive) facies. Its highest stratigraphic occurrence is the "Stewart bed," where it is abundant. Some specimens show faint spiral ribs, whereas others do not. Some specimens, especially at locality 374, have the spiral ribs on one side but not on the other (weathered) side.

Some specimens of *T. a. lawsoni* from localities 374 and 548 are characterized by the presence of a well-developed anterior primary rib and represent the form described by Merriam (1941:78–79, pl. 9, fig. 9) as variety *secondaria.* These Llajas specimens of *T. a. lawsoni* which show the well-developed anterior primary rib are probably just ecotypes.

The primary type material of *secondaria* is UCMP 33998 from UCMP locality 7004 = CSUN locality 374.

Turritella buwaldana Dickerson, 1916

Figure 6h

Turritella buwaldana Dickerson, 1916:500–501, pl. 42, figs. 7a–b. Hanna, 1927:307, pl. 49, figs. 7–8, 12. Merriam, 1941:86–87, pl. 21, figs. 3–9; pl. 22, figs. 1–14. Stewart, 1946:pl. 11, fig. 24. Givens, 1974:63, pl. 5, fig. 15. Saul, 1983:pl. 2, figs. 13–15. Squires, 1983b:fig. 9f.

Turritella kewi Dickerson, 1916:501, pl. 42, fig. 8.

Primary Type Material. UCMP holotype 12130, Domengine Formation, UCMP locality 672.

Molluscan Stage Range. Upper "Meganos"?, "Capay"?, "Domengine" through "Tejon."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Upper part of the Santa Susana Formation?; shallow-marine (transgressive) facies of the Llajas Formation: CSUN localities 371, 372, 373, 455, 467, 469e, 469h, 469j, 484, 486, 499, 500, 505, 514, 538, 539, 540, 548, 705.

Remarks. *T. buwaldana* in the Llajas Formation is characterized by its small size and presence of three primary spiral ribs and two posterior secondaries.

T. buwaldana has been reported from the upper part of the Santa Susana Formation by Merriam (1941), but he noted that these forms are probably subspecifically distinct from those in the Llajas Formation.

Saul (1983) reported *T. b. crooki* Merriam and Turner from the "Capay" portion of the Llajas Formation. Although none was found in the present study, it is possible that *T. b. crooki* and *T. buwaldana* are the same. More taxonomic data are needed to resolve the question (Saul, 1983, pers. commun.).

Turritella uvasana infera Merriam, 1941

Figure 6i

Turritella uvasana infera Merriam, 1941:90, pl. 40, figs. 2–4. Givens, 1974:65–66, pl. 6, figs. 5–7. Saul, 1983:pl. 2, fig. 4.

Primary Type Material. UCMP holotype 33993, "basal conglomerate" of the Llajas Formation, UCMP locality A-994 = CSUN locality 452; UCMP paratypes 15439 and 15443, upper part of the Santa Susana Formation, UCMP locality 7000.

Molluscan Stage Range. Upper "Meganos" through "Capay."

Geographic Distribution. Simi Valley and Pine Mountain area, southern California.

Local Occurrence. Upper part of the Santa Susana Formation; interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies of the Llajas Formation: CSUN localities 452, 705.

Remarks. According to Merriam (1941:90), this taxon occurs in the basal conglomerate of the Llajas Formation. This is misleading, as specimens do not occur in the basal conglomerate proper (equivalent to the coastal alluvial-fan facies). They actually are confined to beds that represent shallow-marine facies interfingering with the coastal alluvial-fan facies.

T. u. infera has been reported from the upper part of the Santa Susana Formation, but the specimens are slightly different variants that have more rounded whorl profiles and heavier ribbing than those from the type locality in the Llajas Formation (Merriam, 1941; Saul, 1983).

Adult whorls of the Llajas specimens have six to seven primary spiral ribs with the posteriormost two more closely spaced and somewhat weaker than the other spiral ribs. Secondary ribs are generally absent.

The illustrated specimen (Fig. 6i) is the same one used by Saul (1983:pl. 2, fig. 4).

Turritella uvasana applinae Hanna, 1927

Figure 6j

Turritella applini Hanna, 1927:307, pl. 49, figs. 1, 4. Clark, 1929:pl. 10, figs. 8, 18.
Turritella uvasana applini Hanna. Merriam, 1941:93–94, pl. 16, figs. 5–6; pl. 18, fig. 2.
Turritella uvasana etheringtoni Merriam, 1941:94, pl. 15, figs. 12–15. Squires, 1977:table 1.
Turritella uvasana applinae Hanna. Givens, 1974:66, pl. 6, figs. 3–4; pl. 7, fig. 19. Givens and Kennedy, 1979:82–83, table 1. Saul, 1983:pl. 2, fig. 18. Squires, 1983b:fig. 9g.

Primary Type Material. UCMP holotype 30971, La Jolla Formation, UCMP locality 3993; UCMP paratype 33894, La Jolla Formation, UCMP locality 3990.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Pine Mountain area, southern California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 440, 444, 449, 469e, 469i, 471d, 471e, 481, 484, 486, 491, 500, 507, 529a, 539, 548, 704. Outer shelf and slope facies: CSUN locality 483. Shallow-marine (regressive) facies: CSUN localities 475, 489, 512b, 512d.

Remarks. Llajas specimens of *T. u. infera* superficially resemble *T. u. applinae,* but the latter has a more convex whorl profile, many more primary spiral ribs, and the presence of numerous well-developed secondary ribs.

The primary type material for *T. u. etheringtoni* is from the Llajas Formation: UCMP holotype 33875, UCMP locality 7003; UCMP paratypes 33876 and 33877, UCMP locality 7004 = CSUN locality 374. Specimens of *T. u. applinae* are especially abundant at locality 374.

Family Architectonicidae Gray, 1850

Genus *Architectonica* Röding, 1798

Type Species. By subsequent designation (Gray, 1847), *Trochus perspectivus* Linné, 1758.

Subgenus *Architectonica* s.s.

Architectonica (*Architectonica*) *llajasensis* Sutherland, 1966

Figure 6k

Architectonica llajasensis Sutherland, 1966:1–4, figs. 1–2.

Primary Type Material. LACMIP holotype 1140, Llajas Formation, LACMIP locality 461-B.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only three specimens were found, and these are from the locality in Devil Canyon. Judging from the megafauna associated with Sutherland's (1966) holotype specimen, the type locality of *A. llajasensis* is probably near CSUN locality 444 in the "Stewart bed."

This species is placed in *Architectonica* s.s. because the umbilicus is bordered by two serrated ridges (see Sutherland, 1966), a characteristic of typical *Architectonica* (Stewart, 1927: 343).

Subgenus *Stellaxis* Dall, 1892

Type Species. By original designation, *Solarium alveatum* Conrad, 1833.

Architectonica (*Stellaxis*) *cognata* Gabb, 1864

Figure 6l

Architectonica cognata Gabb, 1864:117, pl. 20, figs. 72, 72a, 72c, not d and e as stated [not 72b = *A. alveata* (Conrad) *fide* Stewart, 1927:344].
Stellaxis cognata (Conrad). Waring, 1917:98.
Architectonica cognata Gabb. Givens and Kennedy, 1979: 83, table 1.

Architectonica (*Stellaxis*) *cognata* Gabb. Stewart, 1927:343–344, pl. 28, figs. 7–8. Turner, 1938:90, pl. 18, fig. 17. Vokes, 1939:163–164. Stewart, 1946:pl. 11, fig. 4. Weaver, 1943: 363–364, pl. 73, fig. 20; pl. 103, fig. 19. Givens, 1974:68, pl. 7, figs. 1–3.

Primary Type Material. ANSP lectotype 4223, Tejon Formation s.l., 11 km south of Martinez, California.

Molluscan Stage Range. Uppermost "Capay" through "Domengine."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 452, 702, 703. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 444, 447, 455, 486, 490, 491, 538, 704.

Remarks. This species is characterized mostly by a single keel on the periphery of the whorls (Givens, 1974:68). The Llajas specimens have this prominent keel, as well as a less prominent sutural cord, thereby producing an apparent double-keel look. The sutural cord is exposed due to the removal of the shell material in the suture region.

A previously assigned "Capay" age (Turner, 1938; Givens, 1974) for the lower range limit of this species was based on occurrence in the "upper Umpqua" Formation of southwestern Oregon. The "upper Umpqua," however, is actually equivalent to both the "Capay" and "Domengine" "Stages" (Baldwin, 1974; Miles, 1981). A lower range limit of uppermost "Capay," nevertheless, can be substantiated by the occurrence of this species in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation.

Family Cerithiidae Fleming, 1828

Subfamily Cerithiinae Fleming, 1828

Genus *Benoistia* Cossmann, 1899

Type Species. By original designation, *Cerithium muricoides*.

Benoistia umpquaensis Turner, 1938

Figure 6m

Benoistia umpquaensis Turner, 1938:82, pl. 21, figs. 8, 10. Weaver, 1943:387, pl. 76, figs. 11–12.

Tectarius ligniticus Vokes, 1939:164–165, pl. 21, figs. 1, 3, 4.

Benoistea umpquaensis Turner. Givens and Kennedy, 1976: 964–965, pl. 1, figs. 14–21.

Primary Type Material. UCMP holotype 33192, "upper Umpqua" Formation, UCMP locality A-661.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only a single specimen was found, and it is from the "Stewart bed." See Givens and Kennedy (1976) for a detailed morphologic description of this species.

The holotype of *Tectarius ligniticus* is UCMP 15838, Llajas Formation, UCMP locality 7005.

Family Cerithiopsidae H. and A. Adams, 1854

Genus *Cerithiopsis* Forbes and Hanley, 1853

Type Species. By monotypy, *Murex tubercularis* Montagu, 1803.

Cerithiopsis llajasensis n. sp.

Figures 6n–o

Diagnosis. A species of *Cerithiopsis* characterized by teleoconch sculpture of four to five primary spiral ribs crossed by equal-strength collabral costae, with nodes at the intersections. The varices are irregularly spaced.

Cerithiopsis llajasensis n. sp. is similar to *C. orovillensis* Dickerson (1916:489–490, pl. 39, fig. 7) from Eocene strata in northern California. *C. llajasensis* differs from the holotype of *C. orovillensis* in the following features: larger, a more elongate-slender shape, equal strength spiral and collabral sculpture, four to five rather than only four primary spiral ribs on the teleoconch whorls, equal-strength primary spiral ribs, less nodose sculpture, more varices, and an absence of two strong spiral keels above the base of the body whorl.

Cerithiopsis llajasensis n. sp. is similar also to *C. excelsus* Dall (1909:75, pl. 3, fig. 9) from Eocene strata in southwestern Oregon. Givens (1974) regarded *C. excelsus* as *C. excelsum* (Dall). *C. llajasensis* differs from the holotype of *C. excelsum* in the following features: suture more adpressed, absence of a shoulder on the whorls, equally spaced collabral sculpture, fewer primary spiral ribs, equal-strength primary spiral ribs, many more varices, and more swollen varices. The cancellate sculpture of *C. llajasensis* is equal in strength over the shell whereas in *C. excelsum* this is not the case. *C. excelsum* has two prominent spiral ribs and unequally spaced collabral sculpture, thereby producing an uneven cancellate sculpture.

Description. Shell small, turriform and elongate, with many convex whorls. Suture moderately impressed, undulating. Protoconch mammillated, about 3½ whorls, smooth. Teleoconch sculpture cancellate, nodes at intersections of primary spiral ribs and collabral costae. Spiral and collabral sculpture equal strength. Four to five primary spiral ribs per whorl; seven on body whorl proper, five more on base of body whorl. Ribs equally spaced, usually separated by a secondary riblet. No secondary riblets on base of body whorl. Fourteen to 16 collabral costae per whorl. Costae equally spaced, extending from suture to suture. No collabral ornament on base of body whorl. Swollen varices irregularly spaced, usually two per whorl.

Columella smooth, covered by a thin callus. Aperture ovate. Anterior canal short, shallowly notched, bent backwards. Dimensions of largest specimen, height (incomplete) 22.5 mm, body whorl width 6 mm.

Primary Type Material. LACMIP holotype 6515, LACMIP paratype 6516, Llajas Formation, CSUN locality 371.

Molluscan Stage Range. "Domengine."
Geographic Distribution. Simi Valley, California.
Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 489, 491, 498, 517.
Remarks. Specimens of this new species are abundant at locality 371, but preservation is only fair in most of the specimens. The type specimens have the best overall preservation. Fifteen specimens were found at locality 373, one speeimen each from localities 489 and 491, and three specimens each from localities 498 and 517. Preservation is not as good at these other localities as it is at locality 371.

The bent-backwards anterior canal of this species is well developed enough to suggest assignment to *Cerithiopsis. Bittium* is similar to *Cerithiopsis* in having a short and shallow anterior canal, but according to Houbrick (1977) the canal is not bent backwards in *Bittium.*
Etymology. The species is named for the Llajas Formation.

Superfamily Epitoniacea

Family Epitoniidae Lamarck, 1822

Genus *Cirsotrema* Mörch, 1852

Type Species. By monotypy, *Scalaria varicosum* Lamarck, 1822.

Cirsotrema sp.

Figure 6p

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.
Remarks. Only a single specimen was found, and it is from the "Stewart bed." This genus is characterized by thick axial varices more or less reflexed posteriorly and usually not continuous from whorl to whorl; coarse primary spiral ribs; and basal disk bounded by a prominent enlargement of the varices. A species identification could not be made as parts of the aperture and basal keel area are missing.

Superfamily Calyptraeacea

Family Calyptraeidae Blainville, 1824

Genus *Calyptraea* Lamarck, 1799

Type Species. By monotypy, *Patella chinensis* Linné, 1758.

Calyptraea diegoana (Conrad, 1855)

Figure 6q

Trochita diegoana Conrad, 1855:7, 17; 1857:327, pl. 5, fig. 42.
Galerus excentricus Gabb, 1864:136, pl. 20, fig. 95; pl. 29, fig. 232a. Dickerson, 1913:264.
Calyptraea calabasaensis Nelson, 1925:419, pl. 54, figs. 8a–b.
Calyptraea (*Galerus*) *calabasaensis* Nelson. Clark and Woodford, 1927:120, pl. 21, figs. 10–13.
Calyptraea diegoana (Conrad). Stewart, 1927:340–341, pl. 27, fig. 15. Turner, 1938:89–90, pl. 20, figs. 1–2. Weaver, 1943:351–352, pl. 71, figs. 16, 20; pl. 103, fig. 3; 1953:29. Stewart, 1946:pl. 11, fig. 5. Kleinpell and Weaver, 1963: 186, pl. 24, fig. 7. Hickman, 1969:79, 82, pl. 11, figs. 7–8; 1980:33–34, pl. 2, figs. 18–21. Smith, 1975:469, table 1. Givens and Kennedy, 1979:table 2.

Primary Type Material. USNM holotype 1856, Tejon? horizon, San Diego, California.
Molluscan Stage Range. "Martinez" through lower Oligocene.
Geographic Distribution. San Diego, California through Washington.
Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 455, 491, 548. Shallow-marine (regressive) facies: CSUN localities 462, 475, 512d.
Remarks. Specimens were most abundant at locality 371. At all localities, the specimens are unattached.

Family Xenophoridae Philippi, 1853

Genus *Xenophora* Fischer von Waldheim, 1807

Type Species. By subsequent designation (Gray, 1847), *Trochus conchyliophorus* Born, 1780.

Xenophora stocki Dickerson, 1916

Figure 6r

Xenophora stocki Dickerson, 1916:502–503, pl. 37, figs. 4a–b. Givens, 1974:71, pl. 7, fig. 8. Givens and Kennedy, 1979:tables 1, 3.

Primary Type Material. UCMP holotype 11838, Rose Canyon Shale, UCMP locality 2226.
Molluscan Stage Range. "Domengine."
Geographic Distribution. San Diego through Pine Mountain area, southern California.
Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 458, 471d, 472, 477, 479.
Remarks. *Xenophora stocki* is most abundant in the "Stewart bed," especially at locality 374. Specimens at all localities occur as internal molds with only remnants of shell material.

Superfamily Strombacea

Family Strombidae Rafinesque, 1815

Genus *Ectinochilus* Cossmann, 1889

Type Species. By original designation, *Strombus canalis.*

Subgenus *Macilentos* Clark and Palmer, 1923

Type Species. By original designation, *Rimella macilenta* White, 1889.

Ectinochilus (*Macilentos*) *macilentus* (White, 1889)

Figure 6s

Rimella macilenta White, 1889:19, pl. 3, figs. 10–12.
Ectinochilus (*Macilentos*) *macilentus* (White). Clark and Palmer, 1923:280, pl. 51, figs. 9–10. Givens, 1974:72, pl. 7, figs. 13, 16. Squires, 1977:table 1; 1983b:fig. 9b.

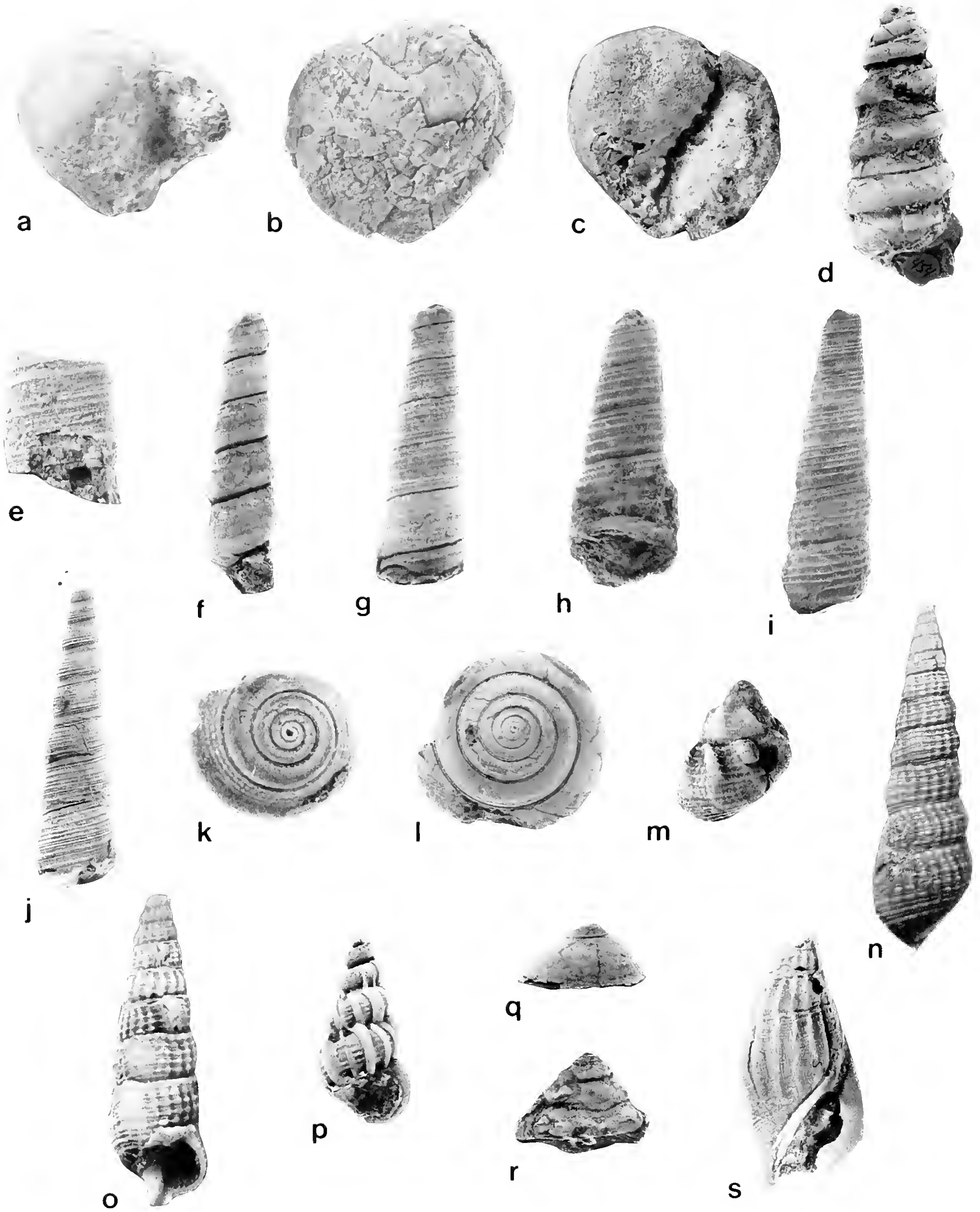

Figure 6. Llajas Formation gastropods. Unless otherwise indicated, views are apertural. **a.** *Nerita* cf. *N.* (*Amphinerita*) *eorex* Vokes, 1939, LACMIP hypotype 6508, CSUN loc. 700, ×6. **b and c.** *Velates perversus* (Gmelin, 1791), UCMP hypotype 37435, UCMP loc. 7193 = CSUN loc. 702, ×1.3. **b,** abapertural view. **d.** *Turritella meganosensis protumescens* Merriam and Turner, 1937, LACMIP 6509, CSUN loc. 454, ×1. **e.** *Turritella andersoni* Dickerson, 1916, LACMIP hypotype 6510, CSUN loc. 469d, ×2. **f and g.** *Turritella andersoni lawsoni* Dickerson, 1916. All parts from CSUN loc. 374 and ×1.25. **f,** LACMIP hypotype 6511. **g,** LACMIP hypotype 6512. **h.** *Turritella buwaldana* Dickerson,

Rimella (*Macilentos*) *macilenta* White. Vokes, 1939:155–156, pl. 20, figs. 1, 2, 4, 5.

Ectinochilus macilentus (White). Stewart, 1946:93, pl. 11, figs. 12–15. Givens and Kennedy, 1979:83, table 1.

Primary Type Material. USNM holotype 20114, Domengine Formation, about 3 km north of New Idria, section 16, T 17 S, R 12 E, Priest Valley quadrangle, Fresno County, California; CAS paratype 769, Llajas Formation, CAS locality 393.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 440, 444, 445, 447, 449, 455, 458, 460, 471d, 472, 481, 484, 491, 493, 494, 498, 499, 508, 518, 538, 539. Outer shelf and slope facies: CSUN locality 482.

Remarks. This species is common in the shallow-marine (transgressive) facies. The two localities at which it is most abundant are 371 and 374. At 371 specimens are very well preserved and some have the protoconch or the fragile outer lip intact.

The diagnosis of the subgenus *Macilentos* by Clark and Palmer (1923) was based on the paratype and other specimens from the Llajas Formation, rather than on White's holotype from central California.

Family Seraphsidae Jung, 1974

Genus *Paraseraphs* Jung, 1974

Type Species. By original designation, *Paraseraphs tetanus* Jung, 1974 [=*Terebellum fusiforme* of authors, not of Lamarck].

Paraseraphs erraticus (Cooper, 1894)

Figure 7a

Tornatina erratica Cooper, 1894:47, pl. 2, fig. 35. Waring, 1917:pl. 15, fig. 11.

Terebellum californicum Vokes, 1939:157, pl. 20, figs. 7–8, 11.

Terebellum (*Terebellum*) *erraticum* (Cooper). Kleinpell and Weaver, 1963:189, pl. 25, figs. 8–9.

Paraseraphs erraticus (Cooper). Jung, 1974:41, pl. 12, figs. 8–14; pl. 13, figs. 1–3. Givens and Kennedy, 1979:87, tables 1, 3.

Primary Type Material. CAS holotype 608, Eocene strata, Rose Canyon, San Diego, California.

Molluscan Stage Range. Uppermost "Capay" through "Transition."

Geographic Distribution. San Diego through central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 469d, 702. Shallow-marine (transgressive) facies: CSUN localities 371, 540.

Remarks. Only a few specimens were found, and most are from locality 371. The largest specimen (Fig. 7a) is 35 mm in height and is nearly twice the size of the holotype.

The presence of *P. erraticus* in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation extends the molluscan stage range of this taxon into the uppermost "Capay." Previously, the lower range limit had been reported as the "Domengine Stage" (Vokes, 1939; Jung, 1974).

Superfamily Cypraeacea

Family Cypraeidae Rafinesque, 1815

Subfamily Cypraeinae Rafinesque, 1815

Genus *Cypraea* Linné, 1758

Type Species. By subsequent designation (Montfort, 1810), *Cypraea tigris* Linné, 1758.

Cypraea castacensis Stewart, 1927

Figure 7b

Cypraea castacensis Stewart, 1927:370, pl. 28, fig. 10. Ingram, 1942:13, pl. 1, figs. 5–6.

Eocypraea castacensis (Stewart). Vokes, 1939:154, pl. 20, figs. 9, 14.

Primary Type Material. UCMP holotype 11690, Tejon? Formation, UCMP locality 452.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 491.

Remarks. Specimens are relatively rare in the Llajas For-

←

1916, LACMIP hypotype 6513, CSUN loc. 373, ×3. **i.** *Turritella uvasana infera* Merriam, 1941, abapertural view, UCLA hypotype 59359, UCLA loc. 6616, ×1.25. **j.** *Turritella uvasana applinae* Hanna, 1927, LACMIP hypotype 6514, CSUN loc. 374, ×1. **k.** *Architectonica* (*Architectonica*) *llajasensis* Sutherland, 1966, dorsal view, LACMIP 6515, CSUN loc. 371, ×3. **l.** *Architectonica* (*Stellaxis*) *cognata* Gabb, 1864, dorsal view, LACMIP hypotype 6516, CSUN loc. 374, ×1. **m.** *Benoistia umpquaensis* Turner, 1938, abapertural view, UCLA hypotype 59274, CSUN loc. 374, ×1. **n and o.** *Cerithiopsis llajasensis* n. sp. All parts from CSUN loc. 371. **n,** LACMIP holotype 6517, ×3.5. **o,** abapertural view, LACMIP paratype 6518, ×3. **p.** *Cirsotrema* sp., UCLA hypotype 59275, CSUN loc. 374, ×1.5. **q.** *Calyptraea diegoana* (Conrad, 1855), side view, LACMIP hypotype 6519, CSUN loc. 371, ×1.5. **r.** *Xenophora stocki* Dickerson, 1916, internal mold, side view, LACMIP hypotype 6520, CSUN loc. 374, ×1. **s.** *Ectinochilus* (*Macilentos*) *macilentus* (White, 1889), LACMIP hypotype 6521, CSUN loc. 371, ×1.5.

mation. One of Vokes' (1939:154, pl. 20, fig. 9) hypotypes is from Devil Canyon, just north of locality 373.

Superfamily Naticacea

Family Naticidae Forbes, 1838

Subfamily Ampullospirinae Cox, 1930

Genus *Eocernina* Gardner and Bowles, 1934

Type Species. By original designation, *Natica hannibali* Dickerson, 1914.

Eocernina hannibali (Dickerson, 1914)

Figure 7c

Natica hannibali Dickerson, 1914:119, pl. 12, figs. 5a–b; 1916: 508, pl. 38, figs. 9a–b.
Natica (*Cryptonatica*) *hannibali* Dickerson. Waring, 1917: pl. 15, figs. 21–23.
Ampullina hannibali (Dickerson). Hanna, 1927:306, pl. 48, figs. 1–3, 10.
Ampullina (*Globularia*) *hannibali* (Dickerson). Clark, 1929: pl. 11, fig. 12.
Cernina (*Eocernina*) *hannibali* (Dickerson). Turner, 1938: 87–88, pl. 19, fig. 3. Vokes, 1939:172, pl. 22, figs. 1, 3. Weaver, 1943:348–349, pl. 71, figs. 8–9, 21, 23.
Eocernina hannibali (Dickerson). Hanna and Hertlein, 1943: fig. 62-17. Marincovich, 1977:229–231, pl. 18, fig. 14; pl. 19, figs. 1–4. Givens and Kennedy, 1979:87, tables 1, 3. Squires, 1983b:fig. 9c.
Globularia (*Eocernina*) *hannibali* (Dickerson). Stewart, 1946: pl. 11, fig. 18. Givens, 1974:75, pl. 9, figs. 1, 3. Squires, 1977:table 1.

Primary Type Material. CAS holotype 243, Umpqua Formation, CAS locality 25.

Molluscan Stage Range. "Capay" through "Transition."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 469a, 542, 545, 702, 703. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 439, 440, 444, 445, 447, 449, 450, 451, 455, 458, 460, 465, 469e, 469g, 470b, 471b, 471e, 477, 479, 480, 484, 486, 488, 493, 494, 497, 498, 499, 500, 508, 509, 510, 514, 517, 523, 538, 704. Outer shelf and slope facies: CSUN locality 482. Shallow-marine (regressive) facies: CSUN localities 512c, 512d.

Remarks. *E. hannibali* is one of the most common species of the Llajas Formation. It occurs in all the marine facies of the formation and is particularly characteristic of the shallow-marine (transgressive) facies. According to Marincovich (1977:231), this species may occur in prolific numbers. This is especially true for the "Stewart bed" in the vicinity of localities 374 and 444. There, *E. hannibali* is the most common megafossil with nearly complete growth series present also.

Genus *Tejonia* Hanna and Hertlein, 1943

Type Species. By monotypy, *Natica alveata* Conrad, 1855, not Troschel, 1852.

Tejonia moragai (Stewart, 1927)

Figure 7d

Natica alveata Conrad, 1855:10; 1857:321, pl. 2, figs. 8, 8a. Not *Natica alveata* Troschel, 1852:159, pl. 5, fig. 3.
Amauropsis alveata (Conrad). Gabb, 1864:110, pl. 19, fig. 59; pl. 21, fig. 111. Dickerson, 1916:pl. 38, fig. 7. Anderson and Hanna, 1925:119–120, pl. 6, fig. 2; pl. 7, fig. 1; pl. 15, fig. 17.
Amauropsis alveatus (Conrad). Arnold, 1907:pl. 39, fig. 8.
Amaurellina moragai Stewart, 1927:334–336, pl. 28, fig. 3 [new name for *Natica alveata* Conrad, 1855, preoccupied]. Clark, 1929:pl. 14, figs. 3, 9. Kleinpell and Weaver, 1963: 188, pl. 25, figs. 1–2.
Amaurellina moragai lajollaensis Stewart, 1927:336, pl. 28, fig. 2.
Amaurellina hendoni Turner, 1938:86–87, pl. 20, figs. 7, 8, 11. Vokes, 1939:173, pl. 22, figs. 7, 10. Weaver, 1943:345, pl. 70, figs. 12–13, 16–17.
Tejonia lajollaensis (Stewart). Hanna and Hertlein, 1943: 172, fig. 62-30. Givens, 1974:74, pl. 8, fig. 5.
Tejonia moragai (Stewart). Givens, 1974:74, pl. 8, fig. 8. Marincovich, 1977:232–236, pl. 19, figs. 6–12. Squires, 1977:table 1. Givens and Kennedy, 1979:tables 1, 3–4.

Primary Type Material. Holotype unknown for *Natica alveata* Conrad (USNM collection?), Tejon Formation, Grapevine Canyon, Tejon quadrangle, Kern County, California. UCMP "holotype" 31387 of *Amaurellina moragai* Stewart, Tejon Formation, UCMP locality 7200. See Marincovich, 1977:235 for a discussion of Stewart's (1927) "holotype."

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 467. Shallow-marine (regressive) facies: CSUN locality 489.

Remarks. At locality 373, *T. moragai* is fairly common and occurs as a growth series. Some specimens have their protoconchs present. Elsewhere, only single specimens were found. This species is characterized by its strongly tabulate adult whorls.

Genus *Pachycrommium* Woodring, 1928

Type Species. By original designation, *Amaura guppyi* Gabb, 1873.

Pachycrommium clarki (Stewart, 1927)

Figure 7e

Amauropsis alveata (Conrad). Arnold, 1910:pl. 4, fig. 21. Waring, 1917:pl. 15, fig. 25. Dickerson, 1915:pl. 5, fig. 9

[not *Natica alveata* Conrad, 1855 = *Tejonia moragai* (Stewart, 1927), treated herein].

Amaurellina (*Euspirocrommium*) *clarki* Stewart, 1927:336–339, pl. 26, figs. 8–9 [new name, in part, for *Amauropsis alveata* (Conrad, 1855), preoccupied]. Clark, 1929:pl. 11, fig. 10. Turner, 1938:86, pl. 20, fig. 3. Weaver, 1943:345, pl. 70, figs. 10, 18. Kleinpell and Weaver, 1963:188, pl. 27, fig. 15.

Amaurellina clarki Stewart. Gardner and Bowles, 1934:246, figs. 6, 8.

Amaurellina? *multiangulata* Vokes, 1939:174, pl. 22, figs. 2, 8, 13.

Pachycrommium? *clarki* (Stewart). Vokes, 1939:175, pl. 22, figs. 11, 30. Givens, 1974:73, pl. 8, figs. 6, 10. Squires, 1977:table 1.

Amaurellina (*Euspirocrommium*?) *clarki* Stewart. Stewart, 1946:pl. 11, fig. 3.

Pachycrommium clarki (Stewart). Marincovich, 1977:238–241, pl. 20, figs. 4–10. Squires, 1983b:fig. 9d.

Primary Type Material. UCMP holotype 31385, UCMP paratype 31386 of *Amaurellina* (*Euspirocrommium*) *clarki* Stewart, Llajas Formation, UCMP locality 7004 = CSUN locality 374.

Molluscan Stage Range. "Capay" through "Tejon."

Geographic Distribution. San Diego, California through northern Washington.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 452, 469a, 702, 703. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 444, 447, 455, 457, 466, 469e, 471e, 479, 484, 486, 488, 491, 492, 493, 494, 498, 500, 505, 506, 507, 508, 513, 514, 518, 528, 537, 538. Outer shelf and slope facies: CSUN locality 482. Outer shelf and slope channel facies: CSUN locality 541.

Remarks. This species is especially abundant at localities 371 and 374, and at both localities it occurs as a growth series.

Subfamily Polinicinae Finlay and Marwick, 1937

Genus *Polinices* Montfort, 1810

Type Species. By original designation, *Polinices albus* Montfort, 1810.

Subgenus *Euspira* Agassiz *in* J. Sowerby, 1838b

Type Species. By subsequent designation (Harris, 1897), *Ampullaria sigaretina* Lamarck, 1804.

Polinices (*Euspira*) *nuciformis* (Gabb, 1864)

Figure 7f

Lunatia nuciformis Gabb, 1864:107, pl. 28, fig. 218. Dickerson, 1916:pl. 39, fig. 4.

Lunatia cowlitzensis Dickerson, 1915:57, pl. 4, figs. 12a–b.

Natica nuciformis (Gabb). Anderson and Hanna, 1925:116, pl. 10, fig. 8.

Polinices (*Euspira*) *nuciformis* (Gabb). Clark and Woodford, 1927: 121, pl. 21, figs. 16–17. Turner, 1938:88, pl. 20, figs. 4–5. Clark, 1938:703–704, pl. 4, figs. 26, 31. Vokes, 1939: 168, pl. 21, figs. 12–14. Weaver, 1943:342–343, pl. 70, figs. 1–2; pl. 103, fig. 2.

Euspira nuciformis (Gabb). Stewart, 1927:323–324, pl. 30, fig. 16; 1946:pl. 11, fig. 16. Weaver, 1953:29. Givens, 1974: 77, pl. 7, fig. 14. Squires, 1977:table 1.

Polinices (*Euspira*) *nuciformis* var. *cowlitzensis* (Dickerson). Weaver, 1943:343, pl. 69, figs. 10–11, 13–19.

Polinices (*Euspira*) *nuciformis* (Gabb). Marincovich, 1977: 281–285, pl. 26, figs. 6–9.

Primary Type Material. ANSP lectotype 4213, ANSP paralectotypes 4213 (two specimens), Tejon Formation, Live Oak Canyon, Kern County, California.

Molluscan Stage Range. Upper Paleocene through "Tejon."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only three specimens were found in the Llajas Formation.

Genus *Neverita* Risso, 1826

Type Species. By monotypy, *Neverita josephina* Risso, 1826.

Subgenus *Neverita* s.s.

Neverita (*Neverita*) *globosa* Gabb, 1869

Figure 7g

Neverita globosa Gabb, 1869:161, pl. 27, fig. 39. Dickerson, 1916:510, pl. 39, figs. 5a–b. Stewart, 1927:326–327, pl. 28, fig. 6. Clark and Woodford, 1927:121–122, pl. 22, figs. 5–10. Turner, 1938:89, pl. 19, figs. 6–7, 13–15. Vokes, 1939: 169, pl. 21, figs. 9, 15–19. Givens and Kennedy, 1979: tables 1–3.

Neverita weaveri Dickerson, 1915:57, pl. 4, figs. 10a–b.

Neverita nomlandi Dickerson, 1917:173–174, pl. 30, figs. 2a–b.

Polinices weaveri (Dickerson). Turner, 1938:86, pl. 20, figs. 14, 16.

Neverita globosa reefensis Vokes, 1939:169, pl. 21, figs. 24–25.

Polinices (*Neverita*) *weaveri* (Dickerson). Weaver, 1943:340, pl. 68, figs. 16–17; pl. 69, fig. 3.

Polinices (*Neverita*) *globosa* (Gabb). Weaver, 1943:339, pl. 68, figs. 21, 24; pl. 69, figs. 5–6; pl. 100, fig. 29.

Polinices (*Neverita*) *nomlandi* (Dickerson). Weaver, 1943: 340, pl. 69, figs. 8, 9, 12.

Neverita (*Neverita*) *globosa* Gabb. Givens, 1974:76. Marincovich, 1977:312–316, pl. 28, figs. 10–15; pl. 29, figs. 1–3.

Neverita (*Glossaulax*?) *globosa* Gabb. Givens and Kennedy, 1976:965–966, pl. 2, figs. 5–14, 16, 18–19.

Neverita globosa Gabb. Givens and Kennedy, 1979:tables 1–3.

Primary Type Material. MCZ holotype 27859, Domengine? Formation, 16 km west of Griswold's, on the road from San Juan to New Idria, and southeast of the "Sheep Well," T 15 S, R 9 E, Priest Valley quadrangle, San Benito County, California.

Molluscan Stage Range. "Meganos" through upper Eocene.

Geographic Distribution. San Diego, California through western Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 704.

Remarks. Only three specimens were found in the Llajas Formation.

Subfamily Sininae Wenz, 1941

Genus *Sinum* Röding, 1798

Type Species. By subsequent designation (Dall, 1915), *Helix haliotoidea* Linné, 1758.

Sinum obliquum (Gabb, 1864)

Figure 7h

Naticina obliqua Gabb, 1864:109, pl. 21, fig. 112. Dickerson, 1915:pl. 5, figs. 5a–b.
Sinum occidentis Weaver and Palmer, 1922:32–33, pl. 11, figs. 8, 26. Weaver, 1943:351, pl. 71, fig. 15.
Sinum coryliforme Anderson and Hanna, 1925:120, pl. 9, fig. 10; pl. 10, fig. 15; pl. 15, fig. 8.
Sinum obliquum (Gabb). Stewart, 1927:327, pl. 30, fig. 7a. Clark, 1938:704, pl. 3, figs. 32, 37. Weaver, 1943:350–351, pl. 71, fig. 13; pl. 103, fig. 6. Hickman, 1969:85–88, pl. 11, figs. 9–10. Marincovich, 1977:347–350, pl. 33, figs. 1–12. Squires, 1977:table 1. Givens and Kennedy, 1979: table 4.

Primary Type Material. ANSP lectotype 4215, ANSP paralectotypes 4215 (seven specimens), Tejon Formation, Fort Tejon area, Kern County, California.

Molluscan Stage Range. "Capay" through lower Oligocene.

Geographic Distribution. San Diego, California through southwestern Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 539.

Remarks. *S. obliquum* is most common at locality 371 where it is well preserved and occurs as a growth series. At locality 539, only a single specimen was found.

Subfamily Naticinae Forbes, 1838

Genus *Natica* Scopoli, 1777

Type Species. By subsequent designation (Anton, 1839), *Nerita vitellus* Linné, 1758.

Subgenus *Naticarius* Duméril, 1806

Type Species. By monotypy, *Nerita canrena* Linné, 1758.

Natica (*Naticarius*) aff. *N.* (*N.*) *uvasana* Gabb, 1864

Figure 7i

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 545. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 486.

Remarks. This taxon is most common at locality 371 where 32 specimens make up a growth series. The largest specimen is 18 mm in height. Elsewhere, only a few specimens were found.

The Llajas specimens agree with the description of *N.* (*N.*) *uvasana* given by Marincovich (1977:390) in possessing irregularly spaced collabral wrinkles immediately below the suture, an open umbilicus, and a robust umbilical callus and funicle. The Llajas specimens differ in that they lack a parietal callus.

Superfamily Tonnacea

Family Cassididae Latreille, 1825

Genus *Galeodea* Link, 1807

Type Species. By monotypy, *Buccinum echinophorum* Linné, 1758.

Subgenus *Caliagaleodea* Clark, 1942

Type Species. By original designation, *Caliagaleodea californica* Clark, 1942.

Galeodea (*Caliagaleodea*) *californica* Clark, 1942

Figure 7j

Galeodea (*Caliagaleodea*) *californica* Clark, 1942:118–119, pl. 19, figs. 15–19.
Galeodea californica Clark. Givens and Kennedy, 1979: table 1.

Primary Type Material. UCMP holotype 34376, UCMP paratype 34377, Llajas Formation, UCMP locality 7004 = CSUN locality 374.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 445, 447, 458.

Remarks. Nearly all the specimens of this species were found at the type locality. The 14 specimens at locality 374 make up a nearly complete growth series, but most occur as internal molds. A few other specimens were found elsewhere in the "Stewart bed" in the vicinity of locality 374.

Subgenus *Gomphopages* Gardner, 1939

Type Species. By original designation, *Galeodea turneri* Gardner, 1939.

Galeodea (*Gomphopages*) *susanae* Schenck, 1926

Figure 7k

Galeodea susanae Schenck, 1926:85, pl. 15, figs. 3–7. Turner, 1938:92, pl. 18, fig. 18. Weaver, 1943:402–403, pl. 78, figs. 2–3.

Galeodea (*Gomphopages*) *susanae* Schenck. Durham, 1942: 184. Givens, 1974:78.

Primary Type Material. CAS holotype 1753, CAS paratype 1754, Llajas Formation, CAS locality 372; CAS paratype 1755, Llajas Formation, CAS locality 364; CAS paratype 1756, near Roseburg, Oregon.

Molluscan Stage Range. "Domengine," "Transition"?.

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. The 16 specimens from locality 371 make up a growth series, and they are extremely well preserved. There is excellent preservation of spines and, in a few cases, the long anterior canal. The largest specimen is 53 mm in height.

Genus *Phalium* Link, 1807

Type Species. By subsequent designation (Dall, 1909), *Buccinum glaucum* Linné, 1758.

Subgenus *Semicassis* Mörch, 1852

Type Species. By subsequent designation (Harris, 1897), *Cassis japonica.*

Phalium (*Semicassis*) *tuberculiformis* (Hanna, 1924)

Figure 7l

Morio (*Sconsia*) *tuberculatus* Gabb, 1864:104, pl. 19, fig. 57. Arnold, 1907:pl. 39, fig. 9.

Not *Cassidaria tuberculata* Risso, 1826:186.

Morio tuberculatus Gabb. Dickerson, 1913:264.

Galeodea tuberculata (Gabb). Dickerson, 1916:pl. 42, fig. 2.

Galeodea (*Morio*) *tuberculata* (Gabb). Waring, 1917:pl. 15, fig. 17.

Galeodea tuberculiformis Hanna, 1924:167 [new name for *Morio* (*Sconsia*) *tuberculatus* Gabb, 1864, preoccupied]. Schenck, 1926:83–84, pl. 14, figs. 12–16. Stewart, 1927: 380–381, pl. 28, fig. 11. Vokes, 1939:149–150, pl. 19, figs. 19, 21, 23–27.

Coalingodea tuberculiformis (Hanna). Durham, 1942:186, pl. 29, figs. 5, 9. Givens, 1974:78–79, pl. 8, fig. 7. Squires, 1977:table 1.

Cassis (*Coalingodea*) *tuberculata* (Gabb). Abbott, 1968b:59–60, pl. 34.

Phalium (*Semicassis*) *tuberculiformis* (Hanna). Givens and Kennedy, 1979:82, 95, tables 1, 3.

Primary Type Material. ANSP lectotype 4343 of *Morio* (*Sconsia*) *tuberculatus* Gabb and *Galeodea tuberculiformis* Hanna, Tejon? Formation, Martinez, California.

Molluscan Stage Range. "Capay"?, "Domengine" through "Transition."

Geographic Distribution. San Diego, California through northwestern Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 440, 444, 445, 455, 458, 471b, 480, 488, 494, 514, 537. Outer shelf and slope channel facies: CSUN locality 541. Shallow-marine (regressive) facies: CSUN localities 462, 512d.

Remarks. This taxon is most common and best preserved at localities 371 and 374, where it occurs in growth series. The beaded appearance of the whorls and the toothed outer lip are well preserved.

Dickerson (1913) reported this species from "Capay"-age strata in central California, but he gave no specific locality information nor did he figure the species. For these reasons, the "Capay"-age occurrence is uncertain.

The presence of *P.* (*S.*) *tuberculiformis* in the Llajas Formation is one of the earliest occurrences of *Phalium* on the West Coast. It is also known from similar age strata in San Diego County (Givens and Kennedy, 1979).

Family Cymatiidae Iredale, 1913

Genus *Cymatium* Röding, 1798

Type Species. By subsequent designation (Dall, 1904), *Murex femorale* Linné, 1758.

Subgenus *Septa* Perry, 1810

Type Species. By monotypy, *Septa scarlatina* Perry, 1810 (=*Murex rubecula* Linné, 1758).

Cymatium (*Septa*) *janetae* Squires, 1983a

Figure 7m

Cymatium (*Septa*) *janetae* Squires, 1983a:355–357, figs. 2a–d.

Primary Type Material. UCLA holotype 59191, Llajas Formation, CSUN locality 444; UCLA paratype 59192, Llajas Formation, CSUN locality 445; UCLA paratype 59193, Llajas Formation, CSUN locality 371.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 444, 498.

Remarks. Only juvenile specimens occur at localities 371 and 498. Only adult specimens occur in the "Stewart bed" at and near localities 374 and 444. The figured specimen (Fig. 7m) is the holotype. *C.* (*S.*) *janetae* is, at present, the earliest species worldwide referable to *Septa* (Squires, 1983a).

Genus *Ranella* Lamarck, 1816

Type Species. By subsequent designation (Children, 1823), *Ranella gigantea* Lamarck, 1816 [=*Murex olearium* Linné, 1758].

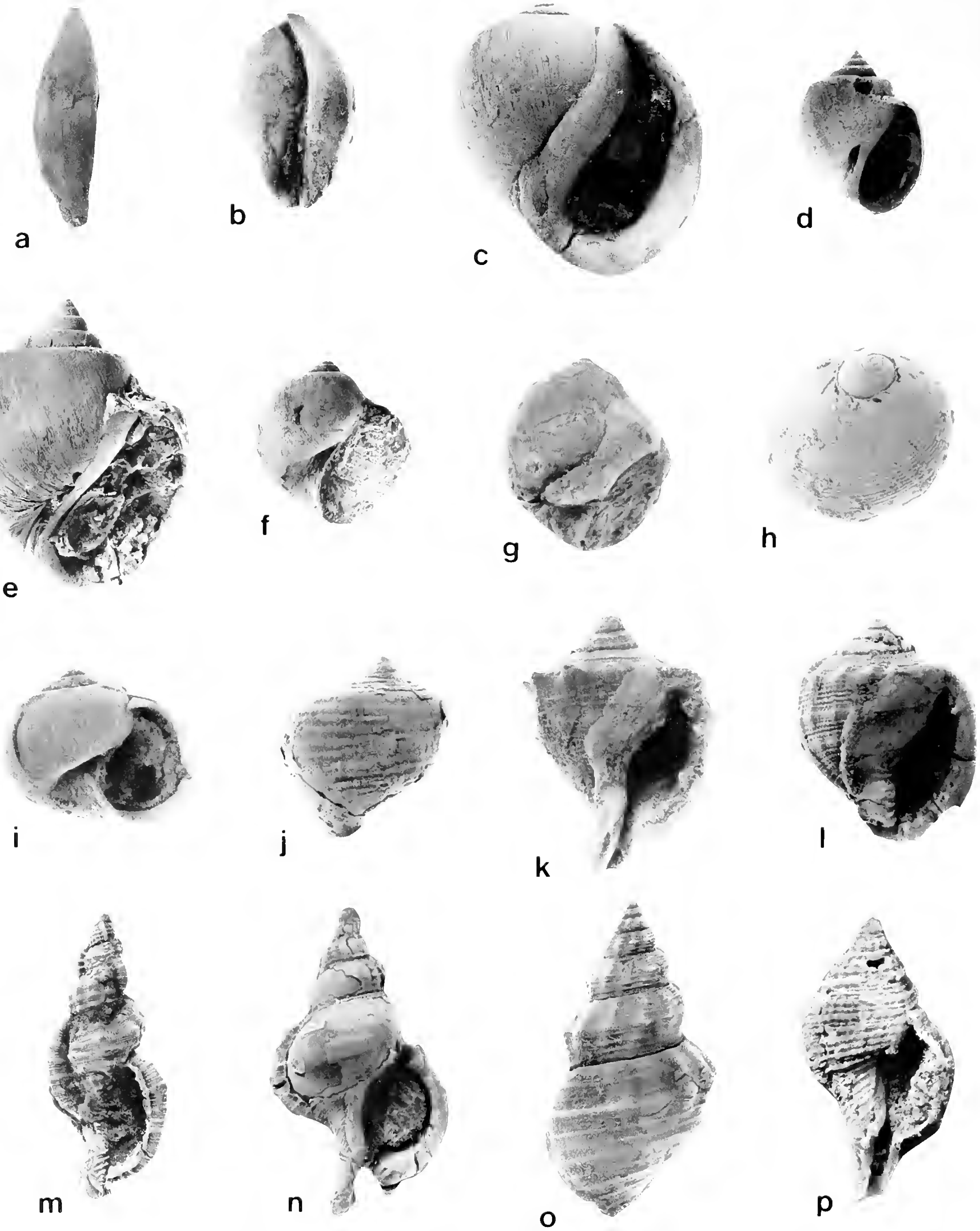

Figure 7. Llajas Formation gastropods (continued). Unless otherwise indicated, views are apertural. **a.** *Paraseraphs erraticus* (Cooper, 1894), abapertural view, LACMIP hypotype 6522, CSUN loc. 371, ×1. **b.** *Cypraea castacensis* Stewart, 1927, LACMIP hypotype 6523, CSUN loc. 374, ×1.25. **c.** *Eocernina hannibali* (Dickerson, 1914), hypotype LACMIP 6524, CSUN loc. 374, ×1. **d.** *Tejonia moragai* (Stewart, 1927), LACMIP hypotype 6525, CSUN loc. 467, ×1. **e.** *Pachycrommium clarki* (Stewart, 1927), LACMIP hypotype 6526, CSUN loc. 371, ×1. **f.** *Polinices* (*Euspira*) *nuciformis* (Gabb, 1864), UCLA hypotype 59276, CSUN loc. 374, ×1. **g.** *Neverita* (*Neverita*) *globosa* Gabb, 1869, LACMIP hypotype 6527, CSUN loc. 704, ×1.5. **h.** *Sinum obliquum* (Gabb, 1864), side view, LACMIP hypotype 6528, CSUN loc. 371, ×2. **i.** *Natica*

Ranella katherineae Squires, 1983a

Figure 7n

"*Ranella*" sp. Smith, 1970:523.
Ranella katherineae Squires, 1983a:357–359, figs. 2e–g.

Primary Type Material. UCLA holotype 45969, Llajas Formation, CSUN locality 374.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only a single, nearly complete adult specimen was found in the Llajas Formation. This specimen is the holotype and the figured specimen (Fig. 7n). *R. katherineae* is one of the earliest West Coast species of *Ranella* s.s. (Squires, 1983a).

Family Bursidae Thiele, 1925

Genus *Olequahia* Stewart, 1927

Type Species. By original designation, *Cassidaria washingtoniana* Weaver, 1912.

Olequahia domenginica (Vokes, 1939)

Figure 7o

Ranella domenginica Vokes, 1939:147–148, pl. 19, figs. 6, 20.
Olequahia hornii domenginica (Vokes). Stewart, 1946: table 1.
Olequahia domenginica (Vokes). Givens, 1974:80, pl. 9, figs. 4–5. Givens and Kennedy, 1979:table 1.

Primary Type Material. UCMP syntypes 15803 and 15804, Domengine Formation, UCMP locality 672.

Molluscan Stage Range. "Domengine Stage."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 444, 445, 471d, 494.

Remarks. Specimens are most common in the "Stewart bed" at locality 374 where they form a growth series.

Vokes (1939:147–148) used non-type, supplementary specimens from the vicinity of locality 374 to augment his description of this taxon.

Genus *Ranellina* Conrad, 1865

Type Species. By original designation, *Ranellina maclurii* Conrad, 1865.

Ranellina pilsbryi Stewart, 1927

Figure 7p

Not *Clavatula*? *californica* Conrad, 1855:11; 1857:322, pl. 2, fig. 11.
Fusus californicus (Conrad). Gabb, 1864:85–86, pl. 28, figs. 205–205a.
Nyctilochus hornii (Gabb). Dickerson, 1915:pl. 7, fig. 8. Dickerson, 1916:pl. 42, fig. 3.
Clavilithes californicus (Conrad). Anderson and Hanna, 1925: 63–64, pl. 13, figs. 1–2.
Ranellina pilsbryi Stewart, 1927:384–385, pl. 30, figs. 8–9 [new name for *Fusus californicus* (Conrad) Gabb, 1864, misidentified]. Turner, 1938:91, pl. 16, fig. 3. Vokes, 1939: 148, pl. 19, figs. 10, 17. Weaver, 1943:417, pl. 82, fig. 7. Givens, 1974:80, pl. 9, fig. 12. Givens and Kennedy, 1979: tables 1, 4.

Primary Type Material. UCMP holotype 31382, UCMP paratype 31383 of *Ranellina pilsbryi* Stewart, Tejon Formation, UCMP locality 7182.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. San Diego, California to southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 486, 498.

Remarks. This species is most common at locality 371 where seven specimens were found.

Smith (1975:table 1) reported "*Ranellina*" sp. aff. *R. pilsbryi* from "Martinez"-age strata of central California.

Family Ficidae Conrad, 1867

Genus *Ficopsis* Conrad, 1866

Type Species. By subsequent designation (Stewart, 1927), *Hemifusus remondii* Gabb, 1864.

Ficopsis cooperiana Stewart, 1927

Figure 8a

Fusus (*Hemifusus*) *cooperii* Gabb, 1864:86, pl. 28, fig. 207. Not *Fusus cooperi* Conrad, 1834:148.
Ficopsis cooperii (Gabb). Dickerson, 1915:61–62, pl. 6, fig. 11; 1916:492–493, pl. 37, fig. 7. Clark, 1929:pl. 9, fig. 13.
Ficopsis cooperiana Stewart, 1927:378–379 [new name for *Fusus* (*Hemifusus*) *cooperii* Gabb, 1864, preoccupied]. Clark, 1929:pl. 9, fig. 13. Givens, 1974:81, pl. 9, figs. 7, 9. Givens and Kennedy, 1979:87, table 3.

Primary Type Material. UCMP holotype 11691 of *Fusus* (*Hemifusus*) *cooperii* Gabb and *Ficopsis cooperiana* Stewart, Eocene strata, UCMP locality 2226.

←

(*Naticarius*) aff. *N.* (*N.*) *uvasana* Gabb, 1864, LACMIP hypotype 6529, CSUN loc. 371, ×2. **j.** *Galeodea* (*Caliagaleodea*) *californica* Clark, 1942, internal mold, abapertural view, LACMIP topotype and hypotype 6530, CSUN loc. 374, ×1. **k.** *Galeodea* (*Gomphopages*) *susanae* Schenck, 1926, LACMIP hypotype 6531, CSUN loc. 371, ×1.5. **l.** *Phalium* (*Semicassis*) *tuberculiformis* (Hanna, 1924), LACMIP hypotype 6532, CSUN loc. 371, ×1. **m.** *Cymatium* (*Septa*) *janetae* Squires, 1983a, UCLA holotype 59191, CSUN loc. 444, ×1. **n.** *Ranella katherineae* Squires, 1983a, UCLA holotype 45969, CSUN loc. 374, ×0.5. **o.** *Olequahia domenginica* (Vokes, 1939), LACMIP hypotype 6533, CSUN loc. 374, ×1. **p.** *Ranellina pilsbryi* Stewart, 1927, LACMIP hypotype 6534, CSUN loc. 371, ×2.5.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only a few specimens were found in the Llajas Formation.

Ficopsis remondii crescentensis Weaver and Palmer, 1922

Figure 8b

Ficopsis angulatus Weaver, 1905:119, pl. 13, fig. 5.

Not *Pyrula angulata* Edwards, 1866:pl. 4.

Ficopsis remondii (Gabb) var. *crescentensis* Weaver and Palmer, 1922:39–40, pl. 11, fig. 14 [new name for *Ficopsis angulatus* Weaver, 1905, preoccupied]. Stewart, 1930:40–41. Turner, 1938:93, pl. 15, fig. 19. Weaver, 1943:399, pl. 77, fig. 10.

Ficopsis remondii crescentensis Weaver and Palmer. Vokes, 1939:152–153. Givens, 1974:82, pl. 9, fig. 11. Squires, 1977:table 1. Givens and Kennedy, 1979:87, tables 1, 3.

Ficopsis crescentensis Weaver and Palmer. Stewart, 1946:pl. 11, fig. 17.

Primary Type Material. UCMP holotype 11887 of *Ficopsis angulatus* Weaver, Eocene strata, UCMP locality 337. UW holotype 205 (CAS 7616) of *Ficopsis remondii crescentensis* Weaver and Palmer, Crescent? Formation, UW locality 358.

Molluscan Stage Range. "Capay" through "Transition."

Geographic Distribution. San Diego, California through northwestern Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 374, 477, 479, 486.

Remarks. Specimens are most common at locality 371 although the largest specimens occur at locality 374. This taxon is characterized by the tri-carination of the body whorl and the cancellate sculpture.

Order Neogastropoda

Superfamily Muricacea

Family Muricidae da Costa, 1776

Subfamily Muricinae da Costa, 1776

Genus *Laevityphis* Cossmann, 1903

Type Species. By original designation, *Typhis coronarius* Deshayes, 1865.

Subgenus *Laevityphis* s.s.

Laevityphis (*Laevityphis*) *antiquus* (Gabb, 1864)

Figure 8c

Typhis antiquus Gabb, 1864:82, pl. 18, fig. 31. Stewart, 1927: 387–388, pl. 27, figs. 7–8.

Laevityphis (*Laevityphis*) *antiquus* (Gabb). Keen, 1944:58, 63. Givens, 1974:82.

Laevityphis antiquus (Gabb). Givens and Kennedy, 1979: table 3.

Primary Type Material. ANSP lectotype 4335, Tejon? Formation, Martinez, California.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only a single specimen was found in the Llajas Formation.

Family Buccinidae Rafinesque, 1815

Genus *Ancistrolepis* Dall, 1895

Type Species. By original designation, *Chrysodomus eucosmius* Dall, 1891.

***Ancistrolepis*? *carolineae* n. sp.**

Figures 8d–e

Diagnosis. Bucciniform shell with two spiral ribs on spire and about six spiral ribs on body whorl, interspaces characteristically concave with numerous fine lirae. Due to the fact that the canal area has been broken off on each of the Llajas specimens, positive generic assignment cannot be made.

Ancistrolepis? *carolineae* n. sp. is very similar to *A. clarki* Tegland (1933:131–132, pl. 12, fig. 14) and *A. clarki* variety? Tegland (1933:132, pl. 12, figs. 15–17) from the Oligocene Blakeley Formation, northwestern Washington. *A.*? *carolineae* differs from *A. clarki* and *A. clarki* var.? in the following features: less convex whorls, narrower and shorter spire, equally spaced primary spiral ribs on the spire, less inflated spiral ribs, and smaller shell size. Unfortunately, the anterior canal area is missing in the Llajas specimens and comparison to the ornamented canal areas of *A. clarki* and *A. clarki* var.? cannot be made. *A. clarki* and *A. clarki* var.? differ from each other only in the nature of the canal area ornamentation.

Description. Medium shell, bucciniform, with five or six angulate whorls. Suture moderately impressed. Protoconch smooth with low, rounded whorls and shallow sutures.

Spire whorls with two very prominent, primary spiral ribs that divide the whorls into three equal concave areas covered with numerous fine lirae. Body whorl with five to six primary spiral ribs, interspaces concave and covered with numerous fine lirae.

Columella smooth and twisted. Aperture straight. Thickened outer lip. Anterior canal area missing. Dimensions of largest specimen (Figs. 8d–e): height (incomplete) 32 mm, body whorl width 20 mm.

Primary Type Material. UCLA holotype 59401, UCLA paratypes 59402 (three specimens), Llajas Formation, CSUN locality 374.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Specimens of this new species were found only at CSUN locality 374 ("Stewart bed"). A total of 12 specimens was found, and preservation is mostly as internal molds. A few specimens (i.e., the primary type material) have portions of the original shell material.

Ancistrolepis Dall is differentiated from *Chrysodomus* in three respects; namely, a shorter canal, a degenerate radula, and in the nature of the operculum. Although only the canal feature can be used in fossil material, Tegland (1933) considered that the outline of the shell and detail of sculpturing of *A. clarki* was so close to the Recent species, *Ancistrolepis eucosimus* Dall (1895:709, pl. 29, fig. 7), the type species of the genus, that reference to that genus rather than *Chrysodomus* was warranted. The Llajas specimens of *A.? carolineae* n. sp. are very similar to those of *A. clarki* and *A. clarki* var.?, and they are not similar to West Coast Paleogene species of *Chrysodomus* in terms of sculpture.

If *A.? carolineae* does belong to *Ancistrolepis*, it would extend the earliest occurrence of this genus to the early middle Eocene, and *A. carolineae* would be the oldest known species referable to this genus. It would be the first occurrence of this genus in California.

Etymology. The species is named for Caroline Squires.

Superfamily Buccinacea

Family Nassariidae Iredale, 1916

Genus *Molopophorus* Gabb, 1869

Type Species. By monotypy, *Bullia* (*Molopophorus*) *striata* Gabb, 1869.

Molopophorus cretaceus (Gabb, 1864)

Figure 8f

Nassa cretacea Gabb, 1864:97, pl. 18, fig. 49.
Molopophorus cretaceus (Gabb). Stewart, 1927:391–392, pl. 28, fig. 9. Vokes, 1939:141–142, pl. 19, fig. 4.

Primary Type Material. ANSP lectotype 4197, Domengine Formation, Bulls Head Point, near Martinez, California.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 467.

Remarks. Only two specimens were found in the Llajas Formation, and the apertures are covered or smashed.

Family Fasciolariidae Gray, 1853

Genus *Clavilithes* Swainson, 1840

Type Species. By subsequent designation (Grabau, 1904), *Fusus parisiensis* Mayer-Eymar, 1877 [=*Fusus longaevus* Lamarck, 1803, not Solander, 1766].

Clavilithes tabulatus (Dickerson, 1913)

Figure 8g

Clavella tabulata Dickerson, 1913:283, pl. 12, fig. 7.
Clavilithes tabulatus (Dickerson). Clark and Vokes, 1936: 874, pl. 1, fig. 3 (holotype refigured). Givens, 1974:85, pl. 10, figs. 4–5.
Clavilithes cf. *C. tabulatus* (Dickerson). Crowell and Susuki, 1959:588–589, pl. 2, figs. 6–7.

Primary Type Material. UCMP holotype 11753, Capay Formation, UCMP locality 1853.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Orocopia Mountains, southern California through central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 703. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 704.

Remarks. Only two specimens were found. The presence of *C. tabulatus* in the middle part of the Llajas extends the molluscan stage range of this taxon into the "Domengine Stage." Previously it had been reported as confined to the "Capay Stage" (Clark and Vokes, 1936; Crowell and Susuki, 1959; Givens, 1974).

***Clavilithes* n. sp. A Clark and Vokes, 1936**

Figure 8h

Clavilithes n. sp. Clark and Vokes, 1936:874, pl. 1, fig. 1. Givens and Kennedy, 1976:973, pl. 4, figs. 9, 12.

Type Material. UCMP hypotype 15468, Llajas Formation, UCMP locality 3296 (Clark and Vokes, 1936). UCR hypotype 4865/13, middle Eocene strata, UCR locality 4865 (Givens and Kennedy, 1976). LACMIP hypotype 6540, Llajas Formation, CSUN locality 704.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 704.

Remarks. Two specimens of this taxon were found with *C. tabulatus* at CSUN locality 704. *C.* n. sp. A is characterized by the presence of nodes on the spire. It is not named at this time pending further taxonomic research by Jack Mount, Rutgers University.

***Clavilithes* n. sp. B Squires, 1983a**

Figure 8i

Clavilithes n. sp. Squires, 1983a:359, figs. 2h–i.

Type Material. UCLA hypotype 59194, Llajas Formation, CSUN locality 445; UCLA hypotype 59195, Llajas Formation, CSUN locality 444.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 445.

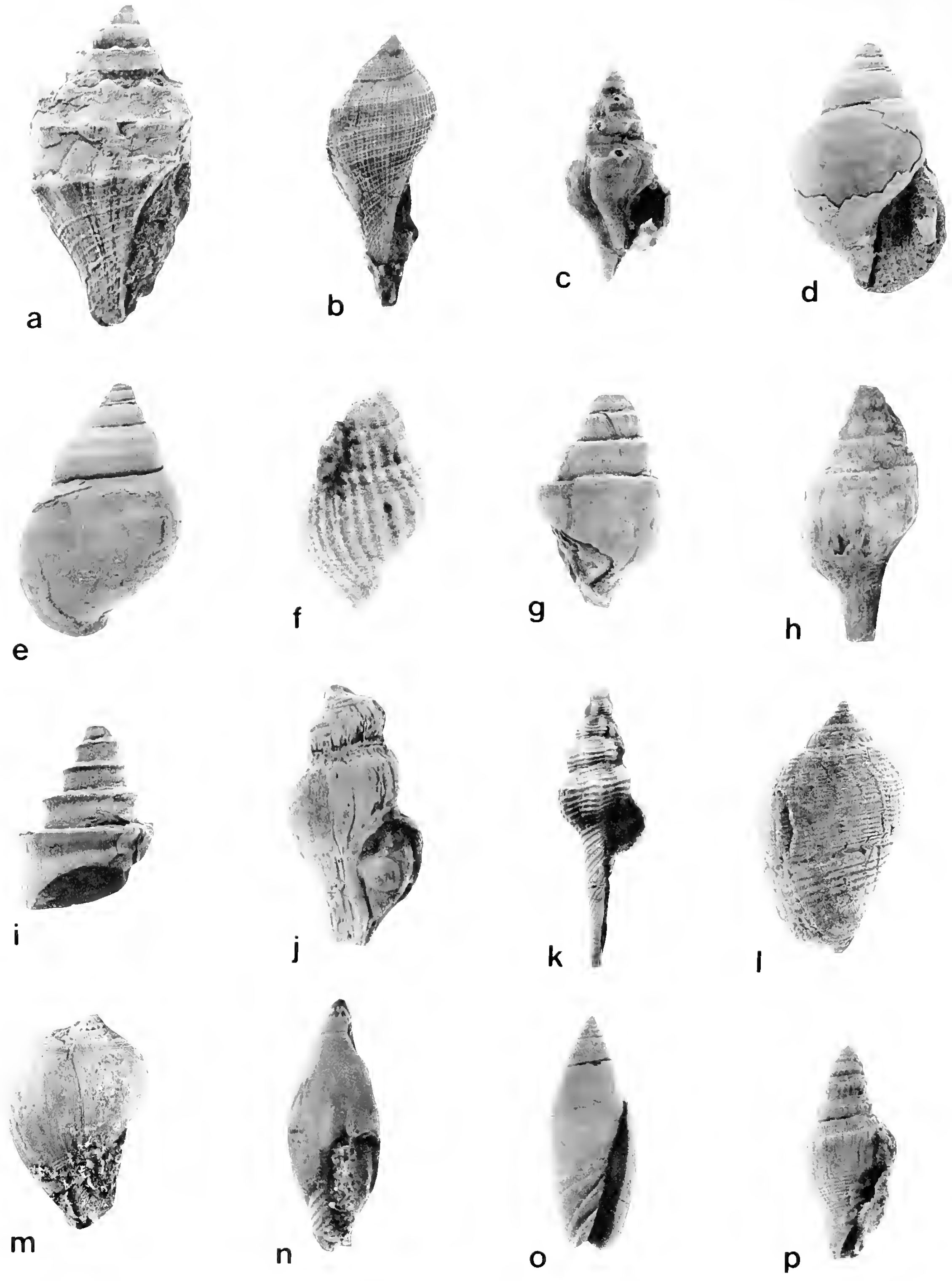

Figure 8. Llajas Formation gastropods (continued). Unless otherwise indicated, views are apertural. **a.** *Ficopsis cooperiana* Stewart, 1927, side view, UCLA hypotype 59277, CSUN loc. 374, ×2. **b.** *Ficopsis remondii crescentensis* Weaver and Palmer, 1922, LACMIP hypotype 6535, CSUN loc. 374, ×1. **c.** *Laevityphis* (*Laevityphis*) *antiquus* (Gabb, 1864), LACMIP hypotype 6536, CSUN loc. 371, ×2. **d and e.** *Ancistrolepis*? *carolineae* n. sp. All parts UCLA holotype 59401, CSUN loc. 374, ×1.25. **e,** abapertural view. **f.** *Molopophorus cretaceus* (Gabb, 1864), abapertural view, LACMIP hypotype 6537, CSUN loc. 467, ×7. **g.** *Clavilithes tabulatus* (Dickerson, 1913), LACMIP hypotype 6538, CSUN loc. 371, ×0.5. **h.** *Clavilithes* n. sp. A Clark and Vokes, 1936, LACMIP hypotype 6539, CSUN loc. 704, ×1.25. **i.** *Clavilithes* n. sp. B

Remarks. This taxon occurs with *C. tabulatus* at CSUN locality 374. *C.* n. sp. B differs from *C.* n. sp. A in the presence of an overhanging carina and in the lack of nodes on the spire. *C.* n. sp. B is not named at this time pending further taxonomic research by Jack Mount, Rutgers University.

Subfamily Fusininae Swainson, 1840

Genus *Fusinus* Rafinesque, 1815

Type Species. By monotypy, *Murex colus* Linné, 1758.

Fusinus teglandae Hanna, 1927

Figure 8j

Fusinus teglandi Hanna, 1927:315, pl. 51, fig. 9.
Fusinus teglandae Hanna. Givens, 1974:85, pl. 10, figs. 6–7.

Primary Type Material. UCMP holotype 31124, Ardath Shale, UCMP locality 5062.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Pine Mountain, southern California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only three poorly preserved specimens were found in the Llajas Formation. The upper spire is missing in all three specimens.

Fusinus aff. *F. ucalius* Vokes, 1939

Figure 8k

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only a single specimen was found in the Llajas Formation. It is unabraded and nearly complete, lacking only the protoconch. This specimen agrees with the description of *Fusinus ucalius* Vokes (1939:137) in having swollen collabral costae, strong spiral cords, and a long straight anterior canal. It differs in that the collabral costae are not obsolete or even subobsolete on the posterior parts of the spire whorls. These collabral costae on the Llajas specimen extend from suture to suture. According to Vokes (1939), *F. voetus* Hanna (1927:315, pl. 51, figs. 1, 2, 4) and *F. meganosensis* Clark and Woodford (1927:111, pl. 19, fig. 13) differ from *F. ucalius* in the same respect. The Llajas specimen differs from *F. voetus* by having a less elongate aperture, more swollen collabral costae, more angulate spire whorls, and only eight (rather than 15) collabral costae on the body whorl. The Llajas specimen differs from *F. meganosensis* by having much stronger collabral costae and spiral cords. In addition, on the body whorl of *F. meganosensis,* the collabral costae tend to become obsolete posteriorly.

Superfamily Volutacea

Family Olividae Latreille, 1825

Genus *Pseudoliva* Swainson, 1840

Type Species. By original designation, *Buccinum plumbea* Chemnitz, 1780? [=*Buccinum crassa* Gmelin, 1788?].

Pseudoliva lineata Gabb, 1864

Figure 8l

Pseudoliva lineata Gabb, 1864:99, pl. 18, fig. 52. Stewart, 1927:400, pl. 28, fig. 14a. Vokes, 1939:139, pl. 18, fig. 23.

Primary Type Material. ANSP lectotype 4200, Tejon Formation s.l., northeast of Martinez, California.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through Martinez, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 484.

Remarks. Only three specimens were found in the Llajas Formation. All show the typical *Pseudoliva* medial spiral groove. *P. lineata* is distinguished by a complete lack of nodes on the shoulder of the whorl, as noted by Turner (1938:78). As mentioned by Vokes (1939:139), Llajas Formation specimens show a spire that is somewhat higher than that of the lectotype figured by Stewart (1927, pl. 28, fig. 14a).

Genus *Strepsidura* Swainson, 1840

Type Species. By original designation, *Strepsidura costata* Swainson, 1840 [=*Fusus ficulnea* Lamarck, 1822, =*Murex turgida* Solander, 1766].

Strepsidura ficus (Gabb, 1864)

Figure 8m

Whitneya ficus Gabb, 1864:104, pl. 28, fig. 216. Dickerson, 1915:69, pl. 9, figs. 5a–d.
Strepsidura ficus (Gabb). Stewart, 1927:404–405, pl. 29, fig. 11. Kleinpell and Weaver, 1963:193, pl. 27, figs. 1–3. Givens, 1974:87, pl. 10, fig. 10.

Primary Type Material. ANSP lectotype 4331, Tejon Formation s.l., Fort Tejon area, California.

Molluscan Stage Range. Uppermost "Capay" through "Tejon."

Geographic Distribution. Simi Valley through Fort Tejon area, southern California.

Squires, 1983a, spire only, UCLA hypotype 59195, CSUN loc. 444, ×0.5. **j.** *Fusinus teglandae* Hanna, 1927, abapertural view, LACMIP hypotype 6540, CSUN loc. 374, ×0.75. **k.** *Fusinus* aff. *F. ucalius* Vokes, 1939, LACMIP hypotype 6541, CSUN loc. 371, ×1.5. **l.** *Pseudoliva lineata* Gabb, 1864, LACMIP hypotype 6542, CSUN loc. 371, ×1.5. **m.** *Strepsidura ficus* (Gabb, 1864), abapertural view, LACMIP hypotype 6543, CSUN loc. 452, ×1.25. **n.** *Ancilla* (*Spirancilla*) *gabbi* Cossmann, 1899, LACMIP hypotype 6544, CSUN loc. 489, ×4. **o.** *Olivella mathewsonii* Gabb, 1864, LACMIP hypotype 6545, CSUN loc. 467, ×2.5. **p.** *Proximitra*? *cretacea* (Gabb, 1864), LACMIP hypotype 6546, CSUN loc. 371, ×2.5.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 452, 545, 703.

Remarks. In some of the specimens, collabral costae are fairly well developed on the earlier whorls.

The presence of *S. ficus* in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation extends the molluscan stage range of this species into the uppermost "Capay." Previously, the lower range limit had been reported as the "Domengine Stage" (Givens, 1974).

Subfamily Olivinae Swainson, 1840

Genus *Ancilla* Lamarck, 1799

Type Species. By monotypy, *Ancilla cinnamonea* Lamarck, 1801.

Ancilla (*Spirancilla*) *gabbi* Cossmann, 1899

Figure 8n

Ancillaria elongata Gabb, 1864:100, pl. 18, fig. 54. Hanna, 1927:323, pl. 53, figs. 9–13. Stewart, 1927:411.

Not *Ancillaria elongata* Gray, 1847:357, pl. 1, fig. 5.

Ancilla gabbi Cossmann, 1899:60 [new name for *Ancillaria elongata* Gabb, 1864, preoccupied]. Turner, 1938:72, pl. 18, fig. 6. Weaver, 1943:500, pl. 95, fig. 18.

Ancilla (*Spirancilla*) *gabbi* Cossmann. Vokes, 1939:131, pl. 18, figs. 6, 10.

Primary Type Material. Holotype lost, UCMP syntypes 12521 (two specimens) of *Ancillaria elongata* Gabb and *Ancilla gabbi* Cossmann, Ardath Shale, near San Diego, perhaps 300 m east of the summit of Soledad Mountain on the east side of the canyon in the bottom of Rose Creek.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego, California through northwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371. Shallow-marine (regressive) facies: CSUN locality 489.

Remarks. Only two specimens were found in the Llajas Formation. Both agree with Gabb's (1864) observations of callused sutures.

Genus *Olivella* Swainson, 1831

Type Species. By subsequent designation (Dall, 1909), *Olivella purpurata* Swainson, 1831 [=*Oliva dama* Mawe, 1823].

Olivella mathewsonii Gabb, 1864

Figure 8o

Olivella mathewsonii Gabb, 1864:100, pl. 18, fig. 53. Anderson and Hanna, 1925:80, pl. 8, fig. 19. Stewart, 1927: 410–411, pl. 29, fig. 13. Weaver, 1943:500–501, pl. 103, fig. 7. Givens, 1974:87. Smith, 1975:469, table 1. Squires, 1977:table 1.

Primary Type Material. ANSP lectotype 4202, Tejon Formation s.l., Martinez, California.

Molluscan Stage Range. Lower "Martinez" through "Tejon."

Geographic Distribution. Simi Valley, California through northwestern Washington.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 469a. Shallow-marine (transgressive) facies: CSUN localities 467, 484, 498.

Remarks. Two specimens were found at locality 469a. At each of the other localities, only one specimen was found. The specimens agree with Gabb's (1864) observations of three columellar plicae at the anterior end of the shell. This taxon may be the same as *O. m. umpquaensis* Turner, 1938: 72, pl. 18, figs. 13–14.

Family Mitridae Swainson, 1831

Subfamily Vexillinae Thiele, 1929

Genus *Proximitra* Finlay, 1927

Type Species. By original designation, *Vexillum rutidolomum* Suter, 1913.

Proximitra? *cretacea* (Gabb, 1864)

Figure 8p

Mitra cretacea Gabb, 1864:103, pl. 28, fig. 215. Stewart, 1927:406, pl. 27, figs. 9–10.

Uromitra (?) *cretacea* (Gabb). Vokes, 1939:134–135, pl. 18, fig. 19.

Proximitra? *cretacea* (Gabb). Givens, 1974:87. Squires, 1977: table 1.

Primary Type Material. ANSP holotype 4302, Tejon Formation s.l., Martinez, California.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. This taxon was found at only one locality in the Llajas Formation, but 46 specimens were collected.

Family Tudiclidae Finlay and Marwick, 1937

Genus *Pseudoperissolax* Clark, 1918

Type Species. By original designation, *Busycon*? *blakei* Conrad, 1855.

Pseudoperissolax blakei praeblakei Vokes, 1939

Figure 9a

Not *Busycon*? *blakei* Conrad, 1855:11; 1857:332, pl. 2, fig. 13.

Perissolax blakei (Conrad). Gabb, 1864:92 (in part), pl. 21, fig. 110.

Pseudoperissolax blakei (Conrad) (subsp.?). Stewart, 1927: 429–430, pl. 28, fig. 1.

Pseudoperissolax blakei praeblakei Vokes, 1939:145–146, pl.

19, figs. 14, 22. Givens, 1974:88, pl. 10, figs. 15–16. Smith, 1975:pl. 2, fig. 16.

Primary Type Material. UCMP holotype 15799, UCMP paratype 15800, Arroyo Hondo Formation, UCMP locality 1817.

Molluscan Stage Range. Lower "Martinez" through "Domengine."

Geographic Distribution. San Diego?, Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only two specimens were found in the Llajas Formation. They are mostly internal molds with shell present only in the spire area. The long anterior canal is missing in the figured specimen (Fig. 9a).

A discussion of the taxonomic reasons for the use of the family Tudiclidae in place of the normally used family Vasidae is given in Zinsmeister (1983b).

Family Harpidae Bronn, 1849

Genus *Eocithara* P. Fischer, 1883

Type Species. By monotypy, *Harpa mutica* Lamarek, 1803.

Eocithara mutica californiensis (Vokes, 1937)

Figure 9b

Harpa (*Eocithara*) *mutica* n. sp. Clark and Vokes, 1936:pl. 2, fig. 5.
Harpa (*Eocithara*) *mutica californiensis* Vokes, 1937:11, pl. 2, figs. 2, 4, 6, 8.
Eocithara mutica californiensis (Vokes). Rehder, 1973:225, pl. 193.

Primary Type Material. UCMP holotype 30438, UCMP paratypes 30439–30449, Llajas Formation, UCMP locality 3296.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 373, 374.

Remarks. Four specimens were found in the Llajas Formation. Preservation is generally excellent with the thin collabral ridges present.

Family Volutidae Rafinesque, 1815

Subfamily Volutinae Rafinesque, 1815

Genus *Cryptochorda* Mörch, 1858

Type Species. By monotypy, *Buccinum stromboides* Herrmannsen.

Subgenus *Cryptochorda* s.s.

Cryptochorda (*Cryptochorda*) *californica* (Cooper, 1894)

Figure 9c

Ancilla (*Oliverato*) *californica* Cooper, 1894:43, pl. 1, figs. 6–11. Dickerson, 1913:264; 1914:115, pl. 12, figs. 4a–b.
Oliverato californica Cooper. Dickerson, 1913:286–287, pl. 13, figs. 4a–b.
Caricella stormsiana Dickerson, 1913:287, pl. 13, figs. 3a–b.
Cryptochorda californica (Cooper). Clark, 1929:pl. 4, figs. 6, 16; pl. 9, figs. 5–6. Clark and Vokes, 1936:874, pl. 1, fig. 5. Turner, 1938:72, pl. 18, figs. 11, 15. Vokes, 1939:139–140. Weaver, 1943:499, pl. 95, figs. 19, 23.

Primary Type Material. CAS syntypes 8a–d (four specimens), Capay Formation, Marysville Buttes, Sutter County, California.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 703.

Remarks. Only two specimens were found in the Llajas Formation.

According to Clark (1921:table 1; 1929), *C.* (*C.*) *californica* [=*Ancilla* (*Oliverato*) *californica*] occurs in "Meganos"-age strata. Such a report, however, cannot be substantiated at this time because of his lack of locality information and because his rock unit names are not clearly defined.

Genus *Lyria* Gray, 1847

Type Species. By original designation, *Voluta nucleus* Lamarck, 1811.

Lyria andersoni Waring, 1917

Figure 9d

Cancellaria irelaniana Cooper, 1894:42, pl. 1, fig. 5. Arnold, 1910:52, pl. 4, fig. 22. [Misidentification.]
Lyria andersoni Waring, 1917:97, pl. 15, fig. 12.
Lyria andersoni Waring. Clark, 1929:pl. 9, figs. 7–8. Clark and Vokes, 1936:876, pl. 1, fig. 17. Turner, 1938:73, pl. 18, fig. 5. Vokes, 1939:136, pl. 18, figs. 22, 24. Hanna and Hertlein, 1943:170, fig. 62-21.

Primary Type Material. SU holotype 195, SU paratype 196, Llajas Formation, SU locality 2696.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 439, 455, 466, 484, 498, 499, 507.

Remarks. This taxon helps to characterize the lower and middle parts of the shallow-marine (transgressive) facies. It is most common in the middle part. Preservation is generally good to excellent.

Subfamily Fulgorariinae Pilsbry and Olsson, 1954

Genus *Lyrischapa* Aldrich, 1911

Type Species. By monotypy, *Lyrischapa harrisi* Aldrich, 1911.

Lyrischapa lajollaensis (Hanna, 1927)

Figure 9e

Pejonia lajollaensis Hanna, 1927:320, pl. 52, figs. 1–2.
Volutospira (*Pejonia*) *lajollaensis* (Hanna). Clark, 1929, pl. 9, figs. 11–12.
Volutocristata lajollaensis (Hanna). Gardner and Bowles, 1934:246, fig. 13. Givens, 1974:88.
Lyrischapa lajollaensis (Hanna). Givens, 1979:124–126, pl. 3, figs. 1–2; pl. 4, figs. 1–3. Givens and Kennedy, 1979: table 1.

Primary Type Material. Holotype lost, UCMP neotype 14634, Ardath Shale, UCMP locality 5062.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Pine Mountain area, southern California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 373, 374, 444, 445, 510, 543, 704.

Remarks. This taxon is most common in the "Stewart bed" at locality 374, where some rather large specimens (47 mm width) occur.

Hypotype specimens figured by Givens (1979) are from the Llajas Formation.

Family Cancellariidae Forbes and Hanley, 1853

Genus *Bonellitia* Jousseaume, 1887

Type Species. By original designation, *Cancellaria bonellii* Bellardi, 1872?

Subgenus *Admetula* Cossmann, 1889

Type Species. By original designation, *Cancellaria evulsa* Solander, 1776.

Bonellitia (*Admetula*) *paucivaricata* (Gabb, 1864)

Figure 9f

Tritonium paucivaricatum Gabb, 1864:95, pl. 28, figs. 209, 209a.
Cancellaria stantoni Dickerson, 1913:282, pl. 12, figs. 2a–b.
Admete (*Bonellitia*) *stantoni* (Dickerson). Weaver and Palmer, 1922:40–42, pl. 11, figs. 1, 5.
Cancellaria paucivaricata (Gabb). Anderson and Hanna, 1925:81, pl. 8, figs. 3–4.
Bonellitia (*Admetula*) *paucivaricata* (Gabb). Stewart, 1927: 413, pl. 29, fig. 5. Turner, 1938:71, pl. 15, figs. 12–13. Weaver, 1943:508, pl. 96, figs. 10, 12, 13; pl. 103, figs. 9, 10, 17. Givens, 1974:89. Squires, 1977:table 1.

Primary Type Material. ANSP lectotype 4194, Tejon Formation, Tejon Pass area, California.

Molluscan Stage Range. "Meganos"?, "Capay" through "Tejon."

Geographic Distribution. Simi Valley, California through southwestern Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only seven specimens were found in the Llajas Formation. According to Clark (1921:table 1; 1926:115), *B.* (*A.*) *paucivaricata* [=*Cancellaria stantoni* and *Admeta stantoni*] occurs in "Meganos"-age strata. Such a report, however, cannot be substantiated at this time because of his lack of locality information and because his rock unit names are not clearly defined. Clark and Woodford (1927), however, reported a questionable occurrence of *B.* (*A.*) *paucivaricata* [=*Admete* (*Bonellitia*) cf. *stantoni*] from localities of late Paleocene/early Eocene age strata.

Superfamily Conacea

Family Turridae Swainson, 1840

Subfamily Turriculinae Powell, 1942

Genus *Pleurofusia* de Gregorio, 1890

Type Species. By original designation, *Pleurotoma* (*Pleurofusia*) *longirostropis* de Gregorio, 1890.

Pleurofusia fresnoensis (Arnold, 1910)

Figure 9g

Pleurotoma fresnoensis Arnold, 1910:53, pl. 4, fig. 23.
Surcula clarki Dickerson, 1913:278, pl. 11, fig. 3.
Pleurofusia fresnoensis (Arnold). Vokes, 1939:117–118, pl. 17, figs. 15–16. Givens, 1974:90, pl. 11, fig. 9. Givens and Kennedy, 1979:95, tables 1, 3.

Primary Type Material. USNM holotype 165631, Domengine Formation, USGS locality 4619.

Molluscan Stage Range. "Capay" through "Transition."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 538, 539.

Remarks. Specimens are most common at locality 371.

According to Clark (1921:table 1; 1926:116), *P. fresnoensis* [=*Turris* (*Surcula*) *clarki* and *Surcula clarki*] occurs in "Meganos"-age strata. Such a report, however, cannot be substantiated at this time because of his lack of locality information and because his rock unit names are not clearly defined.

Smith (1975:table 1) reported *Pleurofusia* sp. aff. *P. fresnoensis* from "Martinez"-age strata of central California.

Genus *Fusiturricula* Woodring, 1928

Type Species. By original designation, *Turris* (*Surcula*) *fusinella*.

Subgenus *Crenaturricula* Vokes, 1939

Type Species. By original designation, *Surcula crenatospira* Cooper, 1894.

Fusiturricula (*Crenaturricula*) *crenatospira* (Cooper, 1894)

Figure 9h

Surcula crenatospira Cooper, 1894:39, pl. 1, figs. 2–4. Dickerson, 1913:278, pl. 11, fig. 4.

Fusiturricula (*Crenaturricula*) *crenatospira* (Cooper). Vokes, 1939:114–115, pl. 17, figs. 4–5.

Primary Type Material. CAS syntypes 9a–b (two specimens), Capay Formation, UCMP locality 1853.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Simi Valley through Marysville Buttes, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only two specimens were found, and these are from the "Stewart bed." According to Vokes (1939:15) this taxon is confined to and is diagnostic of the "Capay Stage." The presence of it in the "Stewart bed" extends its provincial range into the "Domengine Stage."

According to Clark (1921:table 1; 1929), *F.* (*C.*) *crenatospira* [=*Turris* (*Surcula*) *crenatospira* and *Turricula crenatospira*] occurs in "Meganos"-age strata. Such a report, however, cannot be substantiated at this time because of his lack of locality information and because his rock unit names are not clearly defined.

Fusiturricula (*Crenaturricula*) *crenatospira domenginica* Vokes, 1939

Figure 9i

Fusiturricula (*Crenaturricula*) *crenatospira domenginica* Vokes, 1939:115–116, pl. 17, figs. 6–7.

Primary Type Material. UCMP holotype 15768, Llajas Formation, UCMP locality 7002; UCMP paratype 15769, Llajas Formation, UCMP locality 3304.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 444, 445, 498, 548.

Remarks. At locality 374, this taxon occurs along with *F.* (*C.*) *crenatospira,* which is characterized by the presence of collabral sculpturing below the nodes on the spire and body whorls. On *F.* (*C.*) *crenatospira domenginica,* the collabral sculpturing is obsolete. Contrary to Vokes' (1939:115–116) comments, the two taxa have approximately the same number of nodes on the body whorl.

Genus *Surculites* Conrad, 1865

Type Species. By monotypy, *Surcula* (*Surculites*) *annosus* Conrad, 1865.

Surculites mathewsonii (Gabb, 1864)

Figure 9j

Fusus mathewsonii Gabb, 1864:83, pl. 18, fig. 33. Dickerson, 1914:pl. 16, fig. 2.
Bela clathra Gabb, 1869:152, pl. 26, fig. 31.
?*Pleurotoma decipiens* Cooper, 1894:40, pl. 2, fig. 32.
Potamides? *davisiana* Cooper, 1894:44, pl. 1, fig. 13.
Surcula davisiana (Cooper). Dickerson, 1913:279, pl. 12, figs. 6a–b.
Surcula (?) sp. Waring, 1917:pl. 15, fig. 16.
Surcula decipiens (Cooper). Hanna, 1927:324, pl. 54, figs. 6, 8.
Surculites mathewsonii (Gabb). Stewart, 1927:420–421, pl. 26, figs. 12–14. Clark, 1929:pl. 9, figs. 3–4. Turner, 1938: 69–70, pl. 17, figs. 6, 10. Vokes, 1939:123, pl. 17, figs. 8, 19. Weaver, 1943:526, pl. 97, figs. 24, 29; pl. 98, figs. 1, 5; 1953:29. Givens, 1974:90, pl. 11, figs. 5, 7. Zinsmeister, 1974:164, pl. 17, fig. 6; 1983a:table 1. Squires, 1977:table 1. Givens and Kennedy, 1979:87, tables 1, 3.
"*Surculites*" *mathewsonii* (Gabb). Smith, 1975:pl. 2, fig. 15.

Primary Type Material. ANSP lectotype 4180, Tejon Formation s.l., near Martinez, California.

Molluscan Stage Range. Lower "Martinez" through "Transition."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 374, 444, 445, 447, 479, 498.

Remarks. Specimens are fairly common at locality 371 but are more common and larger at locality 374 of the "Stewart bed." At locality 374, the specimens are internal molds. Specimens at locality 371 are strongly angulated, which is in keeping with one of the main characteristics of this species as discussed by Vokes (1939:123).

Genus *Domenginella* Vokes, 1939

Type Species. By original designation, *Turris claytonensis* Gabb, 1864.

Domenginella claytonensis (Gabb, 1864)

Figure 9k

Turris claytonensis Gabb, 1864:92, pl. 18, fig. 46.
Surcula gesteri Dickerson, 1916:499, pl. 42, fig. 4.
Scobinella claytonensis (Gabb). Stewart, 1927:417–418, pl. 27, figs. 11–12.
Domenginella claytonensis (Gabb). Vokes, 1939:122–123, pl. 17, figs. 18, 20.

Primary Type Material. ANSP lectotype 4190, Tejon Formation s.l., near Martinez, California.

Molluscan Stage Range. Uppermost "Capay" through "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 469a. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 455, 466, 484, 486, 498, 517, 538, 539, 548.

Remarks. This taxon is most common at locality 371, where most of the specimens are well-preserved juveniles.

The presence of *D. claytonensis* in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation extends the molluscan stage range of this taxon into the uppermost

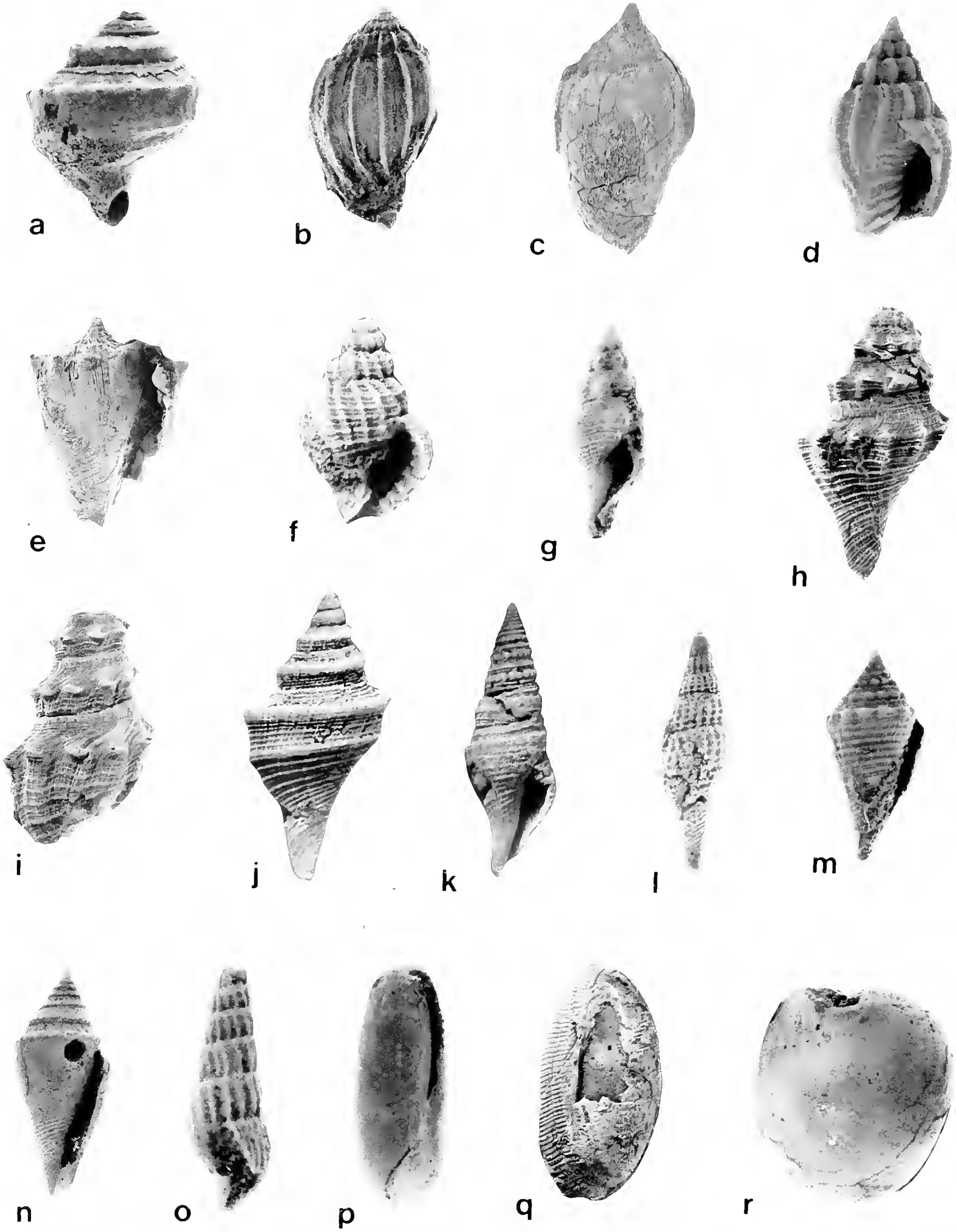

Figure 9. Llajas Formation gastropods (continued). Unless otherwise indicated, views are apertural. **a.** *Pseudoperissolax blakei praeblakei* Vokes, 1939, internal mold, side view, LACMIP hypotype 6547, CSUN loc. 374, ×1.5. **b.** *Eocithara mutica californiensis* (Vokes, 1937), abapertural view, LACMIP hypotype 6548, CSUN loc. 373, ×1.5. **c.** *Cryptochorda* (*Cryptochorda*) *californica* (Cooper, 1894), abapertural view, LACMIP hypotype 6549, CSUN loc. 703, ×1.25. **d.** *Lyria andersoni* Waring, 1917, LACMIP hypotype 6550, CSUN loc. 498, ×2. **e.** *Lyrischapa lajollaensis* (Hanna, 1927), LACMIP hypotype 6551, CSUN loc. 373, ×1. **f.** *Bonellita* (*Admetula*) *paucivariata* (Gabb, 1864), LACMIP hypotype 6552, CSUN loc. 374, ×4.5. **g.** *Pleurofusia fresnoensis* (Arnold, 1910), LACMIP hypotype 6553, CSUN loc. 371, ×3. **h.** *Fusiturricula* (*Crenaturricula*) *crenatospira* (Cooper, 1894), abapertural view, UCLA hypotype 59278, CSUN loc. 374, ×1.5. **i.** *Fusiturricula* (*Crenaturricula*) *crenatospira domenginica* Vokes, 1939, abapertural view, LACMIP hypotype 6554, CSUN loc. 371, ×1. **j.** *Surculites ma-*

"Capay." Previously, the lower range limit had been reported as the "Domengine Stage" (Vokes, 1939).

Genus *Exilia* Conrad, 1860

Type Species. By monotypy, *Exilia pergracilis* Conrad, 1860.

Exilia llajasensis Bentson, 1940

Figure 9l

Exilia llajasensis Bentson, 1940:212, pl. 1, fig. 28; pl. 2, fig. 16.

Primary Type Material. UCMP holotype 12144, Llajas Formation, UCMP locality A-3042; UCMP paratype 12140, Llajas Formation, UCMP locality 3296.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 486, 539.

Remarks. Only two specimens were found in the Llajas Formation. In the primary type specimens, the anterior canal is missing. As can be seen in Figure 9l, the long anterior canal is covered by 10 spiral ribs.

Family Conidae Rafinesque, 1815

Genus *Conus* Linné, 1758

Type Species. By subsequent designation (Children, 1823), *Conus marmoreus* Linné, 1758.

Conus caleocius Vokes, 1939

Figure 9m

Conus caleocius Vokes, 1939:127–129, pl. 18, figs. 1, 7.

Primary Type Material. UCMP holotype 15785, Llajas Formation, UCMP locality 3310.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 498.

Remarks. Four specimens were found. Three of these are from locality 371.

Conus hornii umpquaensis Turner, 1938

Figure 9n

Conus hornii umpquaensis Turner, 1938:69, pl. 15, figs. 1–2. Vokes, 1939:127, pl. 18, figs. 2–3. Stewart, 1946:pl. 11, fig. 6. Weaver, 1943:510–511, pl. 96, fig. 18. Givens and Kennedy, 1979:87, tables 1, 3.

Primary Type Material. UCMP holotype 33656, "upper Umpqua" Formation, UO locality 144.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 374, 449, 455, 484, 486, 491, 498, 538, 539.

Remarks. This taxon characterizes the lower half of the shallow-marine (transgressive) facies. It is especially abundant at locality 371, where it forms a growth series.

Family Terebridae H. and A. Adams, 1854

Genus *Terebra* Bruguière, 1789

Type Species. By subsequent designation (Lamarck, 1799), *Buccinum subulata* Linné, 1758.

Terebra californica Gabb, 1869

Figure 9o

Terebra californica Gabb, 1869:162, pl. 27, fig. 41.

Terebra californica Gabb. Anderson and Hanna, 1925:82, pl. 8, fig. 18. Stewart, 1927:424, pl. 26, fig. 5. Vokes, 1939: 113, pl. 16, fig. 38. Givens, 1974:92.

Primary Type Material. ANSP holotype 4209, Tejon Formation s.l., Martinez, California.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 467.

Remarks. Only two specimens were found. They are very small, with heights of 3 mm.

Subclass Euthyneura

Order Cephalaspidea

Superfamily Cylichnacea A. Adams, 1850

Family Cylichnidae A. Adams, 1850

Genus *Cylichnina* Monterosato, 1884

Type Species. By original designation, *Bulla umbilicata* Montagu, 1803.

thewsonii (Gabb, 1864), abapertural view, LACMIP hypotype 6555, CSUN loc. 371, ×2.5. **k.** *Domenginella claytonensis* (Gabb, 1864), side view, LACMIP hypotype 6556, CSUN loc. 371, ×2.5. **l.** *Exilia llajasensis* Bentson, 1940, LACMIP hypotype 6557, CSUN loc. 539, ×2.5. **m.** *Conus caleocius* Vokes, 1939, LACMIP hypotype 6558, CSUN loc. 498, ×2. **n.** *Conus hornii umpquaensis* Turner, 1938, LACMIP hypotype 6559, CSUN loc. 371, ×2.5. **o.** *Terebra californica* Gabb, 1869, LACMIP hypotype 6560, CSUN loc. 467, × 8. **p.** *Cylichnina tantilla* (Anderson and Hanna, 1925), LACMIP hypotype 6561, CSUN loc. 371, ×2.5. **q.** *Scaphander* (*Mirascapha*) *costatus* (Gabb, 1864), abapertural view, LACMIP hypotype 6562, CSUN loc. 493, ×1.5. **r.** *Megistostoma gabbianum* (Stoliczka, 1868), internal mold, abapertural view, LACMIP hypotype 6553, CSUN loc. 458, ×1.5.

Cylichnina tantilla (Anderson and Hanna, 1925)

Figure 9p

Cylichnella tantilla Anderson and Hanna, 1925:140, pl. 7, figs. 4, 8–9.

Cylichnina tantilla (Anderson and Hanna). Stewart, 1927: 439–441, pl. 27, figs. 2–4. Turner, 1938:67–68, pl. 20, figs. 9–10. Vokes, 1939:110, pl. 16, figs. 28, 33, 39. Weaver, 1943:548–549, pl. 100, figs. 10–12, 14–15. Stewart, 1946: pl. 11, fig. 11. Givens, 1974:93. Squires, 1977:table 1; 1983b, fig. 9a.

Primary Type Material. CAS holotype 958, CAS paratypes 959 and 960, Tejon Formation, CAS locality 711.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. Simi Valley, California through western Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372, 373, 374, 455, 460, 466, 467, 469e, 469f, 484, 486, 491, 492, 498, 499, 507, 508, 517, 537, 538, 540, 543. Shallow-marine (regressive) facies: CSUN locality 475.

Remarks. This easily recognized taxon is especially abundant at localities 371, 373, and 455. At these localities it occurs as growth series.

Genus *Scaphander* Montfort, 1810

Type Species. By original designation, *Bulla lignaria* Linné, 1767.

Subgenus *Mirascapha* Stewart, 1927

Type Species. By original designation, *Cylichna costata* Gabb, 1864.

Scaphander (*Mirascapha*) *costatus* (Gabb, 1864)

Figure 9q

Cylichna costata Gabb, 1864:143–144, pl. 21, fig. 107. Arnold, 1907:pl. 39, fig. 10. Zinsmeister, 1974:170–171, pl. 12, figs. 20–22.

Scaphander costata (Gabb). Hanna, 1927:329, pl. 57, figs. 2, 3, 5.

Scaphander (*Mirascapha*) *costatus* (Gabb). Stewart, 1927: 437–438, pl. 27, fig. 5. Turner, 1938:67, pl. 17, fig. 16. Vokes, 1939:109, pl. 16, figs. 29, 35. Givens, 1974:93–94.

Scaphander costatus (Gabb). Weaver, 1943:545, pl. 100, fig. 2; pl. 103, fig. 21. Weaver, 1953:29. Givens and Kennedy, 1979:88, table 3.

Primary Type Material. ANSP lectotype 4338, Tejon Formation s.l., near Martinez, California.

Molluscan Stage Range. "Martinez" through "Transition."

Geographic Distribution. San Diego, California through western Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 493. Shallow-marine (regressive) facies: CSUN locality 475.

Remarks. Only a few specimens were found in the Llajas Formation.

Family Philinidae Gray, 1850

Genus *Megistostoma* Gabb, 1864

Type Species. By monotypy, *Megistostoma striata* Gabb, 1864.

Megistostoma gabbianum (Stoliczka, 1868)

Figure 9r

Megistostoma striata Gabb, 1864:144, pl. 21, figs. 108a–b. Not *Bullaea striata* Deshayes, 1824:37, pl. 5, figs. 1–3.

Bullaea gabbiana Stoliczka, 1868:434 [new name for *Megistostoma striata* Gabb, 1864, preoccupied].

Philine (*Megistostoma*) *gabbi* Cossmann, 1895:127 [new name for *Megistostoma striata* Gabb, 1864, preoccupied].

Megistostoma gabbianum (Stoliczka). Stewart, 1927:441–442, pl. 26, figs. 1–2. Vokes, 1939:112, pl. 17, figs. 1–3. Givens and Kennedy, 1979:88, table 3.

Megistostoma caminoensis Hanna, 1927:330, pl. 57, figs. 9–10. Turner, 1938:68, pl. 20, fig. 15. Weaver, 1943:541, pl. 99, fig. 24.

Primary Type Material. ANSP holotype 4216 of *Megistostoma striata* Gabb, *Bullaea gabbiana* Stoliczka, and *Philine* (*Megistostoma*) *gabbi* Cossmann, Tejon Formation s.l., near Martinez, California.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 458. Shallow-marine (regressive) facies: CSUN locality 462.

Remarks. Only a few specimens were found in the Llajas Formation, and they occur as internal molds.

Class Bivalvia

Subclass Palaeotaxodonta

Order Nuculoida

Superfamily Nuculacea

Family Nuculidae Gray, 1824

Genus *Acila* H. & A. Adams, 1858

Type Species. By subsequent designation (Stoliczka, 1871), *Nucula divaricata* Hinds, 1843.

Subgenus *Truncacila* Schenck, *in* Grant and Gale, 1931

Type Species. By original designation *Nucula castrensis* Hinds, 1843.

Acila (*Truncacila*) *decisa* (Conrad, 1855)

Figure 10a

Nucula decisa Conrad, 1855:11–12; 1857:pl. 3, fig. 19.
Acila gabbiana Dickerson, 1916:481, pl. 36, fig. 1. Anderson and Hanna, 1925:176, pl. 9, fig. 12.
Nucula (*Acila*) *stillwaterensis* Weaver and Palmer, 1922:6, pl. 8, fig. 8.
Acila lajollaensis Hanna, 1927:270, pl. 25, figs. 1, 3, 5, 7–8, 12, 15.
Acila (*Truncacila*) *decisa* (Conrad). Schenck, 1936:53–56, pl. 3, figs. 1–9, 11–15; pl. 4, figs. 1–2; text figure 7 (22, 23, 25). Turner, 1938:41–42, pl. 5, figs. 2–3. Vokes, 1939:41, pl. 1, figs. 7–8. Weaver, 1943:22–23, pl. 6, figs. 1, 4, 8; pl. 7, figs. 8–9. Givens, 1974:38, pl. 1, fig. 1. Zinsmeister, 1974:67–68, pl. 6, fig. 3. Squires, 1977:table 1. Moore, 1983:A10, pl. 1, fig. 14. Zinsmeister, 1983a:table 1.

Primary Type Material. UCMP neotype 31132, Ardath Shale, UCMP locality 5062.

Molluscan Stage Range. "Martinez" through upper Eocene (*Turritella schencki delaguerrae* Zone of Kleinpell and Weaver, 1963).

Geographic Distribution. San Diego, California through Kamchatka, Alaska.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 467.

Remarks. Specimens are abundant at locality 467. Preservation is excellent. The specimens are disarticulated, but the valves constitute a growth series.

Superfamily Nuculanacea

Family Nuculanidae H. and A. Adams, 1858

Genus *Nuculana* Link, 1807

Type Species. By original designation, *Arca rostrata* Chemnitz, 1784 [=*Arca pernula* Müller, 1776].

Subgenus *Saccella* Woodring, 1925

Type Species. By original designation, *Arca fragilis* Chemnitz, 1784.

Nuculana (*Saccella*) *gabbii* (Gabb, 1864)

Figure 10b

Not *Leda protexta*? Gabb, 1860:303, pl. 48, fig. 23.
Leda protexta? Gabb, 1864:199 (in part), pl. 26, fig. 185.
Nuculana gabbii Conrad, 1866:3 [*nomen nudum*].
Leda gabbii Conrad. Gabb, 1869:197 [new name for *Leda protexta*? Gabb, 1864, misidentified]. Stanton, 1896:1041, pl. 64, fig. 8. Waring, 1917:76, pl. 13, fig. 6. Dickerson, 1915:pl. 1, fig. 1; 1916, pl. 36, fig. 3. Clark and Woodford, 1927:85–86, pl. 14, fig. 2. Clark, 1929:pl. 3, fig. 12.
Leda vaderensis Dickerson, 1915:52, pl. 1, fig. 3.
Leda vogdesi Anderson and Hanna, 1925:177–179, pl. 2, figs. 8–9.
Saccella gabbii (Gabb). Stewart, 1930:55–58, pl. 7, fig. 3 [not pl. 10, fig. 4. =*N.* (*S.*) *alaeformis fide* Zinsmeister, 1974]. Weaver, 1953:28.
Nuculana (*Saccella*) *gabbii* (Gabb). Vokes, 1939:41–42. Kleinpell and Weaver, 1963:195, pl. 28, fig. 1. Givens, 1974:39, pl. 1, fig. 3. Moore, 1983:A16, pl. 2, figs. 7–8.
Nuculana (*Calorhadia*) *gabbii* (Gabb). Zinsmeister, 1974:69–70, pl. 6, fig. 7; 1983a, pl. 1, fig. 3.

Primary Type Material. ANSP lectotype 4476 of *Leda gabbii* Gabb, 1869, Tejon Formation s.l., Martinez, California.

Molluscan Stage Range. "Martinez" through upper Eocene (*Turritella schencki delaguerrae* Zone of Kleinpell and Weaver, 1963).

Geographic Distribution. Simi Valley, California through Kamchatka, Alaska.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 467.

Remarks. Only five disarticulated valves were found in the Llajas Formation. There is considerable variation in the amount of elongation of the rostrum in these specimens, with the illustrated specimen (Fig. 10b) showing the most.

According to Zinsmeister (1974), Stewart (1930) somehow confused *N.* (*S.*) *gabbii* with *N.* (*S.*) *alaeformis* and designated *N.* (*S.*) *alaeformis* (pl. 10, fig. 4) as the lectotype (ANSP 4476) of *N.* (*S.*) *gabbii.*

Subclass Pteriomorpha

Order Arcoida

Superfamily Limnopsacea

Family Glycymerididae Newton, 1922

Subfamily Glycymeridinae Newton, 1922

Genus *Glycymeris* da Costa, 1778

Type Species. By tautonymy, *Arca orbicularis* da Costa, 1778 [=*Arca glycymeris* Linné, 1758].

Subgenus *Glycymeris* s.s.

Glycymeris (*Glycymeris*) *rosecanyonensis* Hanna, 1927

Figure 10c

Glycymeris rosecanyonensis Hanna, 1927:273–274, pl. 27, figs. 4–5, 9, 11. Clark, 1929:pl. 6, fig. 8. Givens and Kennedy, 1979:tables 1, 3.
Glycymeris (*Glycymeris*) *rosecanyonensis* Hanna. Givens, 1974:42. Moore, 1983:A49–A50, pl. 10, figs. 12–13.
Glycymeris (*Glycymerisa*) *rosecanyonensis* Hanna. Squires, 1977:table 1.

Primary Type Material. UCMP holotype 30989, Ardath Shale, UCMP locality 3990.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego through lower Piru Creek, southern California.

Local Occurrence. Shallow-marine (transgressive) facies:

CSUN localities 373, 467, 471d, 520. Shallow-marine (regressive) facies: CSUN localities 476, 489, 512a, 512b.

Remarks. Only a few specimens of this small-sized bivalve were found in the Llajas Formation.

Subgenus *Glycymerita* Finlay and Marwick, 1937

Type Species. By original designation, *Glycymeris concava* Marshall, 1917.

Glycymeris (*Glycymerita*) *sagittata* (Gabb, 1864)

Figure 10d

Axinaea (*Limopsis*?) *sagittata* Gabb, 1864:197–198, pl. 31, figs. 267, 267a.

Glycimeris hannibali Dickerson, 1916:483, pl. 36, figs. 8a–b.

Glycymeris sagittatus (Gabb). Dickerson, 1916:pl. 36, figs. 5a–b.

Glycymeris sagittata (Gabb). Anderson and Hanna, 1925: 181–182, pl. 1, fig. 6. Stewart, 1930:71–73, pl. 12, fig. 10; 1946:pl. 12, fig. 3. Vokes, 1939:45–46, pl. 1, figs. 18–20. Weaver, 1943:54–55, pl. 9, figs. 17–18; pl. 11, fig. 15. Kleinpell and Weaver, 1963:196–197, pl. 28, fig. 10; pl. 29, figs. 1–2.

Glycimeris sagittatus (Gabb). Turner, 1938:43–44, pl. 6, figs. 1–3.

Glycymeris (*Glycymerita*) *sagittata* (Gabb). Givens, 1974: 42–43. Squires, 1977:table 1. Moore, 1983:A54–A55, pl. 12, fig. 17.

Primary Type Material. ANSP lectotype 4422, Tejon Formation, near Fort Tejon (N ½ of section 29, T 10 N, R 19 W, Kern County, California).

Molluscan Stage Range. "Capay" through "Tejon," Oligocene?.

Geographic Distribution. Simi Valley, California through southwestern Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 374, 444, 500, 704.

Remarks. Specimens are uncommon in the Llajas Formation, and leaching has obscured some of the exterior sculpture.

Order Mytiloida

Superfamily Mytilacea

Family Mytilidae Rafinesque, 1815

Genus *Brachidontes* Swainson, 1840

Type Species. By monotypy, *Modiola sulcata* Lamarck, 1819 (not 1805) [=*Mytilus citrinus* Röding, 1798, =*Arca modiolus* Linné, 1767].

Subgenus *Brachidontes* s.s.

Brachidontes (*Brachidontes*) *cowlitzensis* (Weaver and Palmer, 1922)

Figure 10e

Modiola ornata Gabb, 1864:184–185, pl. 24, fig. 166.

Not *Mytilus ornatus* Orbigny, 1843:283, pl. 342, figs. 10–12.

Modiolus ornatus Gabb. Arnold, 1907:pl. 38, fig. 4.

Brachydontes ornatus (Gabb). Anderson and Hanna, 1925: 188, pl. 3, fig. 4.

Modiolus (*Brachydontes*) *ornatus* Gabb. Clark and Woodford, 1927:89, pl. 14, fig. 10. Clark, 1929:pl. 3, fig. 6.

Modiolus (*Brachydontes*) *cowlitzensis* Weaver and Palmer, 1922:16–17, pl. 9, fig. 19 [new name for *Modiola ornata* Gabb, 1864, preoccupied].

Brachidontes cowlitzensis? (Weaver and Palmer). Stewart, 1930:100–103, pl. 8, fig. 12.

Brachidontes cowlitzensis (Weaver and Palmer). Turner, 1938: 45–46, pl. 6, figs. 7–8. Kleinpell and Weaver, 1963:197, pl. 29, fig. 3. Wolfe, 1977:3. Givens and Kennedy, 1979: table 2.

Volsella (*Brachidontes*) *cowlitzensis* (Weaver and Palmer). Weaver, 1943:113–114, pl. 26, fig. 4.

Brachidontes (*Brachidontes*) *cowlitzensis* (Weaver and Palmer). Givens, 1974:43. Squires, 1977, table 1. Moore, 1983: A66–A67, pl. 17, fig. 1.

Primary Type Material. ANSP lectotype 4450 of *Modiola ornata* Gabb, Domengine? Formation, Martinez, California. CAS holotype 7406 of *Modiolus* (*Brachydontes*) *ornatus* Weaver and Palmer, Cowlitz Formation, UW locality 329.

Molluscan Stage Range. "Meganos" through lower Oligocene (*Turritella variata lorenzana* Zone of Kleinpell and Weaver, 1963).

Geographic Distribution. San Diego, California through Gulf of Alaska.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 455, 466, 471d, 492, 514, 528. Shallow-marine (regressive) facies: CSUN locality 512d.

Remarks. Specimens are most common at locality 371, where they are fragile, well-preserved single valves.

Superfamily Pinnacea

Family Pinnidae Leach, 1819

Genus *Pinna* Linné, 1758

Type Species. By subsequent designation (Children, 1823), *Pinna rudis* Linné, 1758.

Pinna lewisi Waring, 1917

Figure 10f

Pinna lewisi Waring, 1914:785; 1917:94, pl. 15, fig. 24.

Pinna (*Pinna*) *lewisi* Waring. Moore, 1983:A79, pl. 21, fig. 10.

Primary Type Material. CAS/SU holotype 5194, Llajas Formation, SU locality 2696.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through south end of San Joaquin Valley, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 548. Shallow-marine (regressive) facies: CSUN locality 475.

Remarks. Only six specimens were found, and five are from locality 475. Preservation is mostly as internal molds, and four specimens are articulated. The following supplementary comments are based on an examination of the holotype. It is mostly an internal mold with 95 percent of the shell missing. There are 16 to 18, very closely spaced radial ribs and about nine comarginal ribs on each valve. The holotype and the Llajas specimens have a median sulcus.

Pinna llajasensis Squires, 1983a

Figure 10g

Pinna n. sp. Vokes, 1939:50, pl. 2, fig. 14. Moore, 1983:A79, pl. 22, fig. 1.

Pinna llajasensis Squires, 1983a:359–360, fig. 21.

Primary Type Material. UCLA holotype 59196, Llajas Formation, CSUN locality 458.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 458.

Remarks. Only two specimens were found and these are from the "Stewart bed." Both are articulated, incomplete specimens (Squires, 1983). The holotype is the figured specimen (Fig. 10g).

P. llajasensis differs from *P. lewisi* in having fewer radial ribs (only 12) which are more widely spaced. *P. llajasensis* also has no comarginal sculpture.

In the original description by Vokes (1939) of his *Pinna* n. sp., he mentioned that his specimen (UCMP 32595, Domengine Formation, UCMP locality 2287) had 23 ribs. The following supplementary comments are based on an examination of the holotype. There are 12 ribs per single valve and about 23 for the entire surface including both valves.

Order Pterioida

Suborder Pteriina

Superfamily Pteriacea

Family Malleidae Lamarck, 1819

Genus *Nayadina* Munier-Chalmas, 1864

Type Species. By monotypy, *Nayadina herberti* Munier-Chalmas, 1864.

Subgenus *Exputens* Clark, 1934

Type Species. By subsequent designation (Vokes, 1939), *Exputens llajasensis* Clark, 1934.

Nayadina (*Exputens*) *llajasensis* (Clark, 1934)

Figures 10h–i

Exputens llajasensis Clark, 1934:270–271, pl. 37, figs. 11–18. Vokes, 1939:51.

Nayadina (*Exputens*) *llajasensis* (Clark). Givens, 1974:44, pl. 1, fig. 9. Moore, 1983:A86–A87, pl. 26, figs. 10, 13.

Primary Type Material. UCMP holotype 32391, UCMP paratypes 32390, 32393, Llajas Formation, UCMP locality 7004 = CSUN locality 374.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Simi Valley through Pine Mountain area, southern California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 445, 447, 471b, 473, 479, 480.

Remarks. Specimens occur mainly in the "Stewart bed" at and in the vicinity of locality 374. In addition, a few specimens were found in glauconitic siltstone at locality 473, about 14 m above the "Stewart bed" at the type section. The bed that locality 473 occurs in probably represents a shallow-marine (transgressive) facies bed that interfingers with the outer shelf and slope facies. At localities 374 and 473, a few of the specimens are articulated.

Superficially, this genus may resemble *Hiatella,* but *Hiatella* is a heterodont with two weak teeth whereas *Nayadina* lacks hinge teeth. A view of the hinge of *N.* (*E.*) *llajasensis* is given in Figure 10i.

Superfamily Pectinacea

Family Spondylidae Gray, 1826

Genus *Spondylus* Linné, 1758

Type Species. By subsequent designation (Schmidt, 1818), *Spondylus gaederopus* Linné, 1758.

Spondylus carlosensis Anderson, 1905

Figure 10j

Spondylus carlosensis Anderson, 1905:194, pl. 13, fig. 1. Arnold, 1910:pl. 2, figs. 6–7. Dickerson, 1915:pl. 1, fig. 7. Anderson and Hanna, 1925:189–190, text figure 10. Vokes, 1939:57, pl. 3, figs. 10, 13. Kleinpell and Weaver, 1963: 199, pl. 31, fig. 6.

Primary Type Material. CAS holotype 56, Domengine Formation, west and north of Coalinga, NW ¼ of section 35, T 20 S, R 14 E, Fresno County, California.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 438, 444, 525.

Remarks. Specimens are relatively uncommon in the Llajas Formation, and they consist of fragments of single valves. The most complete and best preserved specimens are from locality 374.

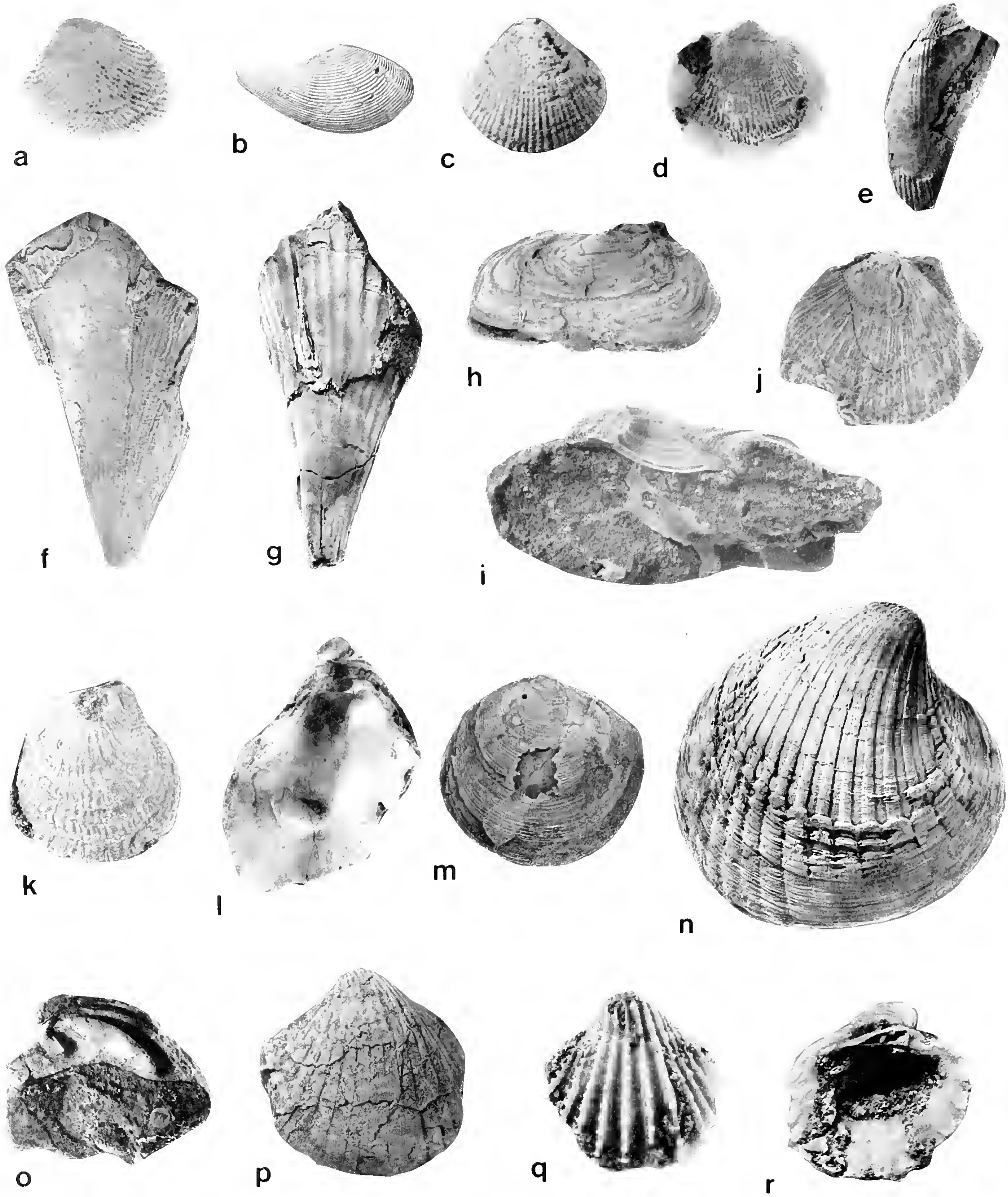

Figure 10. Llajas Formation bivalves. **a.** *Acila* (*Truncacila*) *decisa* (Conrad, 1855), right valve, LACMIP hypotype 6554, CSUN loc. 467, ×3.5. **b.** *Nuculana* (*Saccella*) *gabbi* (Gabb, 1864), right valve, UCLA hypotype 59279, CSUN loc. 467, ×3. **c.** *Glycymeris* (*Glycymeris*) *rosecanyonensis* Hanna, 1927, right? valve, LACMIP hypotype 6565, CSUN loc. 489, ×4.5. **d.** *Glycymeris* (*Glycymerita*) *sagittata* (Gabb, 1864), right? valve, LACMIP hypotype 6566, CSUN loc. 371, ×2. **e.** *Brachidontes* (*Brachidontes*) *cowlitzensis* (Weaver and Palmer, 1922), right valve, LACMIP hypotype 6567, CSUN loc. 371, ×1.5. **f.** *Pinna lewisi* (Waring, 1917), internal mold of right? valve, LACMIP hypotype

Superfamily Anomiacea

Family Anomiidae Rafinesque, 1815

Genus *Anomia* Linné, 1758

Type Species. By subsequent designation (Schmidt, 1818), *Anomia ephippium* Linné, 1758.

Anomia mcgoniglensis Hanna, 1927

Figure 10k

Anomia mcgoniglensis Hanna, 1927:278, pl. 31, figs. 1, 2, 5, 7. Turner, 1938:46, pl. 6, figs. 4–6. Weaver, 1943:100, pl. 22, figs. 4–5. Givens and Kennedy, 1976:974, pl. 4, figs. 13–16. Givens and Kennedy, 1979:table 2.

Primary Type Material. UCMP syntypes 31009–31010, Delmar Formation, UCMP locality 3981.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 438.

Remarks. Only three specimens were found in the Llajas Formation. They occur as single valves unattached to any hard substrate.

Suborder Ostreina

Superfamily Ostreacea

Family Ostreidae Rafinesque, 1815

Subfamily Ostreinae Rafinesque, 1815

Genus *Ostrea* Linné, 1758

Type Species. By subsequent designation (ICZN opin. 94 and 356), *Ostrea edulis* Linné, 1758.

Ostrea idriaensis Gabb, 1869

Figure 10l

Ostrea idriaensis Gabb, 1869:203, pl. 33, figs. 103b–d; pl. 34, figs. 103, 103a. Waring, 1917:78–79, pl. 13, fig. 10. Hanna, 1927:276, pl. 30, figs. 1–2; pl. 31, figs. 3–4. Stewart, 1930:126–127, pl. 8, fig. 3; pl. 17, fig. 1. Vokes, 1935:291–304, pl. 22–24. Merriam and Turner, 1937:table 2. Turner, 1938:46, pl. 6, fig. 9. Weaver, 1943:78–79, pl. 15, fig. 5. Givens, 1974:44. Givens and Kennedy, 1979:tables 2, 4. Not *Ostrea haleyi* Hertlein, 1933:277–282, pl. 18, figs. 5–6.

Primary Type Material. MCZ lectotype 15048, Domengine Formation, about 3 km east of the Hacienda at New Idria, N ½ of section 15, T 17 S, R 12 E, Priest Valley quadrangle, San Benito County, California.

Molluscan Stage Range. "Capay" through "Tejon."

Geographic Distribution. San Diego, California through western Washington.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 458, 468a, 478, 485, 548.

Remarks. Ostreid fragments occur at localities 502, 503, and 542 in the interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies, but generic identifications could not be made. Similarly, ostreid fragments occur at localities 463 and 526 in the lower part of the shallow-marine (transgressive) facies, but generic identifications could not be made. Ostreid fragments and single valves of *O. idriaensis* are fairly common in the uppermost part of the "Stewart bed." The figured specimen (Fig. 10l) is one of the largest specimens.

Subclass Heterodonta

Order Veneroida

Superfamily Lucinacea

Family Lucinidae Fleming, 1828

Subfamily Milthinae Chavan, 1969

Genus *Claibornites* Stewart, 1930

Type Species. By original designation, *Lucina rotunda* Lea, 1833.

Claibornites diegoensis (Dickerson, 1916)

Figure 10m

Lucina diegoensis Dickerson, 1916:484, pl. 37, figs. 1a–b.
Claibornites diegoensis (Dickerson). Givens, 1974:45–46, pl. 1, fig. 15.

Primary Type Material. UCMP holotype 11788, Ardath Shale, UCMP locality 2226.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Pine Mountain area, southern California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 445.

Remarks. At locality 374, only two single valves were found. An articulated specimen was found at locality 445.

6568, CSUN loc. 475, ×1. **g.** *Pinna llajasensis* Squires, 1983a, internal mold of right valve, UCLA holotype 59196, CSUN loc. 458, ×0.5. **h and i.** *Nayadina* (*Exputens*) *llajasensis* (Clark, 1934). All parts from CSUN loc. 374. **h,** right valve, LACMIP topotype and hypotype 6569, ×1. **i,** hinge line, LACMIP topotype and hypotype 6570, ×1.4. **j.** *Spondylus carlosensis* Anderson, 1905, left valve, LACMIP hypotype 6571, CSUN loc. 374, ×1. **k.** *Anomia mcgoniglensis* Hanna, 1927, right valve, UCLA hypotype 59280, CSUN loc. 438, ×1.5. **l.** *Ostrea idriaensis* Gabb, 1869, left valve, LACMIP hypotype 6572, CSUN loc. 458, ×0.5. **m.** *Claibornites diegoensis* (Dickerson, 1916), right valve, UCLA hypotype 59281, CSUN loc. 374, ×1. **n and o.** *Venericardia* (*Pacificor*) *hornii calafia* Stewart, 1930. All parts from CSUN loc. 374 and ×0.5. **n,** left valve, LACMIP topotype and hypotype 6573. **o,** right valve hinge line, LACMIP topotype and hypotype 6574. **p.** *Venericardia* (*Pacificor*) *aragonia joaquinensis* (Vokes, 1939), UCMP hypotype 37433, UCMP loc. 7193 = CSUN loc. 702, ×1. **q and r.** *Glyptoactis domenginica* (Vokes, 1939), LACMIP hypotype 6575, CSUN loc. 371, ×2.5. **q,** left valve exterior. **r,** left valve interior.

Superfamily Carditacea

Family Carditidae Fleming, 1820

Subfamily Venericardiinae Chavan, 1969

Genus *Venericardia* Lamarck, 1801

Type Species. By subsequent designation (Schmidt, 1818), *Venericardia imbricata* Lamarck, 1801.

Subgenus *Pacificor* Verastegui, 1953

Type Species. By original designation, *Venericardia* (*Pacificor*) *mulleri* Verastegui, 1953.

Venericardia (*Pacificor*) *hornii calafia* Stewart, 1930

Figures 10n–o

Venericardia hornii calafia Stewart, 1930:168–170, pl. 11, fig. 2. Turner, 1938:50, pl. 14, fig. 4. Weaver, 1943:134–135, pl. 28, figs. 6–7; pl. 31, figs. 4–5.

Venericardia (*Pacificor*) *calafia* Stewart. Verastegui, 1953: 28–30, pl. 15, figs. 3–5, 7; pl. 16, figs. 1–3; pl. 17, figs. 1–2.

Venericardia (*Pacificor*) *hornii calafia* Stewart. Givens, 1974: 47, pl. 4, fig. 1. Saul, 1983:74, 76, pl. 2, figs. 9, 16–17.

Primary Type Material. UCMP holotype 31450, Llajas Formation, UCMP locality 7004 = CSUN locality 374.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 445, 451, 458, 494, 548, 704.

Remarks. A growth series of this taxon was found at locality 374. At this locality, most of the specimens are single valves, but there are several well-preserved, large-sized articulated specimens. At locality 548, only a single articulated juvenile was found.

Saul (1983) considered *V.* (*P.*) *oregonensis* Verastequi from the Lookingglass Formation of southwestern Oregon to be an immature *V.* (*P.*) *hornii calafia*. *V.* (*P.*) *hertleini* Verastequi is also probably *V.* (*P.*) *hornii calafia* (Saul, 1984, pers. commun.).

Venericardia (*Pacificor*) *aragonia joaquinensis* (Vokes, 1939)

Figure 10p

Venericardia aragonia var. Turner, 1938:49, pl. 13, figs. 6–9.

Megacardita (*Venericor*) *hornii joaquinensis* Vokes, 1939: 69–70, pl. 8, figs. 1–2; pl. 9, figs. 1–2.

Venericardia (*Leuroactis*) *schencki* Verastegui, 1953:50–51, pl. 4, figs. 6–8.

Venericardia (*Leuroactis*) *alisoensis* Verastegui, 1953:52–53, pl. 10, figs. 1–3.

Venericardia (*Leuroactis*) *joaquinensis* (Vokes). Verastegui, 1953:60–61, pl. 11, figs. 1–4; pl. 12, figs. 4–6.

Venericardia (*Leuroactis*) *vokesi* Verastegui, 1953:61–62, pl. 14, figs. 1–3.

Venericardia (*Pacificor*) *aragonia joaquinensis* (Vokes). Saul, 1983:pl. 2, figs. 7–8.

Primary Type Material. UCMP holotype 15616, Avenal Formation, UCMP locality 4170; UCMP paratype 15617, Avenal Formation, UCMP locality 4169; UCMP paratype 15618, Avenal Formation, UCMP locality A-819.

Molluscan Stage Range. Uppermost "Capay" through "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 452, 700, 702, 706.

Remarks. Most specimens in the Llajas Formation are fragments of single valves. Extraction of identifiable specimens from the rock is usually difficult. At locality 700, only a single juvenile was found.

The synonymy of this taxon is based on work by Saul (1984, pers. commun.). *V.* (*P.*) *a. smileyi* (Vokes) may be conspecific with *V.* (*P.*) *a. joaquinensis,* but more taxonomic work is needed to resolve the matter (Saul, 1984, pers. commun.).

The figured specimen (Fig. 10p) is UCMP hypotype 37433 from UCMP locality 7193 = CSUN locality 702. It is the same specimen as used by Saul (1983, pl. 2, fig. 8).

Verastegui (1953) reported *V. (L.) schencki* from the Santa Susana Formation, but his vague locality information makes it impossible to know exactly where he collected his specimens.

The presence of *V.* (*P.*) *a. joaquinensis* in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation refines the lower limit of the molluscan stage range of this taxon as uppermost "Capay."

Subfamily Carditesinae Chavan, 1969

Genus *Glyptoactis* Stewart, 1930

Type Species. By original designation, *Venericardia hadra* Dall, 1903.

Subgenus *Glyptoactis* s.s.

Glyptoactis (*Glyptoactis*) *domenginica* (Vokes, 1939)

Figures 10q–r

Venericardia (*Glyptoactis*?) *domenginica* Vokes, 1939:66, pl. 5, figs. 7–9.

Venericardia (*Glyptoactis*) *domenginica* Vokes. Verastegui, 1953:43–44, pl. 13, fig. 1.

Glyptoactis domenginica (Vokes). Givens, 1974:47. Squires, 1977:table 1. Givens and Kennedy, 1979:tables 1, 3.

Primary Type Material. UCMP holotype 15611, Domengine Formation, UCMP locality A-1219; UCMP paratypes 15612–15613, Tejon Formation, UCMP locality A-1003.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego through Mt. Diablo, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 507, 518, 529a.

Remarks. This taxon is confined to the shallow-marine (transgressive) facies of the Llajas Formation. Specimens are most abundant at locality 371 where there is a growth series. Preservation is excellent, showing the angular nodes on the ribs. No articulated specimens were found.

This species is placed in the subgenus *Glyptoactis* s.s. because the radial ribs are not tripartite. It is the oldest species of this subgenus.

Superfamily Crassatellacea

Family Crassatellidae Férussac, 1822

Subfamily Crassatellinae Férussac, 1822

Genus *Crassatella* Lamarck, 1799

Type Species. By subsequent designation (Schmidt, 1818), *Mactra cygnaea* Lamarck, 1799 (not Chemnitz, 1782) [=*C. gibba* Lamarck, 1801, =*Venus ponderosa* Gmelin, 1791].

Crassatella uvasana Conrad, 1855

Figures 11a–g

Crassatella uvasana Conrad, 1855:9; 1857, pl. 2, fig. 5. Gabb, 1864:214–215, pl. 32, fig. 284. Stewart, 1930:141–143, pl. 12, fig. 9. Turner, 1938:47–48. Givens, 1974:48.

Crassatella alta Conrad, 1855:9; 1857:321 [not Conrad, 1832: 21, pl. 7].

Crassatella grandis Gabb, 1864:181, pl. 24, fig. 163; 1869: 189.

Astarte semidentata Cooper, 1894:48, pl. 3, figs. 44–45.

Crassatellites grandis (Gabb). Arnold, 1910:13, pl. 2, figs. 10, 10a, pl. 3, fig. 14. Dickerson, 1915:80, pl. 1, fig. 8; pl. 2, figs. 1a–b [not Waring, 1917:74, pl. 12, fig. 16 = *Crassatella branneri fide* Nelson, 1925:410].

Crassatellites uvasana (Conrad). Arnold and Hannibal, 1913: 569. Dickerson, 1915:80, pl. 2, fig. 2. Waring, 1917:59, pl. 8, fig. 10.

Crassatellites mathewsonii (Gabb). Dickerson, 1916:pl. 36, figs. 9a–b (probably *C. semidentata* (Cooper) *fide* Turner, 1938:47–48).

Crassatellites uvasanus (Conrad). Anderson and Hanna, 1925: 172–174, pl. 4, figs. 2–3, text figure 7.

Crassatellites semidentata (Cooper). Hanna, 1927:282, pl. 35, figs. 1–2.

Crassatella semidentata (Cooper). Turner, 1938:47–48.

Crassatella uvasana semidentata (Cooper). Vokes, 1939:64–65, pl. 4, figs. 4, 6, 8, 10, 12. Givens, 1974:48. Squires, 1977:table 1. Givens and Kennedy, 1979:tables 1, 3.

Crassatella uvasana uvasana (Conrad). Givens and Kennedy, 1979:table 4.

Primary Type Material. Holotype undetected, USNM collection, Tejon Formation, Grapevine Canyon, Tejon quadrangle, Kern County, California.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 444, 445, 447, 458, 471c, 481, 488, 494. Outer shelf and slope channel: CSUN locality 541.

Remarks. Ninety-six specimens were found, and most occur as single valves. Twelve specimens are articulated. A single, abraded fragment was found at the base of a turbidite-filled channel at locality 541. Numerous well-preserved specimens of *C. uvasana* occur in the "Stewart bed" at localities 374 and 444. Heights range from 20 to 90 mm at locality 374 and from 20 to 65 mm at locality 444. There is a growth series at both localities. Many of the juvenile specimens and a few of the adult specimens are articulated at both localities. For the disarticulated specimens, the ratio of right valves to left valves is approximately 1:1. Based on criteria listed by Fagerstrom (1964), the *C. uvasana* specimens at these "Stewart bed" localities are clearly *in situ*.

There is a gradual change in the external appearance of the shells from juvenile to adult individuals at these localities (Figs. 11a–c). The juvenile specimens have higher and more prominent beaks, a less deep lunule, a less steep posterior dorsal slope, a more concave anterior dorsal margin, and a less obvious escutcheon on the left valve. The adult specimens have a more triangular shape and lower, more rounded beaks. The escutcheon on the right valve is much larger than that on the left. Intermediate-sized specimens (with a height of about 45 mm) are transitional between the two.

The comarginal ribbing is identical in both the juvenile and adult specimens. There are numerous very fine, closely spaced comarginal ribs. At regular intervals there are comarginal rugae. Upon decortication, especially in the beak areas, shell between the rugae has a tendency to chip off, leaving depressed areas outlined by the rugae. Only the adult specimens show cancellate sculpture along the ventral margins of the valves.

Interior shell features of juvenile and adult specimens of *C. uvasana* are identical (Figs. 11d–g). The resilifer extends halfway to the lower margin of the hinge plate and the pit is large. The anterior muscle scar is reniform, and the pallial line is deeply impressed. In both juvenile and adult specimens the right valve has the following features: anterior ventral margin of the hinge plate tends to be swollen and fits into a socket in the left valve; anterior cardinal is large, wedge-shaped, vertically below the beak, its upper end margining part of the resilifer; the floor of the lunule tends to wrap around the anterior cardinal in some specimens (Fig. 11f); posterior cardinal is weak; edge of the escutcheon is swollen and projects as a long ridge that fits into a socket in the left valve.

In both juvenile and adult specimens of *C. uvasana,* the left valve has the following features: posterior ventral margin of the hinge plate is slightly swollen; anterior and posterior cardinals are about equal in size; floor of lunule tends to wrap

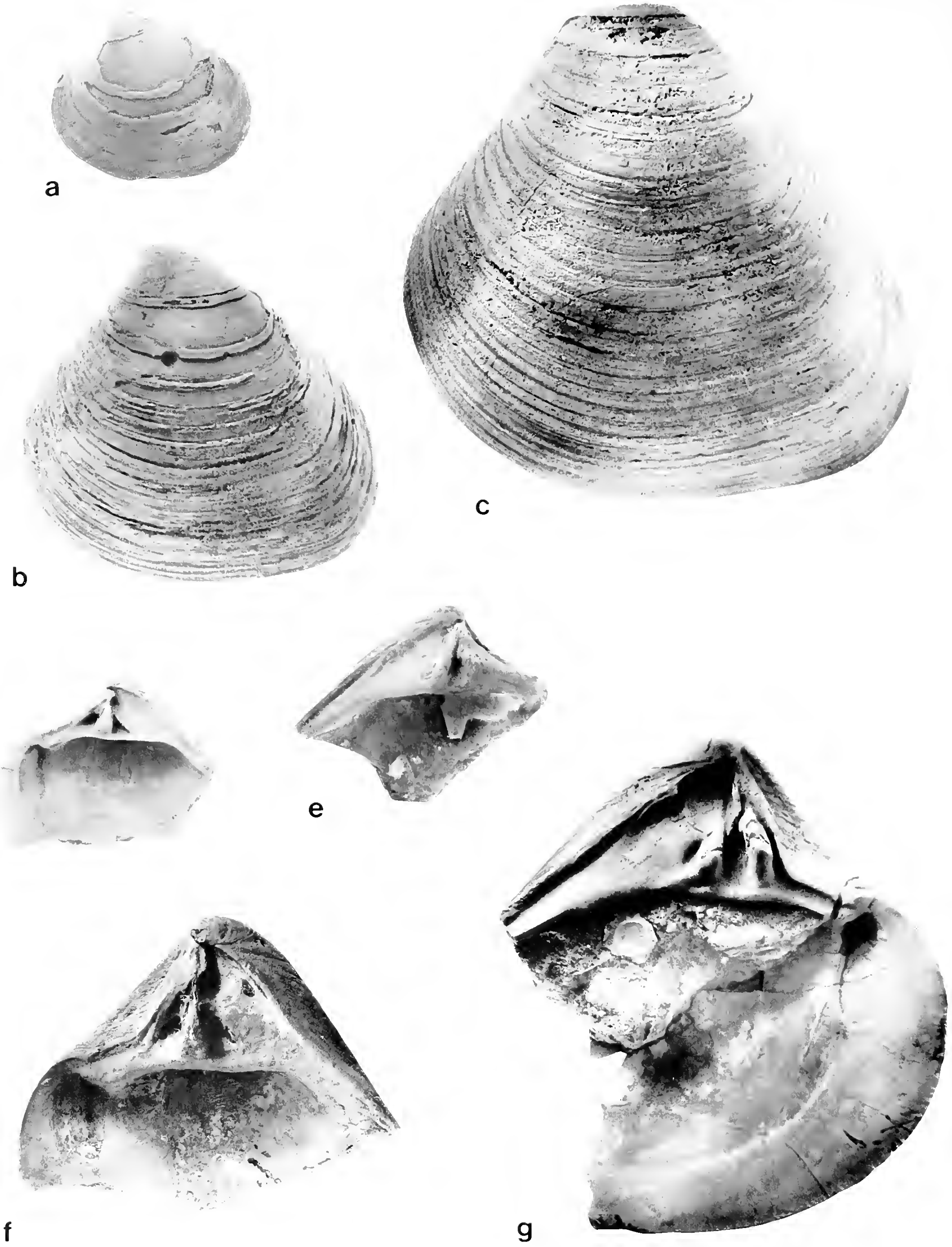

Figure 11. Llajas Formation bivalves (continued). **a through g.** *Crassatella uvasana* Conrad, 1855. All parts from CSUN loc. 374. **a,** left valve, LACMIP hypotype 6576, ×1. **b,** left valve, LACMIP hypotype 6577, ×1. **c,** left valve, LACMIP hypotype 6578, ×1. **d,** right valve interior of juvenile, LACMIP hypotype 6579, ×1. **e,** left valve hinge line of juvenile, LACMIP hypotype 6580, ×1.5. **f,** right valve hinge line of adult, LACMIP hypotype 6581, ×1. **g,** left valve interior of adult, LACMIP hypotype 6582, ×1.

around the anterior cardinal in some specimens, ventral margin of lunule tends to be swollen. In the left valve, as well as in the right valve, the posterior part of the hinge plate is largely occupied by a smooth surface without hinge structures.

If it had not been for the presence of a growth series, the juvenile specimens of *C. uvasana* would have been identified as *C. uvasana semidentata* (Cooper), and the adult specimens would have been identified as *C. uvasana*. Based on the transition of shell characters from the juvenile and adult, as well as the identical shell characters mentioned above, it is concluded that *C. uvasana semidentata* is an unjustified subspecies.

According to Hanna (1927) and Givens (1974), the nature of the beaks is the main distinguishing character between *C. uvasana* and *C. uvasana semidentata*. In actuality, this character can be used to distinguish juvenile from adult specimens of *C. uvasana* as the beaks become more incurved with age. It is interesting to note that if a juvenile specimen is placed on a flat surface, viewed laterally, and elevated along the venter (simulating additional shell material), the beak area then looks identical to that of an adult specimen.

The molluscan stage range of *C. u. semidentata* had been reported as "Domengine" through "Transition" and that of *C. uvasana* as "Tejon" (Givens, 1974). Because the two taxa are identical, the molluscan stage range of *C. uvasana* can be extended to "Domengine" through "Tejon."

Superfamily Cardiacea

Family Cardiidae Lamarck, 1809

Subfamily Cardiinae Lamarck, 1809

Genus *Acanthocardia* Gray, 1851

Type Species. By subsequent designation (Stoliczka, 1870), *Cardium aculeatum* Linné, 1758.

Subgenus *Schedocardia* Stewart, 1930

Type Species. By original designation, *Cardium hatchetigbeense* Aldrich, 1886.

Acanthocardia (*Schedocardia*) *brewerii* (Gabb, 1864)

Figures 12a–b

Cardium brewerii Gabb, 1864:173, pl. 24, fig. 155. Arnold, 1907:pl. 39, fig. 5. McLaughlin and Waring, 1915:fig. 14. Waring, 1917:pl. 14, fig. 9. Anderson and Hanna, 1925: 165–166, pl. 1, fig. 3. Clark, 1929:pl. 12, fig. 7.

Plagiocardium (*Schedocardia*) *brewerii* (Gabb). Stewart, 1930: 256–258, pl. 12, fig. 6. Turner, 1938:52–53, pl. 9, figs. 6–7. Vokes, 1939:75, pl. 11, figs. 1–4. Stewart, 1946:pl. 11, fig. 20.

Plagiocardium brewerii (Gabb). Merriam and Turner, 1937: table 2.

Loxocardium (*Schedocardia*) *brewerii* (Gabb). Weaver, 1943: 153–154, pl. 35, figs. 15, 16, 18; pl. 38, figs. 1, 9; pl. 104, fig. 12.

Cardium (*Trachycardium*) *brewerii brewerii* (Gabb). Kleinpell and Weaver, 1963:201–202, pl. 34, figs. 1–2.

Acanthocardia (*Schedocardia*) *brewerii* (Gabb). Givens, 1974: 48–49, pl. 1, fig. 17.

Acanthocardia brewerii (Gabb). Givens and Kennedy, 1979: table 4.

Primary Type Material. ANSP lectotype 4560, Tejon Formation, east of north end of Grapevine Canyon, Kern County, California.

Molluscan Stage Range. "Capay" through "Tejon."

Geographic Distribution. San Diego, California through southwestern Washington.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN localities 545, 702. Shallow-marine (transgressive) facies: CSUN localities 371, 374, 548, 704.

Remarks. This taxon is somewhat uncommon in the Llajas Formation. It is most common at locality 374 where it occurs as single valves. The largest specimens are also from this locality.

Subfamily Protocardiinae Keen, 1951

Genus *Nemocardium* Meek, 1876

Type Species. By subsequent designation (Sacco, 1899), *Cardium semiasperum* Deshayes, 1858.

Nemocardium linteum (Conrad, 1855)

Figure 12c

Cardium linteum Conrad, 1855:3, 9; 1857:pl. 2, fig. 1. Anderson and Hanna, 1925:166–167, pl. 3, fig. 3.

Cardium cooperii Gabb, 1864:172, pl. 24, figs. 154, 154a. Arnold, 1907:pl. 38, figs. 2–2a. Waring, 1917:pl. 13, fig. 3. Hanna, 1927:285, pl. 41, figs. 6–7.

Cardium dalli Dickerson, 1913:289, pl. 14, figs. 4a–c.

Cardium marysvillensis Dickerson, 1916:482 [new name for *Cardium dalli* Dickerson, 1913, preoccupied].

Cardium (*Protocardium*) *marysvillensis* Dickerson. Clark and Woodford, 1927:94, pl. 15, fig. 12.

Nemocardium linteum (Conrad). Stewart, 1930:275–277, pl. 8, fig. 6. Turner, 1938:52, pl. 10, fig. 10. Vokes, 1939:76–77, pl. 11, figs. 6, 9. Weaver, 1943:159–160, pl. 38, fig. 3; 1953:28. Stewart, 1946:pl. 11, fig. 19. Zinsmeister, 1974: 97–98, pl. 9, figs. 7–9; 1983a:pl. 2, fig. 7. Givens and Kennedy, 1979:table 4.

Cardium (*Nemocardium*) *linteum* Conrad. Kleinpell and Weaver, 1963:202, pl. 34, fig. 4.

Nemocardium (*Nemocardium*) *linteum* (Conrad). Givens, 1974:49. Squires, 1977:table 1.

Primary Type Material. USNM holotype 1834, Domengine Formation, near Martinez, California.

Molluscan Stage Range. "Martinez" through "Tejon."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 373, 374, 438, 444, 445, 458, 479, 488, 493, 513, 525, 548.

Remarks. This taxon is most common in the upper part of the shallow-marine (transgressive) facies. At locality 438, six specimens were found, one of which was articulated. In the "Stewart bed" at locality 374, 21 specimens were found and one was articulated.

Superfamily Solenacea

Family Solenidae Lamarck, 1809

Genus *Solena* Mörch, 1853

Type Species. By subsequent designation (Stoliczka, 1871), *Solen obliquus* Spengler, 1794.

Subgenus *Eosolen* Stewart, 1930

Type Species. By original designation, *Solen plagiaulax* Cossmann, 1906.

Solena (*Eosolen*) *novacularis* (Anderson and Hanna, 1928)

Figure 12d

Solen novacula Anderson and Hanna, 1925:147, pl. 6, fig. 9. Hanna, 1927:294, pl. 43, fig. 1.

Not *Solen novacula* Montagu, 1803:47.

Solen novacularis Anderson and Hanna, 1928:65–66 [new name for *Solen novacula* Anderson and Hanna, 1925, preoccupied].

Solena (*Eosolen*) *coosensis* Turner, 1938:62–63, pl. 9, figs. 1–2. Vokes, 1939:96, pl. 15, fig. 5. Givens, 1974:49–50, pl. 2, fig. 1.

Solena coosensis Turner. Weaver, 1943:229, pl. 52, fig. 16; pl. 53, fig. 13.

Solena novacularis (Anderson and Hanna). Givens and Kennedy, 1979:table 4.

Primary Type Material. CAS holotype 882 of *Solen novacula* Anderson and Hanna and of *Solen novacularis* Anderson and Hanna, Tejon Formation, CAS locality 792.

Molluscan Stage Range. Uppermost "Capay"?, "Domengine" through "Tejon."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 701? Shallow-marine (transgressive) facies: CSUN localities 374, 444, 445, 449, 458, 477, 494, 500.

Remarks. This species helps to characterize the "Stewart bed." At many localities of the "Stewart bed," and especially at locality 374, specimens are fairly common and many are articulated. A solenid at locality 701 may be this species.

A previously assigned "Capay" age (Turner, 1938; Givens, 1974) for the lower range limit of this species was based on occurrence in the "upper Umpqua" Formation of southwestern Oregon. The "upper Umpqua," however, is actually equivalent to both the "Capay" and "Domengine" "Stages" (Baldwin, 1974; Miles, 1981). A lower range limit of uppermost "Capay," nevertheless, is apparent because of the possible occurrence of this species in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation.

Superfamily Tellinacea

Family Tellinidae Blainville, 1814

Subfamily Macominae Olsson, 1961

Genus *Macoma* Leach, 1819

Type Species. By monotypy, *Macoma tenera* Leach, 1819 [=*Tellina calcarea* Gmelin, 1791].

Macoma rosa Hanna, 1927

Figure 12e

Macoma rosa Hanna, 1927:292, pl. 41, figs. 2–5, 8. Clark, 1929:pl. 6, fig. 15. Givens and Kennedy, 1979:table 1.

Primary Type Material. UCMP holotype 31094, Ardath Shale, UCMP locality 3993; UCMP paratype 31095, Ardath Shale, UCMP locality 5089; UCMP paratypes 31096–31097, Ardath Shale, UCMP locality 5085.

Molluscan Stage Range. "Domengine."

Geographic Distribution. San Diego through Simi Valley, California.

Local Occurrence. Shallow-marine (regressive) facies: CSUN localities 462, 489, 512a, 512d, 544.

Remarks. This taxon helps to characterize the shallow-marine (regressive) facies. Specimens are usually few in number and preserved as external and internal molds of articulated individuals.

Family Psammobiidae Fleming, 1828

Subfamily Psammobiinae Fleming, 1828

Genus *Gari* Schumacher, 1817

Type Species. Pending decision by the ICZN, *Gari vulgaris* Schumacher, 1817 (=*Solen amethystus* Wood, 1818).

Gari cf. *G. eoundulata* Vokes, 1939

Figure 12f

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 471d.

Remarks. Specimens are relatively rare in the Llajas Formation. They are preserved as internal molds of single valves, making species identification impossible.

Superfamily Veneracea

Family Veneridae Rafinesque, 1815

Subfamily Pitarinae Stewart, 1930

Genus *Callista* Poli, 1791

Type Species. By subsequent designation (Meek, 1876), *Venus chione* Linné, 1758.

Subgenus *Costacallista* Palmer, 1927

Type Species. By original designation, *Venus erycina* Linné, 1758.

Callista (*Costacallista*) cf. *C.* (*C.*) *hornii* (Gabb, 1864)

Figure 12g

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 373, 465, 466, 467, 704.

Remarks. A few specimens were found as single valves. Hinge-line details were imperfectly preserved, hence a certain species identification could not be made.

Genus *Callocardia* A. Adams, 1864

Type Species. By monotypy, *Callocardia guttata* A. Adams, 1864.

Subgenus *Nitidavenus* Vokes, 1939

Type Species. By original designation, *Cytherea nitida* Deshayes, 1858.

Callocardia (*Nitidavenus*) *tejonensis* (Waring, 1914)

Figure 12h

Isocardia tejonensis Waring, 1914:784–785; 1917:93, pl. 15, fig. 14.
cf. "*Isocardia tejonensis*" Waring. Turner, 1938:58, pl. 11, figs. 1–4.
Nitidavenus tejonensis (Waring). Vokes, 1939:83–84, pl. 12, figs. 11, 13–16.

Primary Type Material. SU holotype 189, SU paratypes 5188–5190, Llajas Formation, SU locality 2696.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. Simi Valley, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 372.

Remarks. Only four single valves were found in the Llajas Formation.

Genus *Pitar* Römer, 1857

Type Species. By monotypy, *Venus tumens* Gmelin, 1791.

Subgenus *Calpitaria* Jukes-Browne, 1908

Type Species. By original designation, *Cytherea sulcataria* Deshayes, 1824.

Pitar (*Calpitaria*) *uvasanus* (Conrad, 1855).

Figures 12i–j

Meretrix uvasana Conrad, 1855:9; 1857:pl. 2, fig. 3. Gabb, 1864:163–164, pl. 30, fig. 248.
Meretrix tejonensis Dickerson, 1915:53–54, pl. 3, figs. 3a–b, not 2a–b. [Unjustified new name for *Meretrix uvasana* Conrad of Gabb, 1864, *fide* Anderson and Hanna, 1925: 160–161 and Stewart, 1930:236.]
Not *Pitaria tejonensis* (Dickerson). Anderson and Hanna, 1925:160–161, pl. 3, fig. 5.
Pitaria uvasana (Conrad). Anderson and Hanna, 1925:161, pl. 5, figs. 3–4.
Pitar (*Calpitaria*) *uvasanus* (Conrad). Stewart, 1930:235–236, pl. 12, fig. 7. Weaver, 1943:178–179, pl. 47, fig. 13. Givens, 1974:53.
Pitar uvasanus uvasanus (Conrad). Givens and Kennedy, 1979:tables 3–4.

Primary Type Material. ANSP neotype 4457, Tejon Formation, Grapevine Canyon, Kern County, California.

Molluscan Stage Range. "Domengine" through "Tejon."

Geographic Distribution. San Diego, California through western Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 371, 374.

Remarks. Specimens are fairly uncommon and generally consist of fragments of single valves. The occurrence of this taxon in the Llajas Formation extends its range into the "Domengine Stage." Previously, it had been reported as ranging from the "Transition" through the "Tejon" (Givens, 1974).

Meretrix tejonensis Dickerson, 1915:53, pl. 3, figs. 2a–b = *Pitar* (*Lamelliconcha*) *dickersoni* Givens, *fide* Givens, 1974: 53–54.

Subgenus *Lamelliconcha* Dall, 1902

Type Species. By original designation, *Cytherea concinna* J. Sowerby, 1835a.

Pitar (*Lamelliconcha*) *joaquinensis* Vokes, 1939

Figure 12k

Meretrix hornii Gabb. Arnold, 1910:pl. 3, fig. 9. [Misidentification.]
Pitar (*Lamelliconcha*) *joaquinensis* Vokes, 1939:85–86, pl. 13, figs. 9–12. Givens, 1974:54, pl. 3, fig. 7.
Pitar? *joaquinensis* Vokes. Stewart, 1946:pl. 12, fig. 12.
Pitar joaquinensis Vokes. Givens and Kennedy, 1979: table 1.

Primary Type Material. UCMP holotype 15674, Domengine Formation, UCMP locality A-1027; UCMP paratype 15675, Domengine? Formation, UCMP locality 4175; UCMP paratype 15676, Domengine Formation, UCMP locality A-1027; UCMP paratype 15677, Avenal Formation, UCMP locality A-1280.

Molluscan Stage Range. "Domengine."

Geographic Distribution. Simi Valley through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only a few single valves were found in the Llajas Formation.

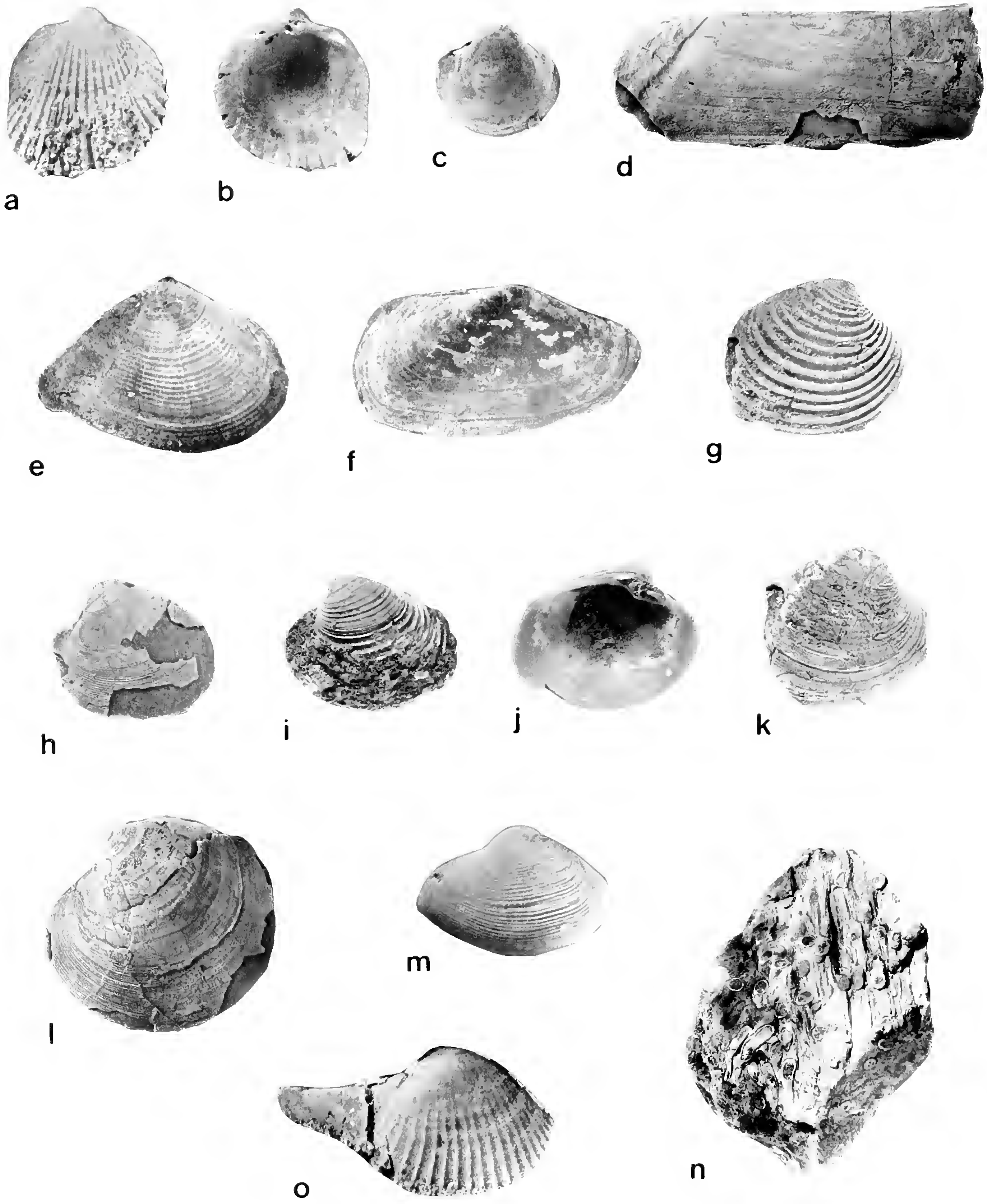

Figure 12. Llajas Formation bivalves (continued). **a and b.** *Acanthocardia* (*Schedocardia*) *breweri* (Gabb, 1864), right valve, LACMIP hypotype 6583, CSUN loc. 371, ×2. **a,** exterior. **b,** interior. **c.** *Nemocardium linteum* (Conrad, 1855), internal mold of right? valve, LACMIP hypotype 6584, CSUN loc. 374, ×1. **d.** *Solena* (*Eosolen*) *novacularis* (Anderson and Hanna, 1928), left valve, LACMIP hypotype 6585, CSUN loc. 374, ×1. **e.** *Macoma rosa* Hanna, 1927, internal mold of right valve, LACMIP hypotype 6586, CSUN loc. 489, ×1.5. **f.** *Gari* cf. *G. eoundulata* Vokes, 1939, internal mold of right valve, LACMIP hypotype 6587, CSUN loc. 471d, ×1. **g.** *Callista* (*Costacallista*) cf. *C.* (*C.*) *hornii* (Gabb, 1864), right valve, LACMIP hypotype 6588, CSUN loc. 465, ×2. **h.** *Callocardia* (*Nitidavenus*) *tejonensis* (Waring, 1914), left valve, LACMIP

Subfamily Tapetinae H. and A. Adams, 1857

Genus *Marcia* H. and A. Adams, 1857

Type Species. By subsequent designation (Kobelt, 1883), "*Venus pinguis* Chemnitz" [=*V. opima* Gmelin, 1791].

Subgenus *Mercimonia* Dall, 1902

Type Species. By original designation, *Venus bernayi* Cossmann, 1888.

Marcia (*Mercimonia*) *bunkeri* (Hanna, 1927)

Figure 12l

Dosinia bunkeri Hanna, 1927:287, pl. 42, figs. 4, 6.

Mercimonia bunkeri (Hanna). Turner, 1938:60, pl. 10, figs. 5–9. Vokes, 1939:77, pl. 11, fig. 12. Givens and Kennedy, 1979:87, table 3.

Marcia (*Mercimonia*) *bunkeri* (Hanna). Weaver, 1943:192, pl. 45, fig. 5; pl. 47, figs. 8, 11.

Primary Type Material. UCMP holotype 30950, Ardath Shale, UCMP locality 5069; UCMP paratype 30951, Ardath Shale, UCMP locality 3976.

Molluscan Stage Range. "Domengine" through "Transition."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 374.

Remarks. Only three specimens were found in the Llajas Formation, and of these, two are articulated.

Order Myoida

Suborder Myina

Superfamily Myacea

Family Corbulidae Lamarck, 1818

Subfamily Corbulinae Lamarck, 1818

Genus *Corbula* Bruguière, 1797

Type Species. By subsequent designation (Schmidt, 1818), *Corbula sulcata* Lamarck, 1801.

Subgenus *Caryocorbula* Gardner, 1926

Type Species. By original designation, *Corbula alabamiensis* Lea, 1833.

Corbula (*Caryocorbula*) *dickersoni* (Weaver and Palmer, 1922)

Figure 12m

Corbula dickersoni Weaver and Palmer, 1922:24–25, pl. 9, figs. 9–10. Clark, 1938:700, pl. 1, fig. 17. Weaver, 1943: 257–258, pl. 61, figs. 13, 16–17, 20.

Corbula (*Caryocorbula*) *dickersoni* Weaver and Palmer. Vokes, 1939:98, pl. 16, figs. 1, 5, 9. Givens, 1974:57, pl. 4, fig. 7.

Primary Type Material. CAS holotype 7452, CAS syntypes 7452A–B, Cowlitz Formation, UW locality 329.

Molluscan Stage Range. Uppermost "Capay" through "Tejon."

Geographic Distribution. Simi Valley, California through southwestern Washington.

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 545. Shallow-marine (transgressive) facies: CSUN localities 371, 373, 455, 484, 498, 501, 507, 540. Shallow-marine (regressive) facies: CSUN locality 475.

Remarks. This taxon is most common at locality 371, where the specimens are similar-sized single valves.

The presence of *C.* (*C.*) *dickersoni* in the zone of interfingering between the coastal alluvial-fan facies and the shallow-marine (transgressive) facies of the Llajas Formation extends the molluscan stage range of this taxon into the uppermost "Capay." Previously, the lower range limit had been reported as the "Domengine" (Vokes, 1939; Givens, 1974).

Suborder Pholadina

Superfamily Pholadacea

Family Teredinidae Rafinesque, 1815

Subfamily Teredininae Rafinesque, 1815

Genus *Teredo* Linné, 1758

Type Species. By subsequent designation (ICZN, 1926, opin. 94), *Teredo navalis* Linné, 1758.

Teredo? sp.

Figure 12n

Local Occurrence. Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies: CSUN locality 469c. Shallow-marine (transgressive) facies: CSUN localities 374, 438, 444, 469, 470a, 488, 534. Outer shelf and slope

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hypotype 6589, CSUN loc. 371, ×1. **i and j.** *Pitar* (*Calpitaria*) *uvasanus* (Conrad, 1855), left valve, LACMIP hypotype 6590, CSUN loc. 371, ×1.5. **i,** exterior. **j,** interior. **k.** *Pitar* (*Lamelliconcha*) *joaquinensis* Vokes, 1939, partial specimen, right valve, LACMIP hypotype 6591, CSUN loc. 371, ×1. **l.** *Marcia* (*Mercimonia*) *bunkeri* (Hanna, 1927), left? valve, UCLA hypotype 59282, CSUN loc. 374, ×1. **m.** *Corbula* (*Caryocorbula*) *dickersoni* (Weaver and Palmer, 1922), right valve, LACMIP hypotype 6592, CSUN loc. 371, ×2.75. **n.** *Teredo*? sp., in petrified wood, LACMIP hypotype 6593, CSUN locality 524, ×0.5. **o.** *Cardiomya* aff. *C. russelli* (Hanna, 1927), internal mold of right valve, LACMIP hypotype 6594, CSUN loc. 512d, ×4.

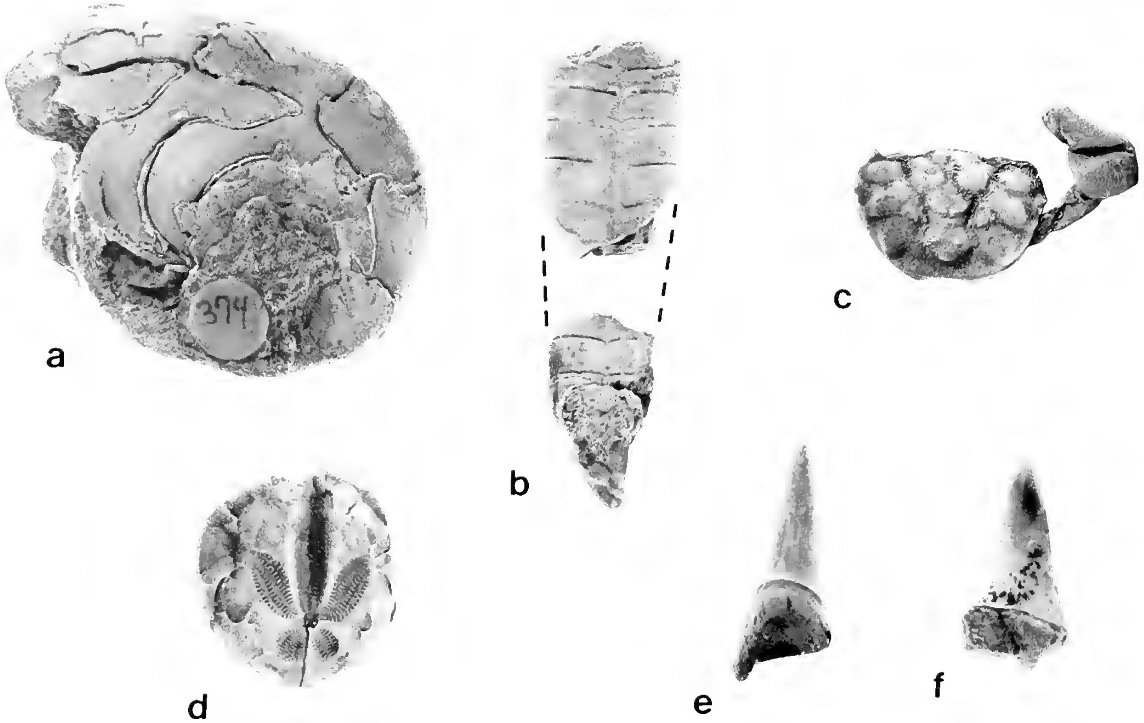


Figure 13. Llajas Formation nautiloid, crab, spatangoid, and shark teeth. **a.** *Aturia myrlae* Hanna, 1927, lateral view, LACMIP hypotype 6595, CSUN loc. 374, ×1.75. **b.** Unidentifiable spirulimorph sepiid, ventral view of partial phragmocone, UCLA hypotype 59197, CSUN loc. 493, ×2.6. **c.** *Glyphithyreus weaveri* (Rathbun, 1926), carapace and portion of right cheliped, dorsal view, UCLA hypotype 59273, CSUN loc. 548, ×1. **d.** *Schizaster diabloensis* Kew, 1920, internal mold, dorsal view, LACMIP hypotype 6596, CSUN loc. 482, ×1. **e.** *Odontaspis* sp., LACMIP hypotype 6597, CSUN loc. 374, ×1. **f.** *Isurus* cf. *I. praecursor* (Leriche, 1906), LACMIP hypotype 6598, CSUN loc. 371, ×3.

facies: CSUN locality 446. Outer shelf and slope channel facies: CSUN locality 541.

Remarks. *Teredo*? sp. occurs in pieces of petrified wood. In most cases, *Teredo*? sp. is represented by calcareous-lined burrows, but unlined burrows can be present in the same piece of wood. Generic determination is uncertain, and it is very possible that future workers will assign these fossils to another genus. Tertiary teredinids are in need of much taxonomic work.

Subclass Anomalodesmata

Order Pholadomyoida

Superfamily Poromyacea

Family Cuspidariidae Dall, 1886

Genus *Cardiomya* A. Adams, 1864

Type Species. By monotypy, *Neaera gouldiana* Hinds, 1843.

Cardiomya aff. *C. russelli* (Hanna, 1927)

Figure 12o

Local Occurrence. Shallow-marine (regressive) facies: CSUN locality 512d.

Remarks. Only a single specimen was found, and it is an internal mold of a right valve. The specimen agrees closely with the description of *C. russelli* given by Hanna (1927: 280–281) in possessing radial ribs and a long, straight smooth rostrum. The Llajas specimen differs in that it has at least 19 radial ribs rather than 16.

Class Cephalopoda

Subclass Nautiloidea

Order Nautilida

Superfamily Nautilacea

Family Aturiidae Hyatt, 1894

Genus *Aturia* Bronn, 1838

Type Species. By subsequent designation (Herrmannsen, 1846), *Nautilus aturi* Basterot, 1825, and virtual tautonymy.

Aturia myrlae Hanna, 1927

Figure 13a

Aturia myrli Hanna, 1927:331, pl. 57, figs. 1, 6.

Aturia myrlae Hanna. Schenck, 1931:454–456, pls. 67–68; text figures 4-3, 4–19. Vokes, 1939:107, pl. 16, fig. 36.

Miller, 1947:100–101, pl. 76, figs. 2–3; pl. 77, figs. 1–2; pl. 92, figs. 6–7.

Primary Type Material. UCMP holotype 31089, Ardath Shale, UCMP locality 3989.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. San Diego through central California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 458.

Remarks. Specimens were found only in the "Stewart bed." The best preserved specimens are from locality 374 where one juvenile (Fig. 13a) and an adult specimen were found. As reported by Schenck (1931), a hypotype of *A. myrlae* is from UCMP 7004 = CSUN locality 374.

Subclass Coleoidea

Order Sepiida

Family Indeterminate

Spirulimorph Sepiid

Figure 13b

Spirulimorph sepiid Squires, 1983a:360, figs. 2j–k.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 493.

Remarks. Only a single partial phragmocone and associated external mold were found in the Llajas Formation. In the absence of the rostrum and the apical part of the phragmocone, the specimen and mold are unidentifiable. This is the first sepiid in the Eocene of western North America (Squires, 1983a).

Phylum Arthropoda

Class Malacostraca

Subclass Eumalacostraca

Order Decapoda

Suborder Pleocyemata

Infraorder Brachyura

Section Brachyrhyncha

Superfamily Xanthoidea

Family Goneplacidae MacLeay, 1838

Subfamily Carcinoplacinae Milne-Edwards, 1852

Genus *Glyphithyreus* Reuss, 1859

Type Species. By original designation, *Glyphithyreus formosus* Reuss, 1859 (=*Plagiolophus wetherelli* Bell, 1858).

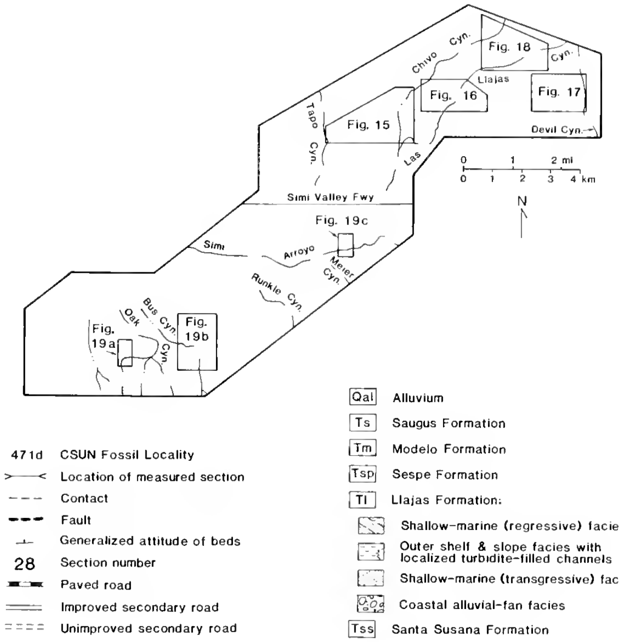


Figure 14. Index map to the Llajas Formation showing locations of areas used as fossil-collecting locality maps in Figures 15–19. An explanation of symbols used on the locality maps is also given.

Glyphithyreus weaveri (Rathbun, 1926)

Figure 13c

Cancer? sp. Weaver, 1905:123, pl. 13, fig. 11.
Cancer (?) sp. A Dickerson, 1916:pl. 42, fig. 11.
Plagiolophus weaveri Rathbun, 1926:35–37, pl. 9, figs. 5–6. Orr and Kooser, 1971:157, text figure 3a, figs. 4a–c, figs. 5a–i.

Primary Type Material. USNM holotype 353351, Eocene strata, Salt Creek, 5.2 km north-northeast of Joaquin Rocks, south part of NW ¼ of section 15, T 18 S, R 14 E, Fresno County, California.

Molluscan Stage Range. "Capay" through "Domengine."

Geographic Distribution. San Diego, California through southwestern Oregon.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 471b, 548.

Remarks. Although fragments of brachyuran chelipeds were found at widely scattered localities in the Llajas Formation, carapaces were found only at localities 471b and 548. At locality 548, most of the specimens have also one or both chelipeds intact.

Phylum Echinodermata

Subphylum Echinozoa

Class Echinoidea

Subclass Euechinoidea

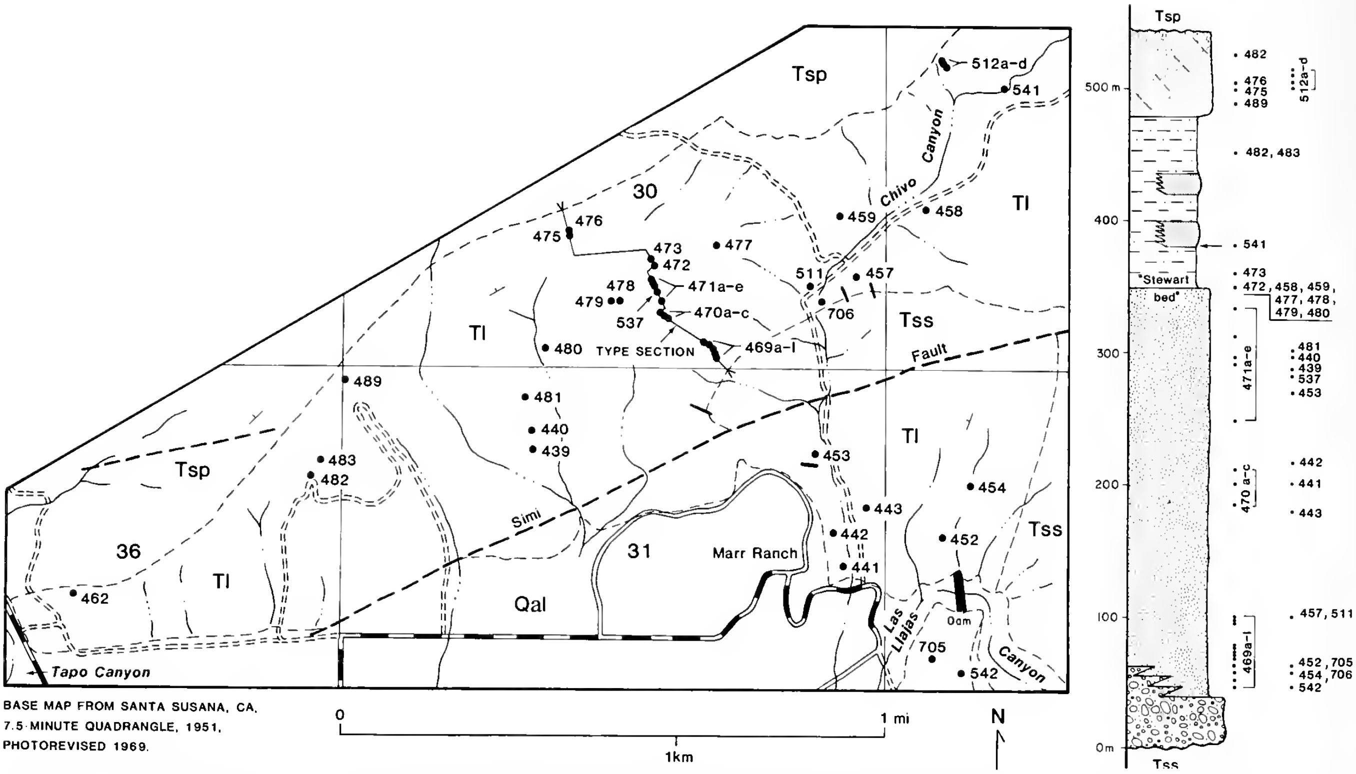


Figure 15. Geologic map showing CSUN fossil-collecting localities, Llajas Formation, type section area. Accompanying columnar section shows stratigraphic position of the fossil-collecting localities. See Figure 14 for explanation of symbols.

Superorder Atelostomata

Order Spatangoida

Suborder Hemiasterina

Family Schizasteridae Lambert, 1902

Genus *Schizaster* L. Agassiz, 1836

Type Species. By subsequent designation (ICZN, 1954, opin. 209), *Schizaster studeri* L. Agassiz, 1836.

Schizaster diabloensis Kew, 1920

Figure 13d

Schizaster diabloensis Kew, 1920:150–151, pl. 41, figs. 5a–c. Clark and Woodford, 1927:123, pl. 22, fig. 14. Clark, 1929:pl. 4, fig. 13. Grant and Hertlein, 1938:120.

Primary Type Material. UCMP holotype 11387, Eocene strata, UCMP locality 1427.

Molluscan Stage Range. Upper Paleocene through "Domengine."

Geographic Distribution. Simi Valley through Marysville Buttes, California.

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 458, 478. Outer shelf and slope facies: CSUN locality 482. Shallow-marine (regressive) facies: CSUN locality 547.

Remarks. Preservation is as internal molds and most specimens are somewhat crushed. At locality 547, *S. diabloensis* is the only megafossil present.

Clark and Woodford (1927) reported this species from the type section area of the Meganos Formation. Marincovich (1977:251) considered the formation to be late Paleocene in age.

Phylum Chordata

Class Chondrichthyes

Subclass Elasmobranchii

Order Lamniformes

Family Odontaspididae Müller and Henle, 1837

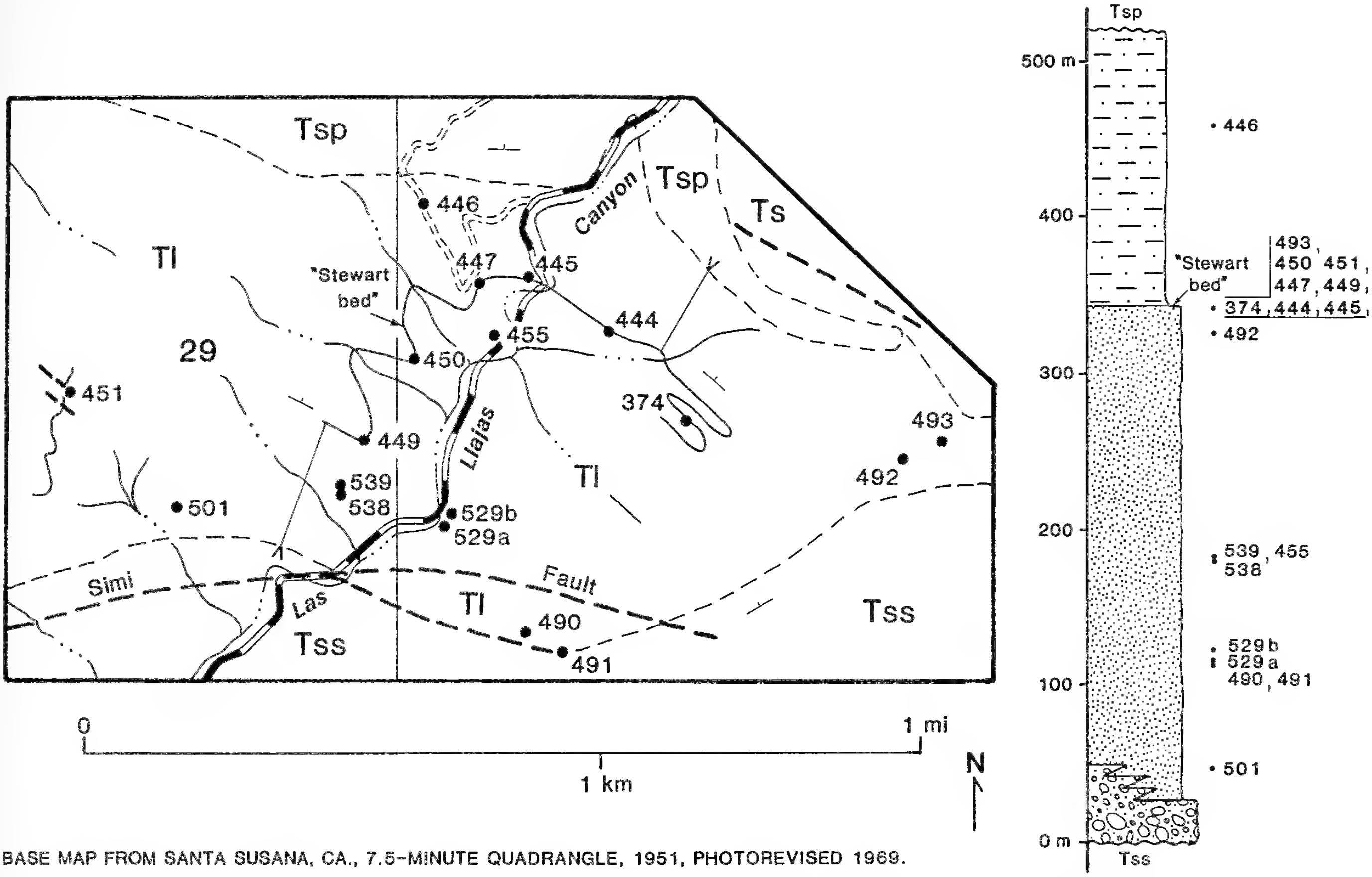
Genus *Odontaspis* L. Agassiz, 1838

Type Species. By monotypy, *Odontaspis ferox* Risso, 1810.

Odontaspis sp.

Figure 13e

Local Occurrence. Shallow-marine (transgressive) facies: CSUN localities 374, 445.



BASE MAP FROM SANTA SUSANA, CA., 7.5-MINUTE QUADRANGLE, 1951, PHOTOREVISED 1969.

Figure 16. Geologic map showing CSUN fossil-collecting localities, Llajas Formation, lower Las Llajas Canyon area. Accompanying columnar section shows stratigraphic position of the fossil-collecting localities. See Figure 14 for explanation of symbols.

Remarks. Only a few specimens were found in the Llajas Formation.

Family Lamnidae Müller and Henle, 1838

Genus *Isurus* Rafinesque, 1809

Type Species. By original designation, *Isurus oxyrhynchus* Rafinesque, 1809.

Isurus cf. *I. praecursor* (Leriche, 1906)

Figure 13f

Local Occurrence. Shallow-marine (transgressive) facies: CSUN locality 371.

Remarks. Only one specimen was found in the Llajas Formation.

LOCALITIES

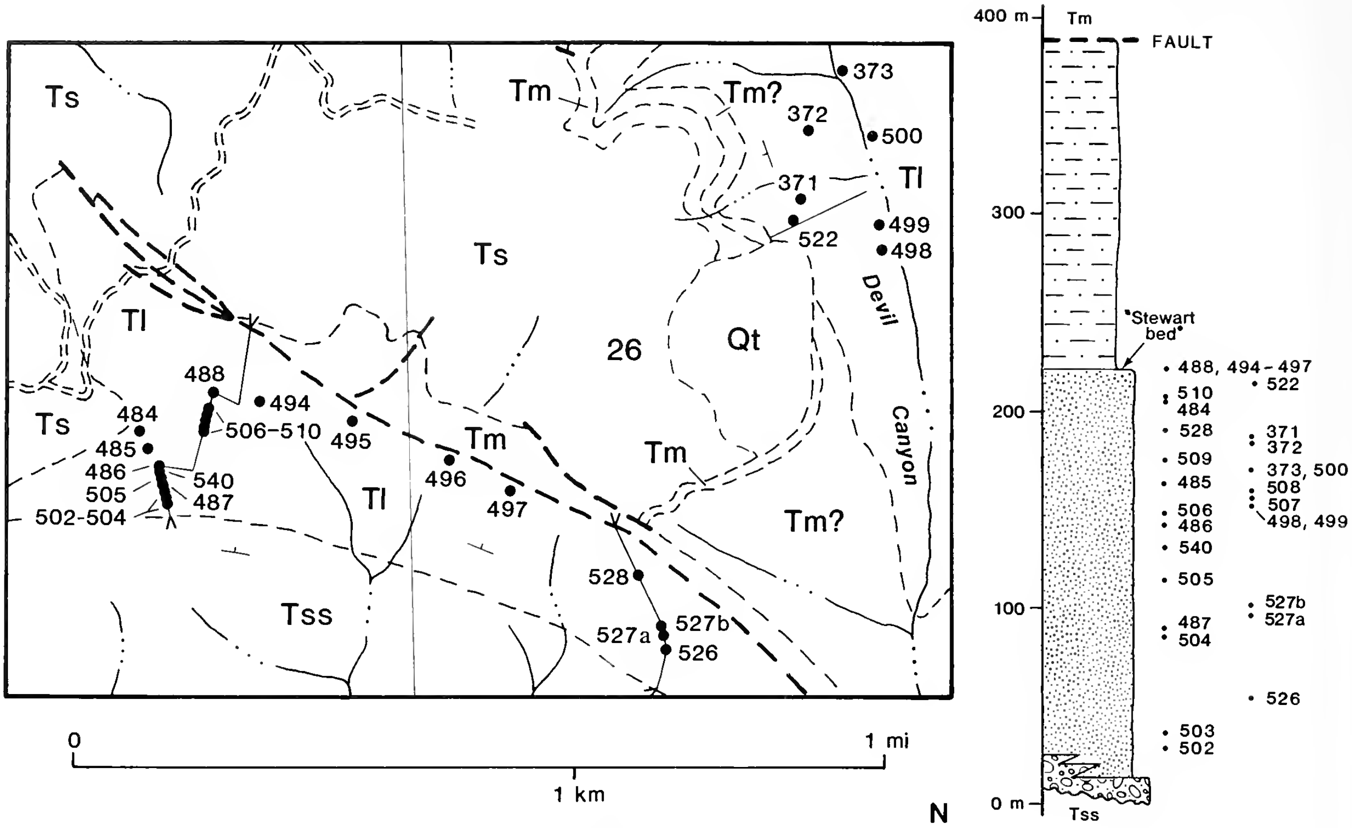
CSUN fossil-collecting localities made by the author in the course of this study are listed first. Localities of other institutions mentioned in this report follow in alphabetical order.

All CSUN localities are in the Llajas Formation, Simi Valley area, California. Unless otherwise noted, they are in the United States Geological Survey 7.5-minute topographic quadrangle of Santa Susana, California (1951), photorevised 1969. In some cases, a locality is in the Santa Susana quadrangle, but the section corner used for referencing is in the United States Geological Survey 7.5-minute topographic quadrangle of Oat Mountain, California (1952), photorevised 1969. These localities are so noted. Abbreviations used are United States Geological Survey (USGS), feet (ft.), meters (m), township (T), range (R), north (N), south (S), east (E), and west (W). Distances are given in both English and metric units, but map contour elevations are given in English units only.

CSUN localities equivalent to localities of University of California Museum of Paleontology (Berkeley) (UCMP); University of California, Los Angeles (UCLA); and California Institute of Technology (CIT) are so indicated. CSUN localities are denoted also as to which marine facies (Squires, 1981) they belong. The general location and the relative stratigraphic position of each CSUN locality are shown in Figures 14 through 19.

CSUN LOCALITIES

371. At elevation of 2000 ft. on south side of a side canyon to Devil Canyon, 1275 ft. (389 m) south and 1150 ft. (350



BASE MAP FROM SANTA SUSANA SUSANA (1951) AND OAT MOUNTAIN (1952), CA., 7.5-MINUTE QUADRANGLES, BOTH PHOTOREVISED 1969.

Figure 17. Geologic map showing CSUN fossil-collecting localities, Llajas Formation, Devil Canyon area. Accompanying columnar section shows stratigraphic position of the fossil-collecting localities. See Figure 14 for explanation of symbols.

m) west of NE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

372. At elevation of 2035 ft. on west side of stream bank of Devil Canyon, 800 ft. (244 m) south and 1200 ft. (366 m) west of NE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

373. At elevation of 1900 ft. on east side of stream bank of Devil Canyon, 450 ft. (137 m) south and 850 ft. (259 m) west of NE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

374. At elevation of 1700 ft. on a small cliff on south side of a side canyon to Las Llajas Canyon, 1950 ft. (594 m) north and 1825 ft. (556 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed" and is equivalent to UCMP locality 7004, UCLA locality 2312, and CIT locality 206. [Shallow-marine (transgressive) facies.]

438. At elevation of 1800 ft. on east side of stream bank of Las Llajas Canyon, 7000 ft. (2134 m) N86°E of NE corner of section 29, T 3 N, R 17 W. Locality is equivalent to UCLA locality 2775. [Shallow-marine (transgressive) facies.]

439. At elevation of 1425 ft. on a ridge, 800 ft. (244 m) south and 1900 ft. (579 m) east of NW corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

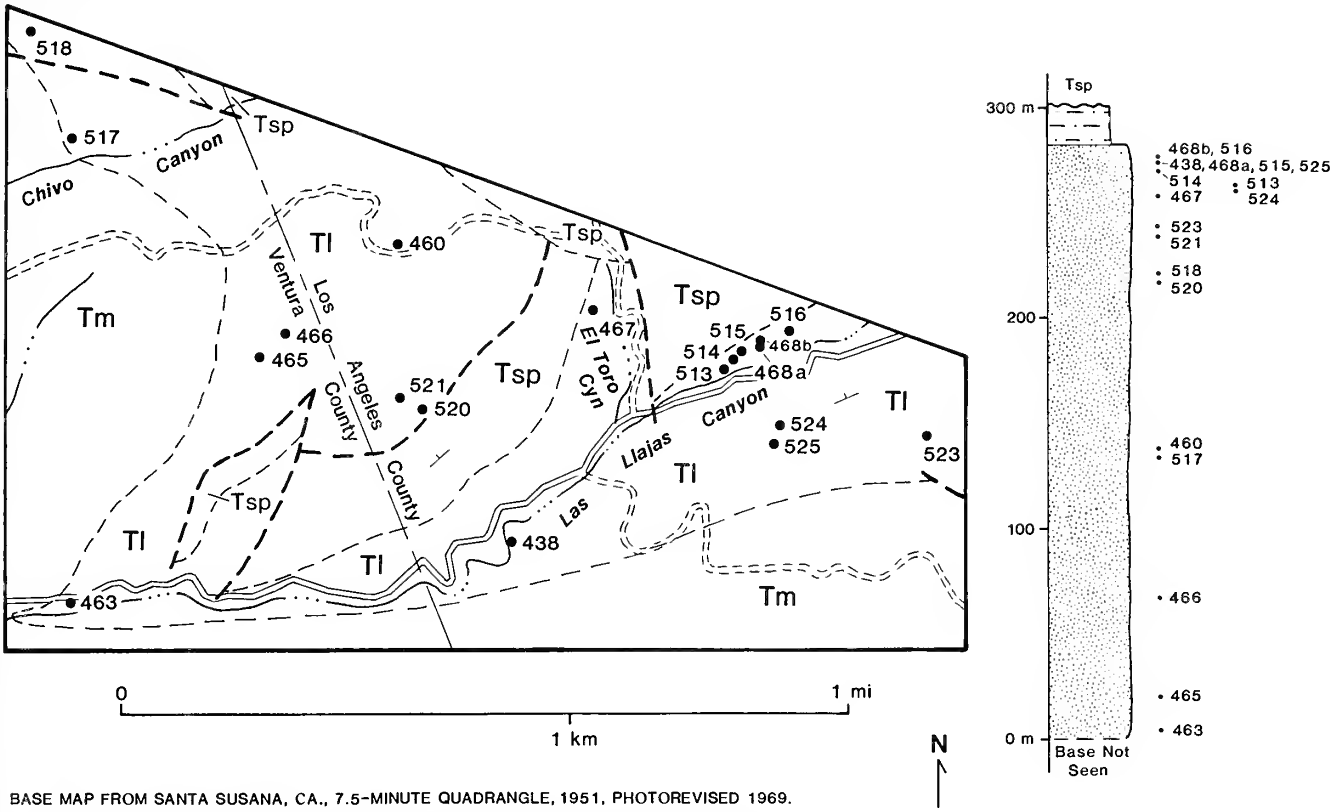
440. At elevation of 1475 ft. on a ridge, 600 ft. (183 m) south and 1875 ft. (571 m) east of NW corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

441. At elevation of 1160 ft. on west side of Chivo Canyon near its mouth, 1890 ft. (576 m) south and 400 ft. (122 m) west of NE corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

442. At elevation of 1185 ft. on west side of Chivo Canyon near its mouth, 1600 ft. (488 m) south and 510 ft. (155 m) west of NE corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

443. At elevation of 1230 ft. on east side of Chivo Canyon near its mouth, 1370 ft. (418 m) south and 200 ft. (61 m) west of NE corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

444. At elevation of 1585 ft. on a small cliff on north side of a side canyon to Las Llajas Canyon, 2500 ft. (762 m) north



BASE MAP FROM SANTA SUSANA, CA., 7.5-MINUTE QUADRANGLE, 1951, PHOTOREVISED 1969.

Figure 18. Geologic map showing CSUN fossil-collecting localities, Llajas Formation, upper Las Llajas Canyon area. Accompanying columnar section shows stratigraphic position of the fossil-collecting localities. See Figure 14 for explanation of symbols.

and 1375 ft. (419 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

445. At elevation of 1485 ft. on a small cliff on west side of Las Llajas Canyon, 2820 ft. (859 m) north and 850 ft. (259 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

446. At elevation of 1760 ft. in roadcut along ridge on west side of Las Llajas Canyon, 3460 ft. (1055 m) north and 200 ft. (61 m) east of SE corner of section 29, T 3 N, R 17 W. [Outer shelf and slope facies.]

447. At elevation of 1550 ft. on a small cliff on west side of Las Llajas Canyon, 2780 ft. (847 m) north and 550 ft. (168 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

449. At elevation of 1700 ft. on a small cliff on west side of Las Llajas Canyon, 1825 ft. (556 m) north and 200 ft. (61 m) west of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

450. At elevation of 1600 ft. on a small cliff on west side of Las Laljas Canyon, 2450 ft. (747 m) north and 125 ft. (38 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

451. At elevation of 1715 ft. on a small cliff on a hillside, 2100 ft. (640 m) north and 2100 ft. (640 m) west of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

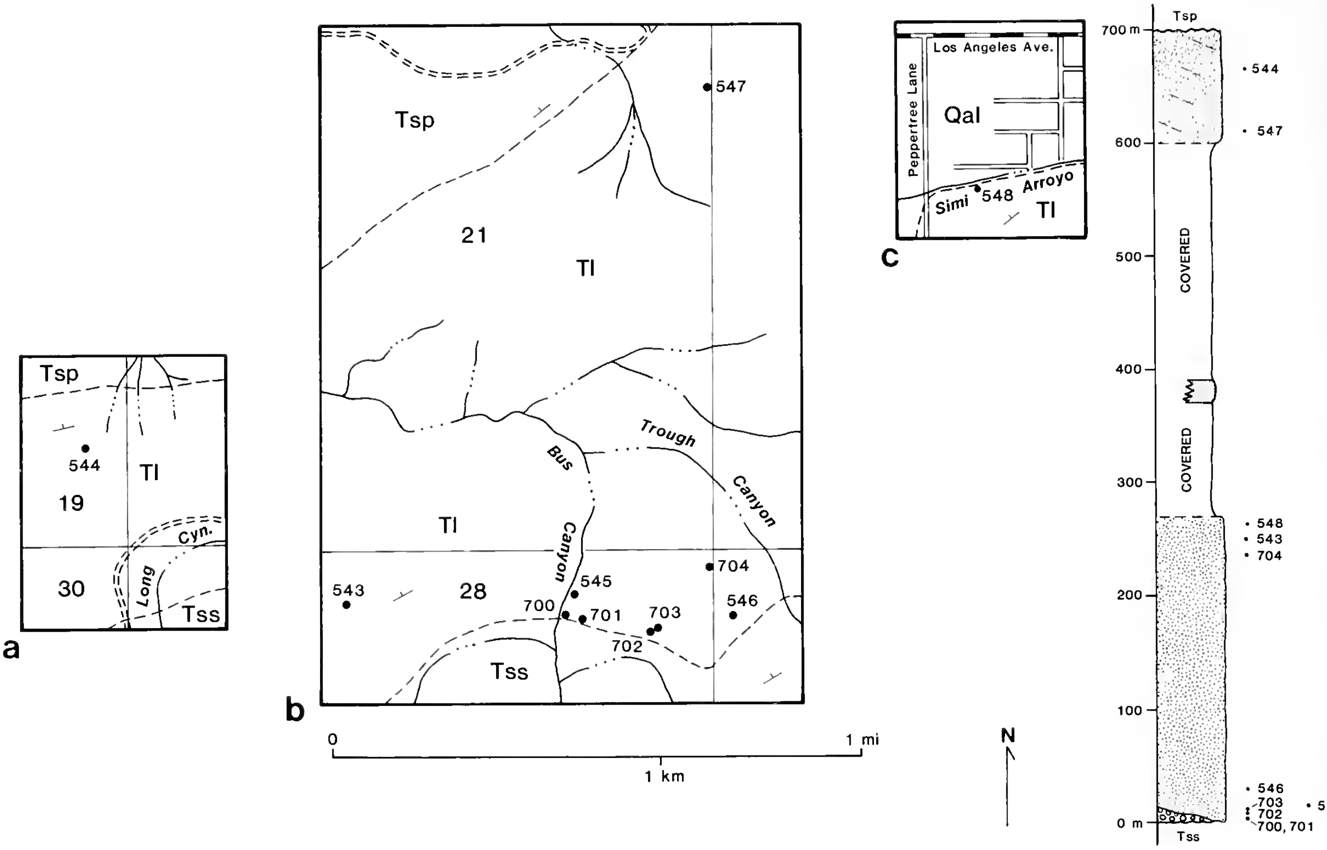
452. At elevation of 1285 ft. on west side of a small canyon branching north near mouth of Las Llajas Canyon, 1650 ft. (503 m) south and 550 ft. (168 m) east of NW corner of section 32, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

453. At elevation of 1275 ft. on west side of Chivo Canyon, 800 ft. (243 m) south and 700 ft. (213 m) west of NE corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

454. At elevation of 1310 ft. on west side of a small canyon branching north near mouth of Las Llajas Canyon, 1100 ft. (335 m) south and 810 ft. (247 m) east of NW corner of section 32, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

455. At elevation of 1475 ft. on east side of stream bank of Las Llajas Canyon, 2500 ft. (762 m) north and 625 ft. (191 m) east of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

457. At elevation of 1300 ft. on east side of Chivo Canyon,



BASE MAP FROM SANTA SUSANA (1951, PHOTOREVISED 1969) AND THOUSAND OAKS (1950, PHOTOREVISED 1967), CA., 7.5-MINUTE QUADRANGLES.

Figure 19. Geologic maps showing CSUN fossil-collecting localities, Llajas Formation, at various areas along the south side of Simi Valley. Accompanying columnar sections shows stratigraphic position of the fossil-collecting localities. See Figure 14 for explanation of symbols. **a.** Long Canyon area. **b.** Lower Bus Canyon area. **c.** Simi Arroyo–Peppertree Lane area.

900 ft. (274 m) north and 300 ft. (91 m) west of SE corner of section 30, T 3 N, R 17 W. Bed is the same one exposed at CSUN localities 4691 and 511. [Shallow-marine (transgressive) facies.]

458. At elevation of 1300 ft. along south side of a ranch road that leads up south side of Chivo Canyon, 1550 ft. (472 m) north and 400 ft. (122 m) east of SW corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

459. At elevation of 1400 ft. on north side of Chivo Canyon, 1500 ft. (457 m) north and 400 ft. (122 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

460. At elevation of 2150 ft. on a hillside just north of a ranch road, 6700 ft. (2042 m) N67°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

462. At elevation of 1225 ft. on a hillside just north of an oilfield road, 2250 ft. (686 m) south and 2675 ft. (815 m) west of NE corner of section 36, T 3 N, R 18 W. Locality is near the Llajas-Sespe contact. [Shallow-marine (regressive) facies.]

463. At elevation of 1650 ft. in streambed, Las Llajas Canyon, 3725 ft. (1135 m) N89°E of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

465. At elevation of 2100 ft. on south side of a hill, 5480 ft. (1670 m) N70°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

466. At elevation of 2150 ft. along east side of a hill, 5700 ft. (1738 m) N69°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

467. At elevation of 1900 ft. on west side of stream bank of El Toro Canyon, 7900 ft. (2408 m) N69°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

468a. At elevation of 1975 ft. on north side of stream bank of Las Llajas Canyon, 6675 ft. (2034 m) N69°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Bed is the same one exposed at CSUN locality 515. [Shallow-marine (transgressive) facies.]

468b. Bed 10 ft. (3 m) stratigraphically above locality 468a.

Bed is the same one exposed at CSUN locality 516. [Shallow-marine (transgressive) facies.]

469a. At elevation of 1400 ft. on north side of a small canyon branching west from Chivo Canyon, 100 ft. (31 m) north and 1650 ft. (503 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation, 144 ft. (44 m) above the base of the formation. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

469b. Bed 26 ft. (8 m) stratigraphically above locality 469a, on a traverse bearing N10°W from locality 469a. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

469c. Bed 13 ft. (4 m) stratigraphically above locality 469b, on a traverse bearing N10°W from locality 469b. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

469d. Bed 13 ft. (4 m) stratigraphically above locality 469c, on a traverse bearing N10°W from locality 469c. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

469e. Bed 20 ft. (6 m) stratigraphically above locality 469d, on a traverse bearing N10°W from locality 469d. [Shallow-marine (transgressive) facies.]

469f. Bed 6.5 ft. (2 m) stratigraphically above locality 469e, on a traverse bearing N10°W from locality 469e. [Shallow-marine (transgressive) facies.]

469g. Bed 6.5 ft. (2 m) stratigraphically above locality 469f, on a traverse bearing N10°W from locality 469f. [Shallow-marine (transgressive) facies.]

469h. Bed 16 ft. (5 m) stratigraphically above locality 469g, on a traverse bearing N10°W from locality 469g. [Shallow-marine (transgressive) facies.]

469i. Bed 9 ft. (3 m) stratigraphically above locality 469h, on a traverse bearing N10°W from locality 469h. [Shallow-marine (transgressive) facies.]

469j. Bed 75 ft. (19 m) stratigraphically above locality 469g, on a traverse bearing N10°W from locality 469g. [Shallow-marine (transgressive) facies.]

469k. Bed 20 ft. (6 m) stratigraphically above locality 469g, on a traverse bearing N10°W from locality 469j. [Shallow-marine (transgressive) facies.]

469l. Bed 13 ft. (4 m) stratigraphically above locality 469k, on a traverse bearing N55°W from locality 469k. Bed is the same one exposed at CSUN localities 457 and 511. [Shallow-marine (transgressive) facies.]

470a. At elevation of 1550 ft. on south side of an amphitheater on west side of Chivo Canyon, 500 ft. (152 m) north and 2100 ft. (640 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation, 266 ft. (81 m) stratigraphically above locality 469l. [Shallow-marine (transgressive) facies.]

470b. Bed 62 ft. (19 m) stratigraphically above locality 470a, on a traverse bearing N60°W from locality 470a. [Shallow-marine (transgressive) facies.]

470c. Bed 33 ft. (10 m) stratigraphically above locality 470b, on a traverse bearing N60°W from locality 470b. [Shallow-marine (transgressive) facies.]

471a. At elevation of 1450 ft. on west side of an amphitheater on west side of Chivo Canyon, 600 ft. (183 m) north and 2125 ft. (655 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation, 125 ft. (38 m) stratigraphically above locality 470c. [Shallow-marine (transgressive) facies.]

471b. Bed 144 ft. (44 m) stratigraphically above locality 471a, on a traverse bearing N27°W from locality 471a. [Shallow-marine (transgressive) facies.]

471c. Bed 20 ft. (6 m) stratigraphically above locality 471b, on a traverse bearing N27°W from locality 471b. [Shallow-marine (transgressive) facies.]

471d. Bed 39 ft. (12 m) stratigraphically above locality 471c, on a traverse bearing N27°W from locality 471c. [Shallow-marine (transgressive) facies.]

471e. Bed 79 ft. (24 m) stratigraphically above locality 471d, on a traverse bearing N27°W from locality 471d. [Shallow-marine (transgressive) facies.]

472. At elevation of 1600 ft. on a ridge, 1000 ft. (305 m) north and 2300 ft. (701 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation and in the "Stewart bed," 46 ft. (14 m) stratigraphically above locality 471e. [Shallow-marine (transgressive) facies.]

473. At elevation of 1650 ft. on a ridge, 1050 ft. (320 m) north and 2300 ft. (701 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation, 46 ft. (14 m) stratigraphically above locality 472. The bed that this locality occurs in probably represents a shallow-marine (transgressive) facies bed that interfingers with the outer shelf and slope facies.

475. At elevation of 1625 ft. on a ridge, 1300 ft. (396 m) north and 3100 ft. (945 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation, approximately 446 ft. (136 m) stratigraphically above locality 473. [Shallow-marine (regressive) facies.]

476. Bed 13 ft. (4 m) stratigraphically above locality 475, on a traverse bearing N15°W from locality 475. [Shallow-marine (regressive) facies.]

477. At elevation of 1625 ft. on a ridge, 1200 ft. (366 m) north and 1700 ft. (518 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

478. At elevation of 1735 ft. just below a saddle along a ridge, 680 ft. (270 m) north and 2670 ft. (814 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

479. At elevation of 1775 ft. just below a saddle along a ridge, 650 ft. (198 m) north and 2700 ft. (823 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

480. At elevation of 1400 ft. near a canyon bottom, 200 ft. (61 m) north and 3400 ft. (1036 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

481. At elevation of 1500 ft. on a ridge, 325 ft. (99 m) south and 1800 ft. (549 m) east of NE corner of section 31, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

482. At elevation of 1435 ft. in a roadcut, 1100 ft. (335 m) south and 300 ft. (91 m) west of NE corner of section 36, T 3 N, R 18 W. [Outer shelf and slope facies.]

483. At elevation of 1525 ft. on west side of a ridge, 925 ft. (282 m) south and 175 ft. (53 m) west of NE corner of section 36, T 3 N, R 18 W. [Outer shelf and slope facies.]

484. At elevation of 2340 ft. on a ridge, 6000 ft. (1829 m) N68°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

485. Bed 135 ft. (41 m) stratigraphically below locality 484, on a traverse bearing S23°E from locality 484. [Shallow-marine (transgressive) facies.]

486. Bed 69 ft. (21 m) stratigraphically below locality 485, on a traverse bearing S23°E from locality 485. [Shallow-marine (transgressive) facies.]

487. Bed 174 ft. (53 m) stratigraphically below locality 486, on a traverse bearing S23°E from locality 486. [Shallow-marine (transgressive) facies.]

488. At elevation of 2175 ft. on a ridge, 5650 ft. (1722 m) N64°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

489. At elevation of 1250 ft. on east side of a canyon, 125 ft. (38 m) south of NW corner of section 31, T 3 N, R 17 W. [Shallow-marine (regressive) facies.]

490. At elevation of 1900 ft. in a saddle along a ridge, 600 ft. (183 m) north and 800 ft. (244 m) east of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

491. At elevation of 1840 ft. on east side of a small canyon, 500 ft. (145 m) north and 1100 ft. (320 m) east of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

492. At elevation of 2230 ft. in a saddle along a ridge, 1700 ft. (518 m) north and 3225 ft. (983 m) east of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

493. At elevation of 2225 ft. in saddle along a ridge, 1825 ft. (556 m) north and 3450 ft. (1052 m) east of SE corner of section 29, T 3 N, R 17 W. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

494. At elevation of 2050 ft. on a small cliff, 5350 ft. (1630 m) N62°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

495. At elevation of 2050 ft. on a small cliff, 4725 ft. (1440 m) N60°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

496. At elevation of 2050 ft. on a hillside, 4100 ft. (1250 m) N59°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

497. At elevation of 2185 ft. on south side of ridge, 3685 ft. (1123 m) N58°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Locality is in the "Stewart bed." [Shallow-marine (transgressive) facies.]

498. At elevation of 1850 ft. on west side of stream bank of Devil Canyon, 1550 ft. (472 m) south and 600 ft. (183 m) west of NE corner of section 26, T 3 N, R 17 W of the USGS 7.5-minute topographic quadrangle of Oat Mountain, California (1952), photorevised 1969. [Shallow-marine (transgressive) facies.]

499. At elevation of 1850 ft. on west side of stream bank of Devil Canyon, 1400 ft. (427 m) south and 630 ft. (192 m) west of NE corner of section 26, T 3 N, R 17 W of the USGS 7.5-minute topographic quadrangle of Oat Mountain, California (1952), photorevised 1969. [Shallow-marine (transgressive) facies.]

500. At elevation of 1875 ft. on east side of stream bank of Devil Canyon, 800 ft. (244 m) south and 675 ft. (206 m) west of NE corner of section 26, T 3 N, R 17 W of the USGS 7.5-minute topographic quadrangle of Oat Mountain, California (1952), photorevised 1969. [Shallow-marine (transgressive) facies.]

501. At elevation of 1500 ft. on east side of a small canyon branching northwest of Las Llajas Canyon, 1400 ft. (427 m) north and 1400 ft. (427 m) west of SE corner of section 29, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

502. At elevation of 2150 ft. on a ridge, 5700 ft. (1737 m) N70°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

503. At elevation of 2160 ft. on a ridge, 5725 ft. (1745 m) N69°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

504. At elevation of 2225 ft. on a ridge, 5750 ft. (1753 m) N71°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

505. Bed 98 ft. (30 m) stratigraphically above locality 504, on a traverse bearing N23°W from locality 504. [Shallow-marine (transgressive) facies.]

506. At elevation of 2280 ft. on a ridge, 5600 ft. (1706 m) N65°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

507. Bed 33 ft. (10 m) stratigraphically above locality 506, on a traverse bearing N6°E from locality 506. [Shallow-marine (transgressive) facies.]

508. Bed 6.5 ft. (2 m) stratigraphically above locality 507, on a traverse bearing N6°E from locality 507. [Shallow-marine (transgressive) facies.]

509. Bed 49 ft. (15 m) stratigraphically above locality 508, on a traverse bearing N6°E from locality 508. [Shallow-marine (transgressive) facies.]

510. Bed 108 ft. (33 m) stratigraphically above locality 509, on a traverse bearing N6°E from locality 509. [Shallow-marine (transgressive) facies.]

511. At elevation of 1225 ft. on north side of Chivo Canyon near a major fork in Chivo Canyon, 800 ft. (244 m) north and 800 ft. (244 m) west of SE corner of section 30, T 3 N, R 17 W. Bed is the same one exposed at CSUN localities 457 and 4691. [Shallow-marine (transgressive) facies.]

512a. At elevation of 1275 ft. on east side of a small canyon branching north of Chivo Canyon, 2275 ft. (693 m) south and 525 ft. (160 m) east of NW corner of section 29, T 3 N, R 17 W. [Shallow-marine (regressive) facies.]

512b. Bed 20 ft. (6 m) stratigraphically above locality 512a, on a traverse bearing N35°W from locality 512a. [Shallow-marine (regressive) facies.]

512c. Bed 16 ft. (5 m) stratigraphically above locality 512b, on a traverse bearing N35°W from locality 512b. [Shallow-marine (regressive) facies.]

512d. Bed 30 ft. (9 m) stratigraphically above locality 512b, on a traverse bearing N35°W from locality 512b. [Shallow-marine (regressive) facies.]

513. At elevation of 1870 ft. (570 m) in the streambed of Las Llajas Canyon, 6825 ft. (2080 m) N71°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

514. At elevation of 1875 ft. on north side of stream bank of Las Llajas Canyon, 6800 ft. (2073 m) N71°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

515. At elevation of 1925 ft. (587 m) on the north side of stream bank of Las Llajas Canyon, 6750 ft. (2057 m) N69°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Bed is the same one exposed at CSUN locality 468a. [Shallow-marine (transgressive) facies.]

516. At elevation of 1975 ft. (602 m) on north side of stream bank of Las Llajas Canyon, 6500 ft. (1981 m) N67°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. Bed is the same one exposed at CSUN locality 468b. [Shallow-marine (transgressive) facies.]

517. At elevation of 1950 ft. in a small canyon bottom, between the letters "n" and "y" in the word "Canyon," 5100 ft. (1555 m) N47°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

518. At elevation of 2125 ft. on a small ridge, 5475 ft. (1669 m) N40°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

520. At elevation of 2070 ft., 6500 ft. (1981 m) N78°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

521. At elevation of 2115 ft. on a ridge, 6360 ft. (1938 m) N88°E of NE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

522. Bed 131 ft. (40 m) stratigraphically above CSUN locality 371, on a traverse bearing S14°W from locality 371. [Shallow-marine (transgressive) facies.]

523. At elevation of 2100 ft. on west side of a canyon branching south of Las Llajas Canyon, 5275 ft. (1608 m) N70°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

524. At elevation of 2035 ft. on ridge along south side of Las Llajas Canyon, 6375 ft. (1943 m) N72°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

525. At elevation of 2050 ft. on a hillside, 6325 ft. (1928 m) N74°W of SE corner of section 23, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

526. At elevation of 2055 ft. on a ridge, 2290 ft. (698 m) N67°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

527a. At elevation of 2075 ft. on a ridge, 2325 ft. (709 m) N65°W of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

527b. Bed 13 ft. (4 m) stratigraphically above locality 527a, on a traverse bearing due north of locality 527a. [Shallow-marine (transgressive) facies.]

528. At elevation of 2185 ft. on a ridge, 1400 ft. (427 m) north and 2250 ft. (686 m) west of SE corner of section 26, T 3 N, R 17 W. Locality is in the Santa Susana quadrangle, but the section corner is in the Oat Mountain quadrangle. [Shallow-marine (transgressive) facies.]

529a. At elevation of 1400 ft. on east side of stream bank of Las Llajas Canyon, 1300 ft. (396 m) north and 350 ft. (107 m) east of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

529b. Bed 26.5 ft. (7 m) stratigraphically above locality 529a, on a traverse bearing N27°E of locality 529a. [Shallow-marine (transgressive) facies.]

537. At elevation of 1500 ft. on west side of an amphitheater on west side of Chivo Canyon, 790 ft. (241 m) north and 2250 ft. (686 m) west of SE corner of section 30, T 3 N, R 17 W. Locality is at the type section of the Llajas Formation. [Shallow-marine (transgressive) facies.]

538. At elevation of 1500 ft. on a ridge on west side of Las Llajas Canyon, 1500 ft. (457 m) north and 350 ft. (107 m) west of SE corner of section 29, T 3 N, R 17 W. [Shallow-marine (transgressive) facies.]

539. Bed 6 ft. (1.8 m) stratigraphically above locality 538, on a traverse bearing N5°E of locality 538. [Shallow-marine (transgressive) facies.]

540. Bed 38 ft. (11.5 m) stratigraphically below CSUN locality 486, on a traverse bearing S28°E from locality 486. [Shallow-marine (transgressive) facies.]

541. At elevation of 1325 ft. on north bank of stream bank of Chivo Canyon, 2800 ft. (853 m) north and 1175 ft. (358 m) east of SE corner of section 29, T 3 N, R 17 W. [Outer shelf and slope channel facies.]

542. At elevation of 1315 ft. on ridge near mouth of Las Llajas Canyon, 2200 ft. (671 m) north and 800 ft. (244 m) east of SW corner of section 32, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

543. At elevation of 1460 ft. on divide between Bus and Montgomery Canyons, 600 ft. (183 m) south and 1500 ft. (457 m) east of NW corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Shallow-marine (transgressive) facies.]

544. At elevation of 1230 ft. on a small ridge, 1025 ft. (312 m) north and 415 ft. (127 m) west of SE corner of section 19, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Shallow-marine (regressive) facies.]

545. At elevation of 1120 ft. on east side of Bus Canyon, 580 ft. (177 m) south and 1410 ft. (430 m) west of NE corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

546. At elevation of 1500 ft. on east side of divide between Bus and Trough Canyons, 700 ft. (213 m) south and 200 ft. (61 m) east of NW corner of section 27, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Shallow-marine (transgressive) facies.]

547. At elevation of 1010 ft. on east side of a roadcut, 650 ft. (198 m) south of NE corner of section 21, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Shallow-marine (regressive) facies.]

548. At elevation of 947 ft. on south side of Simi Arroyo just above the streambed, 1100 ft. (335 m) north and 1750 ft. (553 m) west of SE corner of section 12, T 2 N, R 18 W. Locality is equivalent to UCLA locality 5837. [Shallow-marine (transgressive) facies.]

700. At elevation of 1100 ft. along east side of road in Bus Canyon, 750 ft. (229 m) south and 1500 ft. (457 m) west of NE corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

701. At elevation of 1160 ft. along east side of Bus Canyon, 800 ft. (244 m) south and 1400 ft. (427 m) west of NE corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

702. At elevation of 1420 ft. along a ridge, 900 ft. (274 m) south and 680 ft. (207 m) west of NE corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. Locality is equivalent to UCMP locality 7193 and UCLA locality 7070. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

703. At elevation of 1430 ft. along a ridge, 780 ft. (238 m) south and 580 ft. (177 m) west of NE corner of section 28, T 2 N, R 18 W of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. Locality is a few meters stratigraphically above locality 702. [Lowermost part of shallow-marine (transgressive) facies.]

704. At elevation of 1320 ft. along divide between Bus and Trough Canyons, 180 ft. (55 m) south and 90 ft. (27 m) west of NE corner of section 28 of the USGS 7.5-minute topographic quadrangle of Thousand Oaks, California (1950), photorevised 1967. [Shallow-marine (transgressive) facies.]

705. At elevation of 1240 ft. along a dip-slope just south of the mouth of Las Llajas Canyon, 2450 ft. (747 m) north and 450 ft. (137 m) east of SW corner of section 32, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

706. At elevation of 1250 ft. along a small ridge on east side of Chivo Canyon where it bends sharply to the northeast, 700 ft. (213 m) north and 590 ft. (180 m) west of SE corner of section 30, T 3 N, R 17 W. [Interfingering coastal alluvial-fan facies and shallow-marine (transgressive) facies.]

CAS LOCALITIES

25. On east bank of Little River at its confluence with Umpqua River, near center of section 19, T 26 S, R 3 W. Roseburg quadrangle, Douglas County, Oregon.

364. Exact location unknown. Aliso Creek (now known as Devil Canyon), section 25, T 3 N, R 17 W, near Chatsworth, California, Los Angeles County.

372. Exact location unknown. Aliso Canyon (now known as Devil Canyon), section 23, T 3 N, R 17 W, near Chatsworth, California, Los Angeles County.

393. Devil Canyon, SE ¼ of the NW ¼ of section 26, T 3 N, R 17 W, Santa Susana quadrangle, California.

711. East side of Grapevine Creek near point where it enters valley floor, Tejon quadrangle, Kern County, California.

792. West side of Tecuya Creek, about 1 mile south of where stream flows out on valley floor, Tejon quadrangle, Kern County, California.

HERMAN SCHYMICZEK LOCALITY

HS-A-11(4). Bed 92 ft. (28 m) stratigraphically above CSUN locality 4691, on a traverse bearing due north from locality 4691.

LACMIP LOCALITY

461-B. On the northern slope of a small canyon intersecting Las Llajas Canyon from the east. It is 200 ft. (61 m) from the top of the Llajas Formation, Las Llajas Canyon, Santa Susana Mountains, Ventura County, California.

SU LOCALITY

2696. Chivo Canyon, 5 km N20°E of Bench Mark 961 at Santa Susana, Santa Susana quadrangle, Ventura County, California.

UCMP LOCALITIES

337. About 5 km south of Martinez, on the east side of the road to Walnut Creek, Concord quadrangle, Contra Costa County, California.

452. On road in Grapevine Creek, SW ¼ of the SE ¼ of section 20, T 10 N, R 19 W, Tejon quadrangle, Kern County, California.

672. South portion of crest of Parson's Peak, SE ¼ of the NW ¼ of section 24, T 18 S, R 14 E, Coalinga quadrangle, Fresno County, California.

1427. SW ¼ of section 11, NE of Wall Point, south side of Mount Diablo, California.

1817. Opposite the place where Urruttia Canyon enters Salt Creek, 100 ft. (30 m) up fourth small draw from west end of ridge, SW ¼ of the NW ¼ of section 15, T 18 S, R 14 E, Coalinga quadrangle, Fresno County, California.

1853. Marysville Buttes, N ½ of section 28, T 16 N, R 1 E, Marysville Buttes quadrangle, Sutter County, California.

2226. Longitude 117°14′W, latitude 33°50′N, SE of Soledad Mountain, north of Ladrillo Station, Southern Pacific Railroad, Rose Canyon, La Jolla quadrangle, San Diego County, California.

2287. West side of Domengine Canyon, SW corner of the SW ¼ of the SE ¼ of section 29, T 18 S, R 15 E, Fresno County, California.

2295. Longitude 120.1°W, latitude 36.1°N, near Domengine Ranch, Fresno County, California.

3296. Exact location unknown. Aliso Canyon (now known as Devil Canyon), SE ¼ of the SE ¼ of section 23, T 3 N, R 17 W, Santa Susana quadrangle, Ventura County, California.

3304. Exact location unknown. Aliso Canyon (now known as Devil Canyon, section 36, T 3 N, R 17 W, Santa Susana quadrangle, Los Angeles County, California.

3310. Exact location unknown. Probably Simi Hills, Santa Susana quadrangle, California.

3976. Seven-eighths of a mile (1.4 km) north of Ladrillo Station, Southern Pacific Railroad, in first canyon east of Rose Canyon, elevation 259 ft., La Jolla quadrangle, San Diego County, California.

3981. At 15 m above high-tide level in small gully 0.4 km south of mouth of Soledad Valley, La Jolla quadrangle, San Diego County, California.

3989. 0.2 mi. (0.3 km) north of the top of the "y" of "Tecolote Valley," on the east side of the valley, elevation 100 ft., La Jolla quadrangle, San Diego County, California.

3990. On the east side of canyon in bottom of Rose Creek, 0.3 mi. (0.5 km) east of "t" of "Soledad Mountain," La Jolla quadrangle, San Diego County, California.

3993. In bottom of Rose Creek where creek makes a strong bend to west, 0.2 mi. (0.3 km) south of Bench Mark 176, 2 mi. (3.2 km) east of La Jolla, La Jolla quadrangle, San Diego County, California.

4169. About 500 ft. (152 m) east of ranch house in Big Tar Canyon on east line of section 18, near point where road crosses creek, Garza Peak quadrangle, Kings County, California.

4170. On west side of Big Tar Canyon, where it crosses the Eocene section, Garza Peak quadrangle, Kings County, California.

4175. No locality data available. Probably Domengine Ranch area, north of Coalinga, Domengine Ranch quadrangle, Fresno County, California.

5062. In sea cliff south of mouth of Soledad Valley, due west of midpoint between "P" and "u" of Pueblo," La Jolla quadrangle, San Diego County, California.

5069. 0.4 inches SSE of the "a" in "Morena" in a branch canyon of Tecolote Valley to the north, elevation 150 ft., La Jolla quadrangle, San Diego County, California.

5080. North side of Soledad Valley, at McGonigle Canyon, NE ¼ of section 36, T 14 S, R 4 W, La Jolla quadrangle, San Diego County, California.

5085. 2.62 inches north of the top of the "S" of "Soledad Mountain," on the north side of the creek, on a small ridge formed by the creek and sea cliff, elevation 75 ft., La Jolla quadrangle, San Diego County, California.

5089. 300 ft. (91 m) north of the Scripps Institution pier, in the conglomerate above the mudstone. In the sea cliff, elevation 10 ft., La Jolla quadrangle, San Diego County, California.

7000. Exact location unknown. Las Llajas Canyon, in first canyon on north side of road, Santa Susana quadrangle, California.

7002. At elevation of 1750 ft., in road near top of last western spur which extends northward out of Las Llajas Canyon. In shales striking north just south of east–west fault which is made prominent by the Meganos Conglomerate which parallels it on the north side, Santa Susana quadrangle, Ventura County.

7003. At elevation of 1760 ft. in sandstone exposed in deep washout on south side of second large canyon which enters Llajas Canyon from the east. Washout is about 100 yards east of mouth of canyon. Fossils are found in ledge on west side of washout and near top. Sandstone here dips with slope of canyon side and from west wall of east–west fault which crosses Llajas Canyon south of this locality, Santa Susana quadrangle, Ventura County.

7004. About 300 ft. (91 m) east of locality 7003 in next small canyon which enters Llajas Canyon from the east just south of the most northerly extension of the 1500-ft. contour, Santa Susana quadrangle, Ventura County. Locality is equivalent to CSUN locality 374.

7005. No locality data available. Probably Las Llajas Canyon area, Santa Susana quadrangle, California.

7015. About 5500 ft. (1676 m) S69°E of Bench Mark at Santa Susana, Santa Susana quadrangle, Ventura County.

7182. Boulder from second draw on east side of Live Oak Canyon, Tejon Ranch, Kern County, California.

7193. About 600 ft. (183 m) east of and apparently slightly stratigraphically beneath locality 7194, which is along the top of a 1400-ft. ridge extending NW from third main ridge west of Runkle's Ranch on the ridge on which there is an abandoned well and road leading up to it, Simi Valley, California. Locality is equivalent to CSUN locality 702 and UCLA locality 7070.

7195. In the creek bed about 60 ft. (18 m) north of the second falls or 300 ft. (91 m) north of the mouth of the first small draw which enters Las Llajas Canyon west of the point where the Meganos Conglomerate crosses the road, Santa Susana quadrangle, Ventura County, California.

7200. No locality data available. Probably Live Oak Canyon area, Tejon Ranch, Kern County, California.

A-661. On east bank of Little River between the highway bridge and the first bend of the stream east of the junction with the North Umpqua River, center of section 19, T 26 S, R 3 W, Douglas County, Oregon.

A-819. Lowest reef bed on side of hill just east of and above first saddle south of Big Tar Canyon, Garza Peak quadrangle, Kings County, California.

A-993. Second draw past Marrland Canyon (now known as Las Llajas Canyon) at second small falls up draw approximately 600 ft. (183 m), Santa Susana quadrangle, Ventura County, California.

A-994. About 225 to 300 ft. (69 to 91 m) down the canyon from locality A-993 on west side of canyon about 60 ft. (18 m) from streambed, Santa Susana quadrangle, Ventura County, California.

A-1003. Exact location unknown. Pine Canyon, Mount Diablo, Contra Costa County, California.

A-1027. Valdes Ranch, on branch of Silver Creek, Vallecitos, center of east part of SW ¼ of section 4, T 16 S, R 12 E. Approximately where 120°40′ parallel crosses most northerly intermittent stream indicated on section 4, Panoche quadrangle, Fresno County, California.

A-1219. Base of Domengine Formation on west side, near top, of long ridge extending NW of 2126-ft. hill on line between sections 9 and 16, T 19 S, R 15 E, Domengine Ranch quadrangle, California.

A-1280. Near center of north edge of section 20, on hill immediately south of point where the Big Tar–McLure Valley road crosses saddle at head of steam running into McLure Valley, 45 ft. (14 m) below uppermost fossiliferous layer, Garza Peak quadrangle, Kings County, California.

A-3042. On ridge in blue clay shale member above conglomerate member at base of Llajas Formation, center of SE ¼ of the SE ¼ of section 10, T 3 N, R 17 W, Santa Susana quadrangle, Los Angeles County, California.

UCLA LOCALITY

6616. West end of ridge south of Las Llajas Canyon, 2525 ft. (770 m) north and 575 ft. (175 m) east of SW corner of section 32, T 3 N, R 17 W, Santa Susana quadrangle, Ventura County, California.

UCR LOCALITY

4865. In a roadcut on the southwest side of California State Highway 78, 5.2 km SE of Vista and 4.8 km NW of San Marcos, at longitude 117°12′39″W, latitude 33°09′47″N, in northern San Diego County, California.

UO LOCALITY

144. About 2.5 mi. (4 km) up Fall Creek from Little River on Mathews farm in NE ¼ of section 6, T 27 S, R 3 W, Douglas County, Oregon.

USGS LOCALITIES

4617. On SW flank of Reef Ridge, north of McLure Valley, 2¼ mi. (3.6 km) SSE of El Cerrito oil well, in section 27, T 23 S, R 17 E, Cholame quadrangle, Kings County, California.

4619. North of Coalinga, 15 mi. (24 km) SW of Domengine's Ranch, T 18 S, R 15 E, Coalinga quadrangle, Fresno County, California.

UW LOCALITIES

329. On north bank of the Cowlitz River at bend 1.5 to 2.5 km east of Vader, section 28, T 1 N, R 2 W, Lewis County, Washington.

358. Joice Station, ¼ mi. (0.4 km) east of Tongue Point Railroad, Port Crescent, section 22, T 31 N, R 8 W, Clallam County, Washington.

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LITERATURE CITED

Abbott, R.T. 1968a. Seashells of North America. Golden Press, New York. 280 pp.

———. 1968b. The helmet shells of the world (Cassidae), Part 1. Indo-Pacific Mollusca 2(9):15–200.

———. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Company, New York. 663 pp.

Abbott, R.T., and S.P. Dance. 1982. Compendium of sea shells. E.P. Dutton, New York. 411 pp.

Adams, Arthur. 1850. *In* Sowerby, G.B., Thesaurus conchyliorum, or monographs of genera of shells, vol. 2. London.

———. 1864. On the species of *Neara* found in the seas of Japan. Annales Magasin Naturelle Histoire, sér. 3, 13: 206–209.

Adams, Henry, and Arthur Adams. 1853–1858. The genera of recent Mollusca; arranged according to their organization. 3 vols. John Van Voorst, London. 661 pp.

Addicott, W.O. 1970. Latitudinal gradients in Tertiary molluscan faunas of the Pacific Coast. Palaeogeography, Palaeoclimatology, Palaeoecology 8:287–312.

Advocate, D.M. 1982. Depositional environments of the Maniobra Formation, northwestern Orocopia Mountains, Riverside County, California. California State University, Northridge, Unpublished Master of Science thesis. 130 pp.

Agassiz, L.J.R. 1836. Mémoires de la Société Science Naturelle Neuchâtel, vol. 1. Paris.

———. 1838–1843. Recherches sur les poissons fossiles. Mémoires de la Société Science Naturelle Neuchâtel 3: 73–357.

Aldrich, T.H. 1886. Preliminary report on the Tertiary fossils of Alabama and Mississippi. Geological Survey of Alabama, Bulletin 1 (1):15–60, 6 pls.

———. 1911. New Eocene fossils from the southern Gulf States. Bulletins of American Paleontology 5(22). 24 pp.

Anderson, F.M. 1905. A stratigraphic study in the Mount Diablo Range of California. California Academy of Sciences, Proceedings, ser. 3, 2(2):155–248.

Anderson, F.M., and G.D. Hanna. 1925. Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. California Academy of Sciences, Occasional Papers 11:1–249.

———. 1928. *Solen novacularis,* a name for an Eocene fossil from California. The Nautilus 42(2):65–66.

Anton, H.E. 1839. Verzeichniss der Conchylien welche sich in der Sammlung von Herman Eduard Anton befinden. Halle. 110 pp.

Armentrout, J.M. 1975. Molluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. Pages 14–28 *in* Weaver, D.E., G.R. Hornaday, and Ann Tipton, eds., Future energy horizons of the Pacific Coast; Paleogene symposium and selected technical papers. American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, and Society of Economic Geologists, Pacific Sections, Annual Meeting.

Arnold, Ralph. 1907. New and characteristic species of fossil mollusks from the oil-bearing Tertiary formations of southern California. United States National Museum, Proceedings 32:525–546.

———. 1909. Environment of the Tertiary faunas of the Pacific Coast of the United States. Journal of Geology 17:509–533.

———. 1910. Paleontology of the Coalinga district, Fresno and Kings Counties, California. United States Geological Survey, Bulletin 396:1–173.

Arnold, Ralph, and H. Hannibal. 1913. The marine Tertiary stratigraphy of the North Pacific coast of America. American Philosophical Society, Proceedings 52:559–605.

Baldwin, E.M. 1974. Eocene stratigraphy of southwestern Oregon. Oregon Department of Geology and Mineral Industries, Bulletin 83. 40 pp.

Basterot, B. de. 1825. Description géologique du bassin tertiaire du sud-ouest de la France, première partie comprenant les observations générales sur les Mollusques fossiles. Paris Société Histoire Naturelle, Mémoire 2:1–100.

Bell, Thomas. 1858. A monograph of the fossil malacostracous of Great Britain. Part 1, Crustacea of the London Clay. Palaeontographical Society of London. 44 pp.

Bellardi, Luigi. 1872–1890. I molluschi dei terreni terziari del piemonte e della Liguria. Musei di Zoologia ed Anatomia comparata della R. Università di Torino, Bollettino, pts. 1–5.

Bentson, Herdis. 1940. A systematic study of the fossil gastropod *Exilia.* University of California, Publications in Geological Sciences 25(5):199–238.

Berggren, W.A., D.V. Kent, and J.J. Flynn. Paleogene geochronology and chronostratigraphy. *In* Snelling, N.J., ed., Geochronology and the geological record. Geological Society of London, Special Paper (in press).

Berthiaume, S.A. 1938. Orbitoids from the Crescent Formation (Eocene) of Washington. Journal of Paleontology 12:494–497.

Blainville, H.M.D. de. 1814. Mémoire sur la classification méthodique des animaux mollusques, et établissement d'une nouville considération pour y parvenir. Société Philomathématiques Paris, Bulletin, pp. 175–180.

———. 1816–1830. Vers et zoophytes. *In* Dictionnaire des sciences naturelles. Part 2, Règne organisé. 60 vols.

Blondeau, Alphonse, and E.E. Brabb. 1983. Large foraminifers of Eocene age from the Coast Ranges of California. Pages 41–48 *in* Brabb, E.E., ed., Studies in Tertiary stratigraphy of the California Coast Ranges. United States Geological Survey, Professional Paper 1213.

Born, Ignatius. 1780. Testacea Musei Caesarei Vindobonensis. Joannis Pauli Kraus, Vienna. 442 pp.

Bronn, H.G. 1837–1838. Lethaea geognostica oder Abbildungen und Beschreibungen der für die Gebirgsformationen bezeichnenden Versteinerungen. Schweizerbart, Stuttgart. 1346 pp.

———. 1849. Handbuch der Geschichte der Natur. Index Palaeontologicus, vol. 3 (pt. 3). Stuttgart. 976 pp.

Bruguière, J.G. 1789–1816. Encyclopédie méthodique ou par ordre et matières. Histoire naturelle des Vers, des Mollusques. 758 pp.

Chavan, Andre. 1969. Superfamily Lucinacea Fleming, 1828. Part N, Mollusca 6, Bivalvia, vol. 2, pp. 491–518 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Chemnitz, J.H. 1780–1795. Neues systematisches conchylien cabinet, vols. 4–11. Bauer and Raspe, Nürnberg.

Children, J.G. 1822–1824. Lamarck's genera of shells, translated from the French. Quarterly Journal of Science, vols. 14–16.

Clark, B.L. 1918. The San Lorenzo Series of middle California. University of California, Publications in Geological Sciences 11(2):45–234.

———. 1921. The stratigraphic and faunal relationships of the Meganos Group, middle Eocene of California. Journal of Geology 29:125–165.

———. 1926. The Domengine horizon, middle Eocene of California. University of California, Publications in Geological Sciences 16(5):99–118.

———. 1929. Stratigraphy and faunal horizons of the Coast Range of California. Privately published. 132 pp.

———. 1934. A new genus and two new species of Lamellibranchiata from the middle Eocene of California. Journal of Paleontology 8(3):270–272, pl. 37.

———. 1938. Fauna from the Markley Formation (upper Eocene) on Pleasant Creek, California. Geological Society of America, Bulletin 49(5):683–730.

———. 1942. New middle Eocene gastropods from California. Journal of Paleontology 16(1):116–119.

Clark, B.L., and D.K. Palmer. 1923. Revision of the *Rimella*-like gastropods from the West Coast of North America. University of California, Publications in Geological Sciences 14(7):277–288.

Clark, B.L., and H.E. Vokes. 1936. Summary of marine Eocene sequence of western North America. Geological Society of America, Bulletin 47:851–878.

Clark, B.L., and Woodford, A.O. 1927. The geology and paleontology of the type section of the Meganos Formation (lower middle Eocene) of California. University of California, Publications in Geological Sciences 17(2): 63–142.

Cole, W.S. 1958. Names and variations in certain American larger Foraminifera, particularly the Discocyclinids. Bulletins of American Paleontology 38:411–429.

———. 1964. Discocyclinidae. Part C, Protista 2, vol. 2, pp. 712–717 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Cole, W.S., and E.R. Applin. 1964. Problems of the geographic and stratigraphic distribution of American middle Eocene larger Foraminifera. Bulletin of American Paleontology 47. 48 pp.

Compagno, L.J.U. 1973. Interrelationships of living elasmobranchs. Pages 15–61 *in* Greenwood, P.H., R.S. Miles, and C. Patterson, eds., Interrelationships of fishes. Supplement Number 1, Journal of the Linnean Society of London, Zoology. Vol. 53.

Conrad, T.A. 1832. Fossil shells of the Tertiary formations of North America. Vol. 1, no. 2. Privately published. 17 pp.

———. 1833. On some new fossil and Recent shells of the United States. American Journal of Science and Arts 23(2):339–346.

———. 1834. Observations on the Tertiary and more recent formations of a portion of the southern states. Appendix, descriptions of new Tertiary fossils from the southern states. Academy of Natural Sciences of Philadelphia, Journal 7:116–157.

———. 1855. Report on the fossil shells collected in California by W.P. Blake. Pages 5–20 *in* Preliminary geological report of W.P. Blake, United States 33rd Congress, 1st session, House Executive Document 129.

———. 1857. Descriptions of the fossil shells. Pages 317–329 *in* Williamson, R.S., Report of explorations in California for railroad routes, United States 33rd Congress, 2nd session, Senate Executive Document 78 and House Executive Document 91, vol. 5, pt. 2, appendix 2.

———. 1860. Description of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Academy of Natural Sciences of Philadelphia, Journal, ser. 2, 4:279–296.

———. 1865. Catalogue of the Eocene and Oligocene testacea of the United States. American Journal of Conchology 1:1–35.

———. 1866. Check list of the invertebrate fossils of North America. Eocene and Oligocene. Smithsonian Miscellaneous Collections 7(200):1–41.

———. 1867. Descriptions of new genera and species of Miocene shells, with notes on other fossil and recent species. American Journal of Conchology 3:257–270.

Cooper, J.G. 1894. Catalogue of Californian fossils, parts 2–5. California State Mining Bureau, Bulletin 4:5–65.

Cossmann, A.E.M. 1888. Note rectificative sur la nomenclature d'un genre de coquilles fossiles. Journal Conchyliologie 36:335.

———. 1889. Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. Gastropodes. Annales de la Société Royale Malacologique de Belgique, vol. 24.

———. 1895–1925. Essais de paléoconchologie comparée. 13 livraisons. Les Presses Universitaires de France, Paris.

Costa, E.M. da. 1776. Elements of conchology: or an introduction to the knowledge of shells. London. 318 pp.

———. 1778. Historia naturalis testaceorum Brittanniae. Private publication, London. 254 pp.

Cox, L.R. 1930. The fossil fauna of the Samana Range and some neighbouring areas. Part 8, The Mollusca of the Hangu shales. Memoirs of the Geological Survey of India, Palaeontologica Indica 15:129–222.

Cox, L.R., et al. 1969. Systematic descriptions. Part N, Mollusca 6, Bivalvia, vols. 1 and 2, pp. 225–952 *in*

Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Crowell, J.C., and Takeo Susuki. 1959. Eocene stratigraphy and paleontology, Orocopia Mountains, southeastern California. Geological Society of America, Bulletin 70: 581–592.

Cushman, J.A. 1917. Orbitoid Foraminifera of the genus *Orthrophragmina* from Georgia and Florida. United States Geological Survey, Professional Paper 108-G:115–124.

———. 1920. The American species of *Orthophragmina* and *Lepidocyclina*. United States Geological Survey, Professional Paper 125D:39–108.

Cushman, J.A., and H.H. McMasters. 1936. Middle Eocene Foraminifera from the Llajas Formation, Ventura County, California. Journal of Paleontology 10(6):497–517.

Dall, W.H. 1886. Reports on the results of dredging . . . in the Gulf of Mexico (1877–1878) and in the Caribbean Sea (1879–1880) . . . . Report on the Mollusca. Part 1, Brachiopoda and Pelecypoda. Harvard Museum of Comparative Zoology, Bulletin 12(6):171–318.

———. 1891. On some new or interesting west American shells obtained from the dredgings of the U. S. Fish Commission steamer *Albatross* in 1888. United State National Museum, Proceedings 14:173–191.

———. 1892. Contributions to the Tertiary fauna of Florida. Part 2. Transactions of the Wagner Free Institute of Science 3:201–473.

———. 1895. Report on Mollusca and Brachiopoda dredged in deep water chiefly near the Hawaiian Islands, with illustrations of hitherto unfigured species from northwest America. United States National Museum, Proceedings 17:675–733.

———. 1902. Illustrations and descriptions of new unfigured, or imperfectly known shells, chiefly American, in the U.S. National Museum. United States National Museum, Proceedings 24(1264):499–566.

———. 1903. Synopsis of the Carditacea and of the American species. Academy of Natural Sciences of Philadelphia, Proceedings 54:695–716.

———. 1904. An historical and systematic review of the frogshells and tritons. Smithsonian Miscellaneous Collections 47:114–144.

———. 1909. Contributions to the Tertiary paleontology of the Pacific Coast. I. The Miocene of Astoria and Coos Bay, Oregon. United States Geological Survey, Professional Paper 59:1–278, 23 pls.

———. 1915. A monograph of the molluscan fauna of the *Orthaulax pugnax* zone of the Oligocene of Tampa, Florida. United States National Museum, Bulletin 90. 173 pp.

Dance, S.P. 1976. The collector's encyclopedia of shells, 2nd ed. McGraw-Hill Book Company, New York. 288 pp.

Defrance, D.F. 1827. Dictionnaire des sciences naturelles, vol. 14, Cuvier, F.G., ed. Strasbourg. 517 pp.

Dell, R.K., and S.P. Dance. 1963. The molluscan genus *Ranella* and the distribution of *Ranella olearium* (Linnaeus). Malacological Society of London, Proceedings 35:159–167.

Deshayes, M.G.P. 1824–1837. Descriptions des coquilles fossiles des environs de Paris. 2 vols. Chez l'auteur and others, Paris. 814 pp.

———. 1825. Anatomie et monographie du genre Dentale. Société d'Histoire Naturelle de Paris 2:322–378.

———. 1856–1866. Description des animaux sans vertèbres découverts dans le bassin de Paris. J.-B. Baillière et fils, Paris. 656 pp.

Dickerson, R.E. 1913. Fauna of the Eocene at Marysville Buttes, California. University of California, Publications in Geological Sciences 7(12):257–298.

———. 1914. The fauna of the *Siphonalia sutterensis* zone in the Roseburg Quadrangle, Oregon. California Academy of Sciences, Proceedings, ser. 4, 4:113–128.

———. 1915. Fauna of the type Tejon: its relation to the Cowlitz phase of the Tejon Group of Washington. California Academy of Sciences, Proceedings, ser. 4, 5(3): 33–98.

———. 1916. Stratigraphy and fauna of the Tejon Eocene of California. University of California, Publications in Geological Sciences 9(17):363–524.

———. 1917. Climatic zones of Martinez Eocene time. California Academy of Sciences, Proceedings, ser. 4, 7: 193–196.

Douvillé, Henri. 1923. Les orbitoides et leur evolution en Amérique. France Société Géologie, Bulletin, sér. 4, 22: 55–100.

Duméril, A.M.C. 1806. Zoologie analytique, ou méthode naturelle de classification des animaux. Paris. 344 pp.

Durham, J.W. 1942. Notes on Pacific Coast Galeodeas. Journal of Paleontology 16(2):183–191.

———. 1950. Cenozoic marine climates of the Pacific Coast. Geological Society of America, Bulletin 61:1243–1264.

Edwards, F.E. 1866. *Pyrula angulata.* Plate 4 *in* Lowry's chart of the characteristic British Tertiary fossils.

Eisenberg, J.M. 1981. A collector's guide to seashells of the world. McGraw-Hill Book Company, New York. 240 pp.

Ekman, S. 1953. Zoogeography of the sea. Sedgwick and Jackson, London. 417 pp.

Fagerstrom, A. 1964. Fossil communities in paleoecology: their recognition and significance. Geological Society of America, Bulletin 75:1197–1216.

Férussac, A.E. de. 1822. Tableaux systématiques des animaux mollusques. Paris. 111 pp.

Filewicz, M.V., and M.E. Hill, III. 1983. Calcareous nannofossil biostratigraphy of the Santa Susana and Llajas Formations, north side Simi Valley. Pages 45–60 *in* Squires, R.L., and M.V. Filewicz, eds., Cenozoic geology of the Simi Valley area, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume and Guidebook.

Finlay, H.I. 1927. A further commentary on New Zealand molluscan systematics. Transactions of the Proceedings of the New Zealand Institute 57:320–485.

Finlay, H.I., and J. Marwick. 1937. The Wangaloan and associated molluscan faunas of Kaitangata-Green Island subdivision. New Zealand Geological Survey Branch, Palaeontology Bulletin 15. 140 pp.

Fischer, Paul. 1880–1887. Manuel de Conchyliologie et de Paléontologie Conchyliologique. F. Savy Librairie, Paris. 1369 pp.

Fischer von Waldheim, G. 1806–1807. Muséum Demidoff, ou catalogue systématique et raisonné des curiosités de la nature et de l'art . . . . 3 vols. Moscou.

Fisher, A.G. 1966. Spatangoids. Part U, Echinodermata 3, pp. 543–628 *in* R.C. Moore, ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Fleming, John. 1817–1821. Conchology. 7 vols. D. Brewster's Edinburgh encylopaedia.

———. 1828. A history of British animals . . . . 8 vols. Bell and Bradfute, Edinburgh. 565 pp.

Forbes, Edward. 1838. Malacologie Monensis. A catalogue of the Mollusca inhabiting the Isle of Man and the neighboring sea. Edinburgh. 63 pp.

Forbes, Edward, and S.C. Hanley. 1848–1853. A history of British Mollusca and their shells. 4 vols. John Van Voorst, London. 2059 pp.

Gabb, W.M. 1860. Description of new species of American Tertiary and Cretaceous fossils. Academy of Natural Sciences of Philadelphia, Journal, ser. 2, 4(4):375–406.

———. 1864. Description of the Cretaceous fossils. Pages 55–243, pls. 9–32, *in* Meek, F.B., and W.M. Gabb, Palaentology of California, Geological Survey of California, vol. 1, Palaeontology. Caxton Press, Philadelphia.

———. 1869. Cretaceous and Tertiary fossils. Geological Survey of California, vol. 2, Palaeontology. Caxton Press, Philadelphia. 299 pp., 36 pls.

———. 1873. On the topography and geology of San Domingo. American Philosophical Society, Transactions 15:49–259.

Galloway, J.J. 1928. A revision of the family Orbitoididae. Journal of Paleontology 2:45–69.

Gardner, Julia. 1926. The nomenclature of the superspecific groups of *Corbula* in the lower Miocene of Florida. The Nautilus 40:41–47.

———. 1939. Notes on fossils from the Eocene of the Gulf Province. United States Geological Survey, Professional Paper 193-B:17–33.

Gardner, Julia, and Edgar Bowles. 1934. Early Tertiary species of gastropods from the Isthmus of Tehuantepec. Journal of the Washington Academy of Sciences, 24(6): 241–248.

Givens, C.R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. University of California, Publications in Geological Sciences 109:1–107, 11 pls.

———. 1979. The gastropod genus *Volutocristata* Gardner and Bowles (Eocene; California, Mexico): a synonym of *Lyrischapa* Aldrich (Eocene; Gulf Coast). Tulane Studies in Geology and Paleontology 15(4):117–127.

Givens, C.R., and M.P. Kennedy. 1976. Middle Eocene mollusks from northern San Diego County, California. Journal of Paleontology 50(5):954–975.

———. 1979. Eocene molluscan stages and their correlation, San Diego area, California. Pages 81–95 *in* Abbott, P.L., ed., Eocene depositional systems, San Diego, California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Field Trip Guide, Geological Society of America Annual Meeting.

Glaessner, M.F. 1969. Decapoda. Part R, Arthropoda 4, pp. 400–533 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Gmelin, J.F. 1788–1793. Linné's Systema Naturae. Editio 13. 3 vols.

Goldfuss, A. 1826–1833. Petrefacta Germaniae. Arnz, Düsseldorf. 252 pp.

Grabau, A.W. 1904. Phylogeny of *Fusus* and its allies. Smithsonian Miscellaneous Collections 44(1417):1–192.

Grant, U.S., IV, and H.R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California. San Diego Society of Natural History, Memoirs 1:1–1036.

Grant, U.S., IV, and L.G. Hertlein. 1938. The West American Cenozoic Echinoidea. University of California, Publications in Mathematical and Physical Sciences 2: 1–226.

Grassé, P.P. 1968. Mollusques gastéropodes et scaphopodes. Traité de Zoologie Anatomie, Systématique, Biologie. Libraires de L'Académie de Médecine, Paris. Vol. 5, 1083 pp.

Gray, J.E. 1808–1856. Synopsis of the contents of the British Museum. British Museum, London. 370 pp.

———. 1847. A list of the genera of Recent Mollusca, their synonyms and types. Zoological Society of London, Proceedings 15:129–219.

Gregorio, M.A. de. 1890. Monographie de la faune Eocénique de l'Alabama et surtout de celle de Claiborne de l'étage Parisien. Annales de Géologie et de Paléontologie, livraisons 7 et 8. 316 pp.

Habe, Tadashige. 1968. Shells of the western Pacific in color, vol. 2, revised edition. Hoikusha Publishing Company, Osaka. 233 pp.

Hanna, G.D. 1924. Rectifications of nomenclature. California Academy of Sciences, Proceedings, ser. 4, 13(10): 151–186.

Hanna, G.D., and L.G. Hertlein. 1943. Characteristic fossils of California. California Division of Mines and Geology, Bulletin 118(2):165–182.

Hanna, M.A. 1927. An Eocene invertebrate fauna from the La Jolla Quadrangle, California. University of California, Publications in Geological Sciences 16(8):247–398.

Harris, G.G. 1897. Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History), Part 1. The Australasian Tertiary Mollusca. London. 407 pp.

Heckel, P.H. 1972. Recognition of ancient shallow marine environments. Pages 226–286 *in* Rigby, J.K., and W.K. Hamblin, eds., Recognition of ancient sedimentary environments. Society of Economic Paleontologists and Mineralogists, Special Publication 16.

Herrmannsen, A.N. 1846–1852. Indicis generum malacozoorum primordia. 2 vols. Theodore Fischeri, Cassel. 1494 pp.

Hertlein, L.G. 1933. A new gryphaeoid oyster from the Eocene of California. San Diego Society of Natural History, Transactions 7:277–282.

Hertlein, L.G., and U.S. Grant, IV. 1944. The Cenozoic Brachiopoda of western North America. University of California, Publications in Mathematical and Physical Sciences 3:1–236.

———. 1972. The geology and paleontology of the marine Pliocene of San Diego, California (Paleontology: Pelecypoda). San Diego Society of Natural History, Memoir 2, pt. 2B. 409 pp., 57 pls.

Hickman, C.J.S. 1969. The Oligocene marine molluscan fauna of the Eugene Formation in Oregon. University of Oregon Museum of Natural History, Bulletin 16:1–112.

———. 1980. Paleogene marine gastropods of the Keasey Formation in Oregon. Bulletins of American Paleontology 78:1–112.

Hinds, R.B. 1843. Descriptions of new shells from the collection of Captain Sir Edward Belcher . . . during the years 1836–1842 . . . . Zoological Society of London, Proceedings 11:36–49.

Houbrick, R.S. 1977. Reevaluation and new description of the genus *Bittium* (Cerithiidae). The Veliger 20(2):101–106.

Howell, B.F. 1962. Worms. Part W, Miscellanea, pp. 144–177 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Hyatt, Alpheus. 1894. Phylogeny of an acquired characteristic. American Philosophical Society, Proceedings 32: 349–647.

Ingram, W.M. 1940. A new *Gisortia.* Journal of the Washington Academy of Sciences 30(9):376–377.

———. 1942. Type fossil Cypraeidae of North America. Bulletins of American Paleontology 27(104):1–32.

International Commission on Zoological Nomenclature. 1964. International code of zoological nomenclature. International Trust for Zoological Nomenclature, London. 176 pp.

Iredale, T. 1913. The generic name to be used for *Murex tritonis* Linné. The Nautilus 27:55–56.

———. 1916. On some new and old molluscan names. Malacological Society of London, Proceedings 12:27–37.

Jeletzky, J.A. 1966. Comparative morphology, phylogeny, and classification of fossil Coleoidea. The University of Kansas Paleontological Contributions, Mollusca, artiele 7, pp. 1–162.

Jousseaume, F.P. 1887. La famille des Cancellariidae. Le Naturaliste, annales 9, sér. 2, pp. 155–157, 163, 192–194, 213, 214, 221–223.

Jukes-Browne, A.J. 1908. On the genera of Veneridae represented in the Cretaceous and older Tertiary deposits. Malacological Society of London, Proceedings 8:148–177.

Jung, Peter. 1974. A revision of the Family Seraphsidae (Gastropoda:Strombacea). Palaeontographica Americana 8(47):5–72.

Keen, A.M. 1944. Catalogue and revision of the gastropod subfamily Typhinae. Journal of Paleontology 18(1):50–72.

———. 1951. The molluscan names in Reiner's "Tavole." The Nautilus 65(1):8–15.

———. 1971. Sea shells of tropical West America, 2nd ed. Stanford University Press, Stanford. 1064 pp.

Keen, A.M., and Herdis Bentson. 1944. Check list of California Tertiary marine Mollusca. Geological Society of America, Special Papers 56:1–280.

Keen, A.M., and Eugene Coan. 1974. Marine molluscan genera of western North America, 2nd ed. Stanford University Press, Stanford. 208 pp.

Keenan, M.F. 1932. The Eocene Sierra Blanca limestone at the type locality in Santa Barbara County, California. Transactions of the San Diego Society of Natural History 7:53–84.

Kennett, J.P. 1982. Marine geology. Prentice-Hall, Englewood Cliffs, New Jersey. 813 pp.

Kennett, J.P., et al. 1975. Cenozoic paleoceanography in the southwest Pacific Ocean, Antarctic glaciation, and the development of the cirum-Antarctic current. Pages 1155–1169 *in* Kennett, J.P., et al., eds., Initial reports of the Deep Sea Drilling Project, vol. 29. United States Government Printing Office, Washington, D.C.

Kew, W.S.W. 1919. Structure and oil resources of the Simi Valley, southern California. United States Geological Survey, Bulletin 691:323–347.

———. 1920. Cretaceous and Cenozoic Echinoidea of the Pacific Coast region of North America. University of California, Publications in Geological Sciences 12:23–236.

———. 1924. Geology and oil resources of a part of Los Angeles and Ventura Counties, California. United States Geological Survey, Bulletin 753:1–202.

Kira, Tetsuaki. 1965. Shells of the western Pacific in color, vol. 1, 2nd ed. Hoikusha Publishing Company, Osaka. 224 pp.

Kleinpell, R.M., and D.W. Weaver. 1963. Oligocene biostratigraphy of the Santa Barbara embayment, California. University of California, Publications in Geological Sciences 43:1–250.

Kobelt, Wilhelm. 1883. Iconographie der schalentragenden europäischen Meeresconchilien. Heft 3. Wiesbaden.

Laiming, Boris. 1940a. Some foraminiferal correlations in the Eocene of San Joaquin Valley, California. Sixth Pacific Science Congress, Proceedings 2:535–568.

———. 1940b. Foraminiferal correlations in Eocene of San Joaquin Valley, California. American Association of Petroleum Geologists, Bulletin 24:1923–1939.

———. 1943. Eocene foraminiferal correlations in California. California Division of Mines, Bulletin 118:193–198.

Lamarck, J.B. de. 1799. Prodome d'une nouvelle classification des coquilles . . . . Mémoires de la Société d'Histoire naturelle de Paris, pp. 63–91.

———. 1801. Système des animaux sans vertèbres ou tableau général des classes, des ordres, et des genres de ces animaux. Paris. 432 pp.

———. 1802–1809. Mémoires sur les fossiles des environs de Paris. Annales du Muséum National d'Histoire Naturelle, vols. 1–9, 12, 14. Variously paged.

———. 1811. Suite de la détermination des espèces de mollusques testacés: continuation du genre Volute et Mitre. Annales du Muséum d'Histoire Naturelle Paris 17:54–80, 195–222.

———. 1815–1822. Histoire naturelle des animaux sans vertèbres. 7 vols. Paris.

Lambert, Jules. 1902. Description des échinides fossiles de la province de Barcelone. Mémoires de la Société Géologique de France, Paléontologie, Mémoire 24:1–128.

Latreille, P.A. 1825. Familles naturelles du règne animal, exposées succintement et dans un order analytique, avec l'indication de leurs genres. Second édition. Paris.

Lea, Isaac. 1833. Contributions to geology. Carey, Lea, and Blanchard, Philadelphia. 227 pp.

Leach, W.E. 1819. A list of invertebrate animals discovered by H.M.S. ship Isabella, in a voyage to the arctic regions. Appendix II, pp. 61–64 *in* Ross, C.J., Voyage of discovery . . . exploring Baffin's Bay. Appendix I, pp. 1–252.

Leriche, Maurice. 1906. Contribution à l'étude des Poissons fossiles du Nord de la France et des régions voisines. Mémoire Société Géologie Nord 5:1–430.

Lewis, W.D. 1940. The geology of the upper Las Llajas Canyon area, Santa Susana Mountains, California. California Institute of Technology, Unpublished Master of Science thesis. 74 pp.

Lindner, Gert. 1978. Seashells of the world. Van Nostrand Reinhold Company, New York. 271 pp.

Link, H.F. 1807. Beschreibung der Naturalien-Sammlung der Universität zu Rostok, vol. 1. Variously paged.

Linné, Carl von. 1758. Systema naturae per regna tria naturae, Editio decima, reformata, Regnum animale, vol. 1. Holmiae. 824 pp.

———. 1766–1767. Systema naturae per regna tria naturae, Editio duodecima, reformata, Regnum animale, vol. 1. Holmiae. 1327 pp.

Ludbrook, N.H. 1960. Scaphopoda. Part I, Mollusca 1, pp. 37–41 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

MacLeay, W.S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. Vol. 5, Invertebratae, pp. 53–71, *in* Andrew Smith, M.D., Illustrations of the zoology of South Africa.

Mallory, V.S. 1959. Lower Tertiary biostratigraphy of the California Coast Ranges. American Association of Petroleum Geologists, Tulsa. 416 pp.

Marincovich, Louie, Jr. 1977. Cenozoic Naticidae (Mollusca:Gastropoda) of the northeastern Pacific. Bulletins of American Paleontology 70(294):169–494.

Marshall, W.B. 1917. The Wangaloa beds. New Zealand Institute, Transactions 49(38):450–460, 4 pls.

Mawe, John. 1823. The Linnaean system of conchology. London. 207 pp.

Mayer-Eymar, Karl. 1877. Systematisches Verzeichniss der Versteinerungen des Parisian der Umgegend von Einsiedeln. Beitragen Geologisch Karte Schweiz 14(26):100 pp.

McLaughlin, R.P., and C.A. Waring. 1915. Petroleum industry of California. California Mining Bureau Bulletin 69. 519 pp. Atlas.

McMasters, J.H. 1932. The Eocene Llajas Formation, Ventura County, California. Stanford University, Unpublished Master of Arts thesis. 70 pp.

McMillan, N.F. 1968. British shells. Frederick Warne and Company, London. 196 pp.

Meek, F.B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country. United States Geological Survey, Territory Annual Report 9:1–629, 45 pls.

Merriam, C.W. 1941. Fossil Turritellas from the Pacific Coast region of North America. University of California, Publications in Geological Sciences 26(1):1–214.

Merriam, C.W., and F.E. Turner. 1937. The Capay middle Eocene of northern California. University of California, Publications in Geological Sciences 24(6):91–114.

Miles, G.A. 1981. Planktonic foraminifers of the lower Tertiary Roseburg, Lookingglass, and Flournoy Formations (Umpqua Group), southwest Oregon. Pages 85–103 *in* Armentrout, J.M., ed., Pacific Northwest Cenozoic biostratigraphy. Geological Society of America, Special Paper 184.

Miller, A.K. 1947. Tertiary nautiloids of the Americas. Geological Society of America, Memoir 23:1–234.

Milne-Edwards, Henri. 1852. Observations sur les affinités zoologiques et la classification naturelle des crustacés. Annales Science Naturelle, Zoologie, sér. 3, 18:109–166.

Milne-Edwards, Henri, and Jules Haime. 1848–1850a. Recherches sur les polypes. Annales Science Naturelle de Paris, vols. 9–13, 15–16.

———. 1850b. A monograph of the British fossil corals. Introduction; corals from the Tertiary and Cretaceous formations. Palaeontographical Society, London. 85 pp.

Montagu, George. 1803–1808. Testacea Britannica, or natural history of British shells, marine, land and freshwater. 2 vols. London. 789 pp.

Monterosato, T.A. di. 1884. Nomenclatura generica e spezifica di alcune conghiglie mediterranee. Palermo. 152 pp.

Montfort, P.D. 1808–1810. Conchyliologie systématique et classification méthodique de coquilles. 2 vols. Paris. 676 pp.

Moore, E.J. 1983. Tertiary marine pelecypods of California and Baja California: Nuculidae through Malleidae. United States Geological Survey, Professional Paper 1228-A:A1–A108, 27 pls.

Mörch, O.A.L. 1852–1853. Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra et Gadea Comes de Yoldi. 8 vols. Hafniae.

———. 1858. Note sur le genre *Volutharpa* Fischer. Journal de Conchyliologie, sér. 2, 3:40–44.

Morris, P.A. 1966. Pacific Coast shells, 2nd ed. Houghton Mifflin Company, Boston. 297 pp.

———. 1975. Shells of the Atlantic and Gulf Coasts and the West Indies, 3rd ed. Houghton Mifflin Company, Boston. 330 pp.

Muir-Wood, H.M., G.F. Elliott, and Kotora Hatai. 1965. Mesozoic and Cenozoic Terebratellidina. Part H, Brachiopoda, vol. 2, pp. 816–857 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

Müller, O.F. 1776. Zoologiae Danicae prodromus seu animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium, 8 vols. Havniae. 282 pp.

Müller, Johannes, and F.G.J. Henle. 1837. Ueber die Gattungen der Plagiostomen. Archiv Naturgeschichte 3:394–401, 434.

———. 1838. On the generic characters of cartilaginous fishes, with descriptions of new genera. Charlesworth's Magazine of Natural History 2:33–37, 88–91.

Munier-Chalmas, E.C.P.A. 1864. Société Linnaeus Normandie, Bulletin 8:99, 108.

Nelson, R.N. 1925. A contribution to the paleontology of the Martinez Eocene of California. University of California, Publications in Geological Sciences 15(11):397–466.

Newton, R.B. 1922. Eocene Mollusca from Nigeria. Geological Survey of Nigeria, Bulletin 3:1–140.

Nilsen, T.H. 1973. Facies relations in the Eocene Tejon Formation of the San Emigdio and western Tehachapi Mountains, California. Pages 7–23 *in* Fischer, Pete, ed., Sedimentary facies changes in Tertiary rocks, California Transverse and southern Coast Ranges. Society of Economic Paleontologists and Mineralogists, Los Angeles.

Nomland, J.O. 1916. Corals from the Cretaceous and Tertiary of California and Oregon. University of California, Publications in Geological Sciences 9(5):59–76.

Nordsieck, Fritz. 1968. Die europäischen Meeres-gehauseschnecken (Prosobranchia). Gustav Fischer Verlag, Stuttgart. 273 pp.

———. 1969. Die europäischen Meeresmuscheln (Bivalvia). Gustav Fischer Verlag, Stuttgart. 256 pp.

Okada, Hisatake, and David Bukry. 1980. Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation (Bukry, 1973; 1975). Marine Micropaleontology 5:321–325.

Olsson, A.A. 1961. Mollusks of the tropical eastern Pacific: Panama-Pacific Pelecypoda. Paleontological Research Institution, Ithaca. 574 pp., 86 pls.

Orbigny, A.D. d'. 1843. Paléontologie française. Terrains crétaces 3:1–807.

Orr, W.N., and M.A. Kooser. 1971. Oregon Eocene decapod Crustacea. The Ore Bin 33:119–129.

Palmer, D.B.K. 1923. A fauna from the middle Eocene shales near Vacaville, California. University of California, Publications in Geological Sciences 14(8):289–318.

Palmer, K.V.W. 1927–1929. The Veneridae of eastern America, Cenozoic and Recent. Palaeontographica Americana 1(5):209–522, 45 pls.

———. 1967. A comparison of certain Eocene molluscs of the Americas with those of the western Tethys. Pages 183–193 *in* Adams, C.G., and D.V. Ager, eds., Aspects of Tethyan biogeography. Systematics Association Publication, no. 7.

———. 1974. Composition with relationships of Paleocene and Eocene molluscan fauna of the East Americas. Pages 468–485 *in* Contributions to the geology and paleobiology of the Caribbean and adjacent areas. Verhandlungen der Naturforschenden Gesellschaft in Basel, vol. 84.

Palmer, K.V.W., and D.C. Brann. 1965–1966. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Bulletins of American Paleontology 48:1–1057 (2 parts).

Perry, George. 1810–1811. Arcana, or the Museum of Natural History; containing the most recent discovered objects . . . . London.

Peterson, G.L., and P.L. Abbott. 1979. Mid-Eocene climatic change, southwestern California and northwestern Baja California. Palaeogeography, Palaeoclimatology, Palaeoecology 26:73–87.

Philippi, R.A. 1853. Handbuch der Conchyliologie und Malakozoologie. Halle. 547 pp.

Pilsbry, H.A., and A.A. Olsson. 1954. Systems of the Volutidae. Bulletins of American Paleontology 35(152):271–306.

Poli, G.S. 1791–1795. Testacea utriusque Siciliae, eorumque historia et anatomia. 3 vols. Parma.

Poore, R.Z. 1980. Age and correlation of California Paleogene benthic foraminiferal stages. United States Geological Survey, Professional Paper 1162-C. 8 pp.

Powell, A.W.B. 1942. The New Zealand Recent and fossil Mollusca of the family Turridae, with general notes on turrid nomenclature and systematics. Bulletin of Auckland Institute and Museum, no. 2. 188 pp.

Quayle, E.H. 1932. Fossil corals of the genus *Turbinolia* from the Eocene of California. Transactions of the San Diego Society of Natural History 7(10):91–109.

Rafinesque, C.S. 1809. Indice d'ittiologia Siciliana. Messina, pp. 12–167.

———. 1815. Analyse de la nature, ou tableau de l'univers et des corps organisées. Palermo.

Rathbun, M.J. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. United States National Museum, Bulletin 138:1–155.

Rehder, H.A. 1973. The family Harpidae of the world. Indo-Pacific Mollusca 3(16):207–274.

Reuss, A.E. 1859. Zur Kenntnis fossiler Krabben. Akademie Wissenschaftlich Wien, Denkschrift 17:1–90, 24 pls.

Rios, E.C. 1970. Coastal Brazilian seashells. Museu Oceanográfico de Rio Grande. 255 pp.

Risso, J.A. 1810–1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes. 5 vols. Paris.

Röding, P.F. 1798. Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturae quae olim collegerat. J.F. Bolten, M.D., ed., Pars Secunda. Typis Johan Christi Trappii, Hamburg. 199 pp.

Römer, Eduard. 1857. Kritische Untersuchung der Arten des Molluskengeschlechts Venus bei Linné und Gmelin mit Berücksichtigung der später Beschriebenen Arten. J. Georg Luckhardt, Cassel. 136 pp.

Ross, C.A. 1974. Paleogeography and provinciality. Pages 1–17 *in* Ross, C.A., ed., Paleogeographic provinces and provinciality. Society of Economic Paleontologists and Mineralogists, Tulsa.

Sacco, Frederico. 1890–1904. I Molluschi dei terreni terziari del Piemonte e della Liguria descritti da Luigi Bellardi. Musei di Zoologia ed Anatomia comparata della R. Università di Torino, Bollettino pts. 6–30.

Saul, L.R. 1983. Notes on Paleogene turritellas, venericardias, and molluscan stages of the Simi Valley area, California. Pages 71–80 *in* Squires, R.L., and M.V. Filewicz, eds., Cenozoic geology of the Simi Valley area, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume and Guidebook.

Savin, S.M., R.G. Douglas, and F.C. Stehli. 1975. Tertiary marine paleotemperatures. Geological Society of America, Bulletin 86:1499–1510.

Schenck, H.G. 1926. Cassididae of western America. University of California, Publications in Geological Sciences 16(4):69–98.

———. 1929. *Discocyclina* in California. Transactions of the San Diego Society of Natural History 5(14):211–240.

———. 1931. Cephalopods of the genus *Aturia* from western North America. University of California, Publications in Geological Sciences 19(19):435–490.

———. 1936. Nuculid bivalves of the genus *Acila*. Geological Society of America, Special Paper 4:1–149.

Schmidt, F.C. 1818. Versuch über die beste Einrichtung zur Aufstellung, Behandlung und Aufbewahrung der verschieden Naturkorper und Gegenstande der Kunst. Gotha. 252 pp.

Schumacher, C.F. 1817. Essais d'un nouveau système des habitations des vers testacés. 4 vols. Cophenhagen. 287 pp.

Schymiczek, H.B. 1983a. Benthic Foraminifera and paleobathymetry of the Eocene Llajas Formation, north side of Simi Valley, California. Pages 97–108 *in* Squires, R.L., and M.V. Filewicz, eds., Cenozoic geology of the Simi Valley area, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume and Guidebook.

———. 1983b. Benthic Foraminifera and paleobathymetry of the Eocene Llajas Formation, southwestern Santa Susana Mountains, California. California State University, Northridge, Master of Science thesis. 76 pp.

Schymiczek, H.B., and R.L. Squires. 1981. Biostratigraphy of discocyclinid-bearing beds, Eocene Llajas Formation, southwestern Santa Susana Mountains, California. American Association of Petroleum Geologists, Bulletin 65:989.

Scopoli, J.A. 1777. Introductio ad historiam naturaleum sistens genera lapidum, plantarum et animalus . . . . Pragae. 506 pp.

Seiden, Hyman. 1972. Geology of Las Llajas Canyon, Ventura County, California. University of California Los Angeles, Unpublished Master of Science thesis. 33 pp.

Shepard, F.P., R.R. Lankford, and E.D. Milow. 1957. La Jolla area field trip syllabus. Pacific Section, Society of Economic Paleontologists and Mineralogists, Field Trip Guide. 10 pp.

Smith, J.P. 1919. Climatic relations of the Tertiary and Quaternary faunas of the California region. California Academy of Sciences, Proceedings, ser. 4, 9(4):123–173.

Smith, J.T. 1970. Taxonomy, distribution, and phylogeny of the cymatiid gastropods *Argobuccinum, Fusitriton, Mediargo,* and *Priene.* Bulletins of American Paleontology 56:445–573.

———. 1975. Age, correlation, and possible Tethyan affinities of mollusks from the Lodo Formation of Fresno County, California. Pages 464–483 *in* Weaver, D.W., G.R. Hornaday, and Ann Tipton, eds., Future energy horizons of the Pacific Coast; Paleogene symposium and selected technical papers. American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, and Society of Economic Geologists, Pacific Sections, Annual Meeting.

Solander, D.C. 1766. Description of species. Pp. 1–43 *in* Gustavo Brander, Fossilia Hantoniensia collecta, et in Museuo Britannico deposita. London.

Sowerby, James. 1812a–1846a. Mineral conchology, 7 vols. London.

———. 1837b–1844b. Mineral-conchologie Grossbritanniens . . . . Deutsch bearbeitet von E. Desor. Durchgesehen und mit Anmerkungen und Berichtigungen versehen von L. Agassiz. Solothurn. 689 pp.

Spengler, Lorenz. 1794–1802. Over det taskallede slaegt tellinerne. 5 vols. Skriv. Naturhist. Selskabet. Copenhagen.

Squires, R.L. 1977. Middle Eocene molluscan assemblage and stratigraphy, lower Piru Creek, Transverse Ranges, California. California Division of Mines and Geology, Special Report 129:81–86.

———. 1979. New macrofossil occurrences, Stewart bed, middle Eocene Llajas Formation, Llajas Canyon, Santa Susana Mountains, California. Geological Society of America, Cordilleran Section Meeting [Abstracts] 11(3): 129.

———. 1981. A transitional alluvial to marine sequence: the Eocene Llajas Formation, southern California. Journal of Sedimentary Petrology 51(3):923–938.

———. 1983a. New mollusks from the lower middle Eocene Llajas Formation, southern California. Journal of Paleontology 57:354–362.

———. 1983b. Eocene Llajas Formation, Simi Valley, southern California. Pages 81–95 *in* Squires, R.L., and M.V. Filewicz, eds., Cenozoic geology of the Simi Valley area, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume and Guidebook.

Stanton, T.W. 1896. The faunal relations of the Eocene and Upper Cretaceous on the Pacific Coast. United States Geological Survey, Annual Report 17:1005–1060.

Stewart, R.B. 1927. Gabb's California fossil type gastropods. Academy of Natural Sciences of Philadelphia, Proceedings 78:287–447, pls. 20–32.

———. 1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. Academy of Natural Sciences of Philadelphia, Special Publication 3:1–314, 17 pls.

———. 1946. Geology of Reef Ridge Coalinga district California. United States Geological Survey, Professional Paper 205C:81–115, pls. 11–17.

Stipp, T.F. 1943. Simi oil field. Pages 415–424 *in* Geologic formations and economic development of the oil and gas fields of California. California Division of Mines, Bulletin 118, pt. 3.

Stoliczka, Ferdinand. 1868. The Gastropoda of the Cretaceous rocks of southern India. Memoirs of the Geological Survey of India, Palaeontologica Indica, ser. 5, 2:1–498.

———. 1870–1871. Cretaceous fauna of southern India. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. Geological Survey of India, Palaeontologica Indica, ser. 6, 3:1–535.

Suter, Henry. 1913. Manual of the New Zealand Mollusca. Government Printer, Wellington. 1120 pp.

Sutherland, J.A. 1966. A new species of *Architectonica* from the Santa Susana Mountains, Ventura County, California. Los Angeles County Museum, Contributions in Science 117:1–4.

Swainson, William. 1820–1833. Zoological illustrations, 2 ser. London.

———. 1840. A treatise on malacology or shells and shellfish. London. 419 pp.

Tebble, Norman. 1976. British bivalve seashells, 2nd ed. Her Majesty's Stationery Office, Edinburgh. 212 pp.

Tegland, N.M. 1933. The fauna of the type Blakeley upper Oligocene of Washington. University of California, Publications in Geological Sciences 23:81–174.

Thiele, Johannes. 1925. Gastropoden der deutschen Tiefsee-expedition II. Wissenschaftlich Ergebnis Deutsch Tiefsee-Expedition 17(2):36–282.

———. 1929–1935. Handbuch der systematischen Weichtierkunde. 2 vols. Jena. 1134 pp.

Troschel, F.H. 1852. Verzeichniss der durch Herrn Dr. v. Tschudi in Peru gesammelten Conchylien. Archiv für Naturgeschichte 18(1):151–208.

Turner, F.E. 1938. Stratigraphy and Mollusca of the Eocene of western Oregon. Geological Society of America, Special Paper 10:1–130.

Vail, P.R., R.M. Mitchum, Jr., and S. Thompson, III. 1977. Seismic stratigraphy and global changes of sea level, part 4: Global cycles of relative changes of sea level. Pages 83–97 *in* Payton, C.E., ed., Seismic stratigraphy—applications to hydrocarbon exploration. American Association of Petroleum Geologists, Tulsa, Oklahoma.

Vaughan, T.W. 1900. Eocene and lower Oligocene coral faunas of the United States with a few doubtfully Cretaceous species. United States Geological Survey, Monograph 39:1–263.

———. 1936. New species of orbitoidal Foraminifera of the genus *Discocyclina* from the lower Eocene of Alabama. Journal of Paleontology 10:255–256.

———. 1945. American Paleocene and Eocene larger Foraminifera. Geological Society of America, Memoir 9(1): 1–175.

Verastegui, Pedro. 1953. The Pelecypod genus *Venericardia* in the Paleocene and Eocene of western North America. Palaeontographica Americana 3(25):1–112.

Vokes, H.E. 1935. Notes on the variation and synonymy of *Ostrea idriaensis* Gabb. University of California, Publications in Geological Sciences 23(9):291–304.

———. 1937. The gastropod genus *Harpa* in the Eocene of the western United States. Journal of Paleontology 11(1):10–12, pl. 2.

———. 1939. Molluscan faunas of the Domengine and Arroyo Hondo Formations of the California Eocene. Annals of the New York Academy of Sciences 38:1–246.

———. 1940. Paleoecology of the fauna of the Domengine Formation, middle Eocene, California. Sixth Pacific Science Congress, Proceedings 2:597–605.

———. 1980. Genera of the Bivalvia: a systematic and bibliographic catalogue (revised and updated). Paleontological Research Institution, Ithaca. 307 pp.

Waring, C.A. 1914. Eocene horizons of California. Journal of Geology 22(8):782–785.

———. 1917. Stratigraphic and faunal relations of the Martinez to the Chico and Tejon of southern California. California Academy of Sciences, Proceedings, ser. 4, 7(4): 41–124.

Weaver, C.E. 1905. Contribution to the palaeontology of the Martinez Group. University of California, Publications in Geological Sciences 4(5):101–123.

———. 1912. A preliminary report on the Tertiary paleontology of western Washington. Washington Geological Survey, Bulletin 15:1–80, 15 pls.

———. 1943. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington, Publications in Geology 5(1–3):1–789.

———. 1953. Eocene and Paleocene deposits at Martinez, California. University of Washington Publications in Geology 7:1–102.

Weaver, C.E., and K.V.W. Palmer. 1922. Fauna from the Eocene of Washington. University of Washington Publications in Geology 1(3):1–56.

Weaver, C.E., et al. 1944. Correlation of the marine Cenozoic formations of western North America. Geological Society of America, Bulletin 55:569–598.

Weaver, C.S., and duPont, J.E. 1970. Living volutes. Delaware Museum of Natural History, Monograph Series No. 1, Greenville, Delaware. 375 pp.

Wells, J.W. 1956. Scleractinia. Part F, Coelenterata, pp. 328–444 *in* Moore, R.C., ed., Treatise on invertebrate paleontology. University of Kansas Press, Lawrence.

———. 1957. Corals. Pages 1087–1104 *in* Hedgpeth, J.W., ed., Treatise on marine ecology and paleoecology. Geological Society of America, Memoir 67, vol. 1.

Wenz, Wilhelm. 1938–1944. Gastropoda. Vol. 6, 7 parts, pp. 1–1639 *in* Schindewolf, O.H., ed., Handbuch der Paläozoologie. Gebrüder Borntraeger, Berlin.

White, C.A. 1889. On invertebrate fossils from the Pacific Coast. United States Geological Survey, Bulletin 51:1–102.

Wolfe, J.A. 1977. Paleogene floras from the Gulf of Alaska region. United States Geological Survey, Professional Paper 997. 108 pp.

Wood, William. 1818–1828. Index testaceologicus. 8 vols. Privately published, London. 188 pp.

Woodring, W.P. 1925. Miocene Mollusca from Bowden Jamaica, pelecypods and scaphopods. Carnegie Institute of Washington, Publication 366:1–564, 40 pls.

———. 1928. Miocene mollusks from Bowden, Jamaica. Part 2, Gastropods and discussion of results. Carnegie Institute of Washington, Publication 385:1–564.

———. 1966. The Panama land bridge as a sea barrier. American Philosophical Society, Proceedings 110:425–433.

Woodward, S.P. 1851–1856. A manual of the Mollusca: or rudimentary treatise of recent and fossil shells. John Weale, London. 330 pp.

Zinsmeister, W.J. 1974. Paleocene biostratigraphy of the Simi Hills, Ventura County, California. University of California, Riverside, Unpublished Ph.D. dissertation. 236 pp.

———. 1982. Late Cretaceous–early Tertiary molluscan biogeography of the southern circum-Pacific. Journal of Paleontology 56:84–102.

———. 1983a. Late Paleocene ("Martinez Provincial Stage") molluscan fauna from the Simi Hills, Ventura County, California. Pages 61–70 *in* Squires, R.L., and M.V. Filewicz, eds., Cenozoic geology of the Simi Valley area, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume and Guidebook.

———. 1983b. New late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology 57:1282–1303.

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CONTRIBUTIONS IN SCIENCE

MOLLUSCAN PALEONTOLOGY AND BIOSTRATIGRAPHY OF THE LOWER MIOCENE UPPER PART OF THE LINCOLN CREEK FORMATION IN SOUTHWESTERN WASHINGTON

Ellen J. Moore

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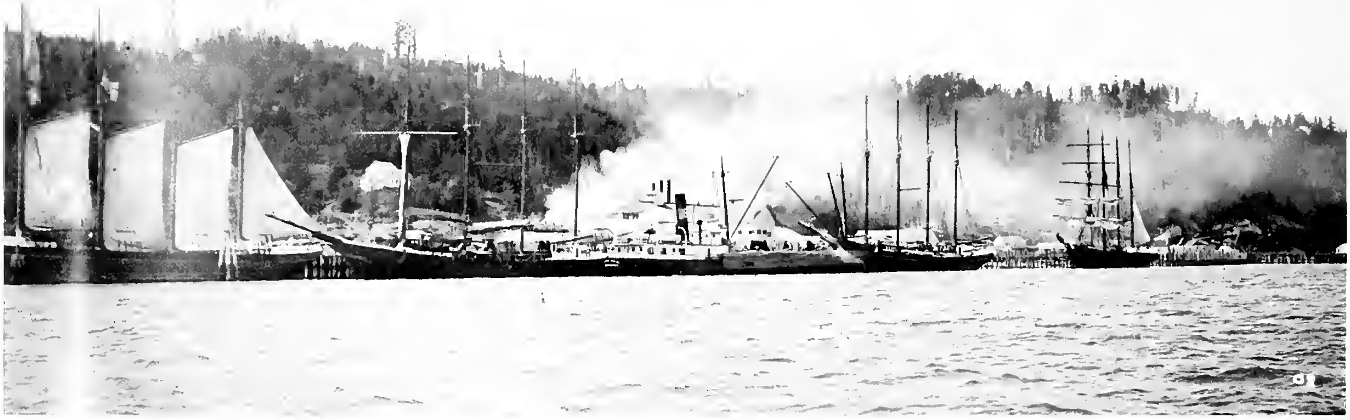

Vessels loading lumber at Knappton, Washington, in 1908. When it was founded in 1867, Knappton was called Cementville, and concretionary rocks served as the raw material for the cement. (Photograph courtesy of Dale Estoos and David Lee Myers.)

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900 Exposition Boulevard
Los Angeles, California 90007

PREFACE

Knappton, Washington, on the Columbia River north of Astoria, Oregon, was named for Jabez Burrell Knapp, who built a cement plant there in 1867, calling the town Cementville. The plant included a large kiln and a cement-barrel factory, but was unable to continue production for more than a few years because of lack of sufficient raw material: fossiliferous concretions and concretionary layers. Knapp then built a sawmill, which supported the company town for 70 years. In 1941, the planing mill caught fire and the blaze quickly spread to other buildings. The wooden water main burned through, leaving the fire fighters helpless, and the town was destroyed. Only a monument and pilings remain at the site to reflect its past history.

A few fossil mollusks were collected from the Knappton area in the early 1900's and deposited in the National Museum of Natural History at Washington, D.C., and the California Academy of Sciences at San Francisco. The small collections contain usually poorly preserved material from both the upper part of the Lincoln Creek Formation and the overlying Astoria Formation, which were not differentiated at that time.

Controversy over the age of the Astoria Formation, whose type locality is just across the river, began in 1865 and revolved especially around the presence of the fossil cephalopod *Aturia.* This cephalopod also was known to occur in the upper part of the Lincoln Creek Formation on the Washington side of the Columbia River, and casual references to Knappton occasionally appeared in the scientific literature. It was not until 1979, however, that a detailed geologic map of the Knappton area was prepared by Ray E. Wells and issued by the U.S. Geological Survey.

The first major collections of fossils from Knappton were made by James L. Goedert and his wife, Gail. The presence of vertebrate fossils, chiefly whales, at Knappton led Goedert to contact the Los Angeles County Museum of Natural History in 1979. His offer to donate the collections to the Los Angeles Museum, and the recognition of the importance of the invertebrate fossils in those collections by Edward C. Wilson, Curator of Invertebrate Paleontology, has led to publications on the barnacles by Victor A. Zullo, the sponges by J. Keith Rigby and D.E. Jenkins, and the mollusks described herein.

This paper is dedicated to James L. Goedert whose generosity has made it possible for specialists to study the remarkable Knappton fossils.

CONTENTS

MOLLUSCAN PALEONTOLOGY AND BIOSTRATIGRAPHY OF THE LOWER MIOCENE UPPER PART OF THE LINCOLN CREEK FORMATION IN SOUTHWESTERN WASHINGTON

Ellen J. Moore[1]

ABSTRACT. The uppermost part of the Lincoln Creek Formation in the Knappton area of southwestern Washington is assigned to the lower Miocene upper part of the Juanian Molluscan Stage (=Saucesian Foraminiferal Stage) and the *Liracassis apta* Molluscan Zone. This part of the Lincoln Creek Formation is correlated with the upper part of the Pysht Formation of the Twin River Group in northwestern Washington.

Fossils, invertebrates and vertebrates, are preserved in concretions that erode out of landslides and accumulate as float along the Columbia River. The molluscan fauna of the upper part of the Lincoln Creek Formation consists of 33 species in 30 genera, including five newly described species in the genera "*Bathybembix,*" *Ancistrolepis, Musashia, Modiolus,* and *Acesta.* Eastern Pacific species in the genus *Musashia* are reviewed. The fauna lived at depths between 100 and 350 m, a bathymetric range substantiated by the inferred ranges of 16 associated phyla also preserved as fossils at Knappton. The nautiloid cephalopod *Aturia,* which is common in the collections, indicates that the water temperature may have been as high as 16°C at a depth of 100 m. The abundance of preserved organic material suggests that free oxygen was depleted in the sediment below the level of bioturbation.

INTRODUCTION

Fossiliferous concretions that have eroded out of landslide blocks from the upper part of the Lincoln Creek Formation occur as float along the Columbia River near the site of Knappton in southwestern Washington (Figs. 1, 2). The Lincoln Creek Formation in this area is part of a homocline, and the sequence dips eastward. The upper part consists of poorly bedded, locally laminated, bioturbated, concretionary dark-gray siltstone. The formation is unconformable upon the upper Eocene siltstones of Cliff Point unit (Wells, 1979).

The invertebrate fauna described in this report is from the uppermost part of the Lincoln Creek Formation (LAM Loc. 5842) and is early Miocene in age. The fauna is assigned to the upper part of the Juanian Mollusean Stage (=Saucesian Foraminiferal Stage) and the *Liracassis apta* [*Echinophoria apta*] Molluscan Zone. The Lincoln Creek Formation is overlain by the lower Miocene part of the Astoria Formation, assigned to the Pillarian Molluscan Stage and the *Vertipecten fucanus* Molluscan Zone (Fig. 3).

Although the fossiliferous concretions are collected as float on the bank of the Columbia River, an approximate stratigraphy is preserved in the landslides because wedge-shaped blocks move south toward the river bank parallel with the strike of the rocks. One locality, informally called the "glass sponge bed" (LAM Loc. 5852), and others below it, called the "decapod crustacean bed" (LAM Loc. 5843) and the "gooseneck barnacle bed" (LAM Loc. 5844), all lie stratigraphically below the major mollusk-bearing unit (the *Aturia* bed) described here (LAM Loc. 5842). Faunas in these four beds are segregated in the float in proper stratigraphic position. The lack of mixing is also characteristic of faunas typical of the overlying Astoria Formation (LAM Loc. 5863).

The geology in the area is complicated by landslides, faults, by few road cuts, and by vegetative cover (Figs. 4, 5). Generally, only sections 100 m or less can be measured in tidal exposures, and the relationship between exposures is often difficult to discern (Figs. 6, 7). Mapping by Wells (1979) portrays the complexities in the area.

Despite the poor exposures, some interpretations can be made. The concretions are continuously being reworked from the landslides and new accumulations appear with sufficient regularity to be collected every two weeks at low tide. The concretions therefore are randomly distributed throughout the unit.

Most of the concretions are spherical and composed of fine-grained siltstone with calcareous cement. A few are cemented by quartz in the central part and calcite at the rim. I believe that the concretions formed early in diagenesis, because the mollusks preserved in the concretions are almost always complete specimens that are neither broken nor

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[1] U.S. Geological Survey, 345 Middlefield Road MS-915, Menlo Park, California 94025, and Research Associate, Invertebrate Paleontology Section, Natural History Museum of Los Angeles County.

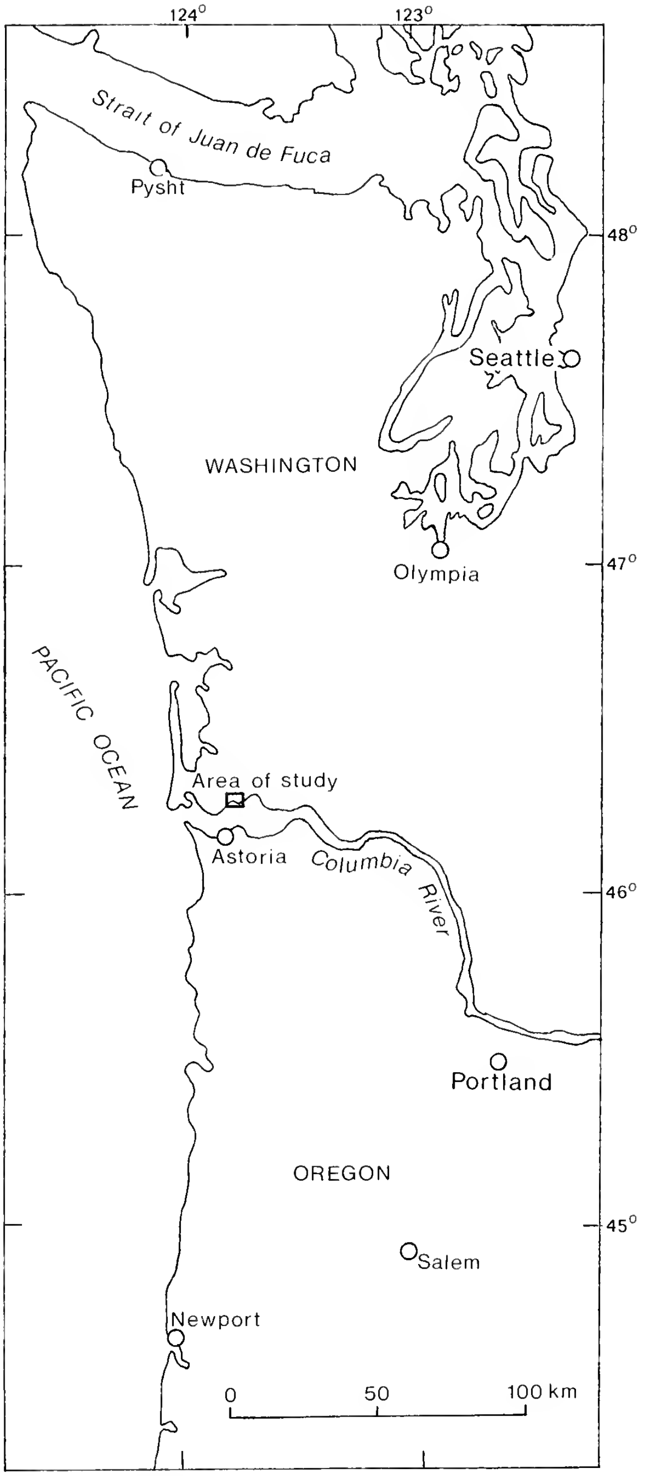

Figure 1. Index map of the Pacific coast showing localities mentioned in the text.

crushed. Delicate features of snails such as the long, narrow siphonal canal of *Priscofusus* and the T-shaped axial ribs of *Ancistrolepis* are preserved intact. Some of the concretions do not have any obvious organic center, but most contain fossils, many are bioturbated, and most contain fecal pellets.

Of particular interest as an aid to diagenetic interpretation is the preservation of complex sequences of laminated calcite, sparry calcite, barite, and quartz, precipitated in that order, within the phragmocone chambers of the cephalopod *Aturia*. This sequential mineralization is currently being studied, but it is obvious now that the laminated calcite was precipitated first followed by sparry calcite, barite, and quartz.

PREVIOUS WORK

James L. Goedert, in collaboration with Gail H. Goedert, began collecting fossils in the Knappton area in the late 1970's and donated the collections to the Natural History Museum of Los Angeles County. The first invertebrate collections were made over a relatively large area and assigned the locality number LAM 5787. Later observations led Goedert to realize that the concretions and other fossiliferous material on the terrace represented separate faunal zones. Thus he separated subsequent collections into three localities: the lowest (LAM Loc. 5844) contains abundant gooseneck barnacles (*Arcoscalpellum*) and the trace fossil *Tisoa;* the middle (LAM Loc. 5843) contains many decapod crustaceans; and the uppermost (LAM Loc. 5842) contains siliceous sponges, mollusks including large specimens of the cephalopod *Aturia,* and abundant marine vertebrates. Still later, he was able to separate the siliceous sponge-bearing locality (LAM Loc. 5852) from the other three localities. At that time, he divided the collecting area into four informal faunal units. Beginning at the base of the section these are: Unit I (LAM Loc. 5844), Unit II (LAM Loc. 5843), Unit III (LAM Loc. 5852), and Unit IV (LAM Loc. 5842) (Fig. 3).

Victor A. Zullo (1982) described the barnacles from Units I and IV. From Unit I, he described two species of gooseneck barnacles, *Arcoscalpellum knapptonensis* and *A. raricostatum,* and assigned the unit to the upper Eocene. From Unit IV, Zullo described the archaeobalinid *Solidobalanus* (*Hesperibalanus*) sp. aff. *S.* (*H.*) *sookensis* (Cornwall) and assigned the unit to the upper Oligocene.

J. Keith Rigby and David E. Jenkins (1983) described sponges from Units II, III, and IV. *Eurete goederti* was described from Unit III and *Aphrocallistes polytretos* was described from Units II, III, and IV. Rigby and Jenkins also identified *A. polytretos* in three other places: a limestone quarry in the Bear River area northwest of Knappton (LAM Loc. 5802) that is in the upper Eocene siltstones of Cliff Point unit (Wells, 1979); in the type area of the lower and middle Miocene Astoria Formation at Astoria, Oregon; and in the upper Oligocene and lower Miocene Yaquina Formation, south of Newport, Oregon. Thus *E. goederti* is early Miocene in age and the range of *A. polytretos* is late Eocene to middle Miocene.

J. Dale Nations, Northern Arizona University, is studying the decapod crustaceans from Units II and IV, Carole S. Hickman, University of California, is studying micromollusks from the section at Knappton, and Bruce J. Welton, Chevron Oil Field Research Company, the fish. Birds and marine mammals, collected throughout the section but most

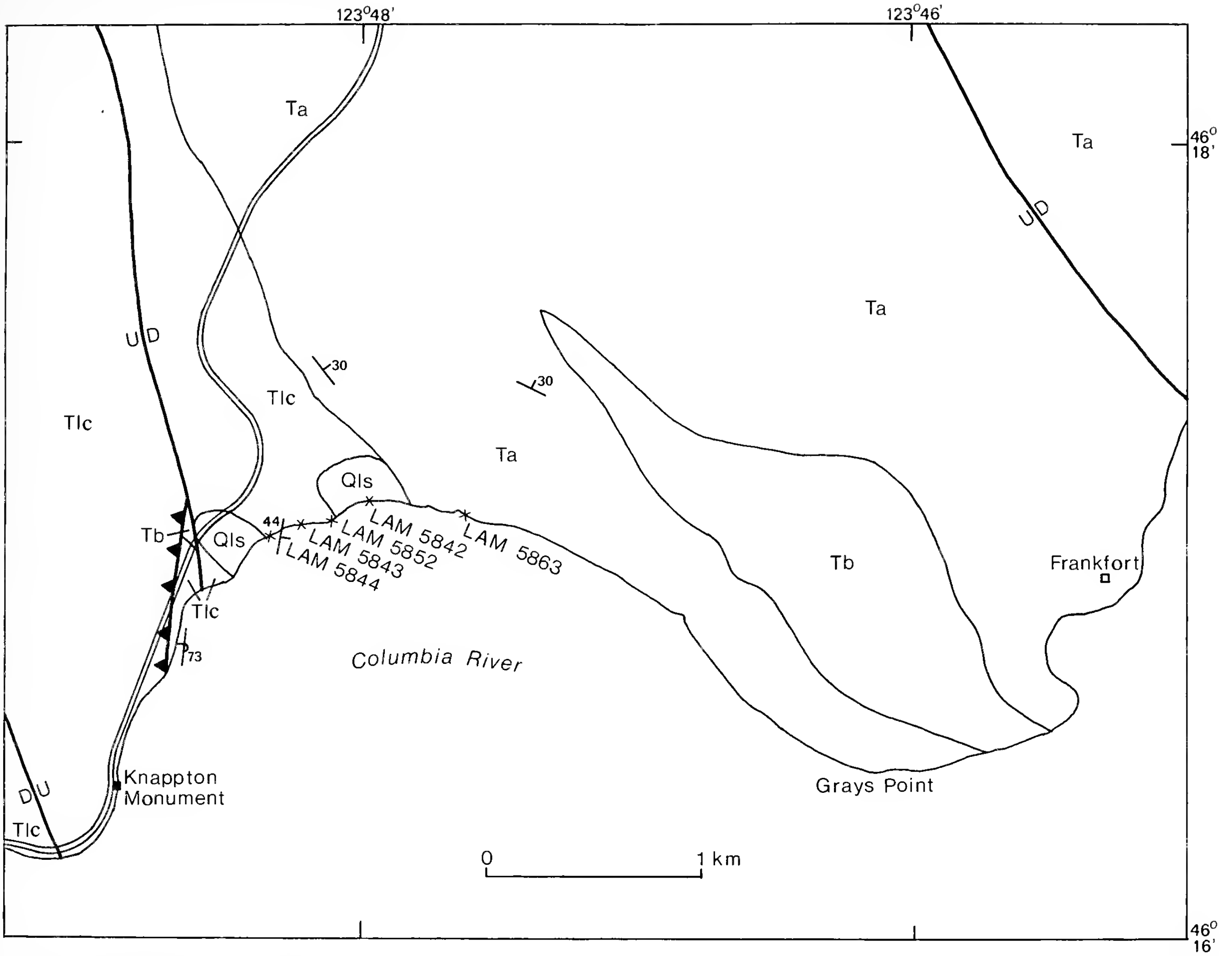

Figure 2. Geologic map of the Knappton area, Washington, modified from Wells (1979), showing fossil localities. Tlc = Lincoln Creek Formation, Ta = Astoria Formation, Tb = Tertiary basaltic sill, and Qls = Quarternary landslide material.

commonly from Unit IV, are in the vertebrate collections of the Natural History Museum of Los Angeles County.

CHRONOSTRATIGRAPHY

Molluscan stages were proposed for the Pacific northwest Tertiary section by Addicott (1976c) and by Armentrout (1975, 1977), and molluscan zones by Durham (1944), with revisions and additions by both Addicott (1976c) and Armentrout (1977). Subsequent work (Allison, 1978; Marincovich, 1979; Moore, 1984) has demonstrated the usefulness of these stages and zones (Fig. 3).

Stratigraphic sections representing the major Oligocene part of the Juanian Molluscan Stage have been extensively studied and their molluscan faunas described and illustrated (Tegland, 1933; Weaver, 1942; Durham, 1944; Armentrout, 1973; Addicott, 1976a, 1976b).

The upper part of the Lincoln Creek Formation is assigned to the upper part of the Juanian Molluscan Stage, equivalent to the upper part of the *Liracassis apta* Molluscan Zone (Fig. 3). The upper part of the formation is of early Miocene age and equivalent in age to the earliest part of the Saucesian Foraminiferal Stage.

The upper part of the Lincoln Creek Formation in southwestern Washington, assigned to the part of the Juanian that is of late Oligocene age, contains a molluscan fauna that remained essentially the same in species composition throughout the late Oligocene. The strata exposed near Knappton, which represent the highest exposed part of the Lincoln Creek Formation and the part of the Juanian Molluscan Stage that is of earliest Miocene age, contains five new species, representing about 15% of the molluscan fauna in the unit. I interpret this as indicating that this part of the section is rarely preserved and that the fauna is transitional between the well-known part (upper Oligocene) of the Juanian and the Pillarian (lower Miocene). The fauna has more

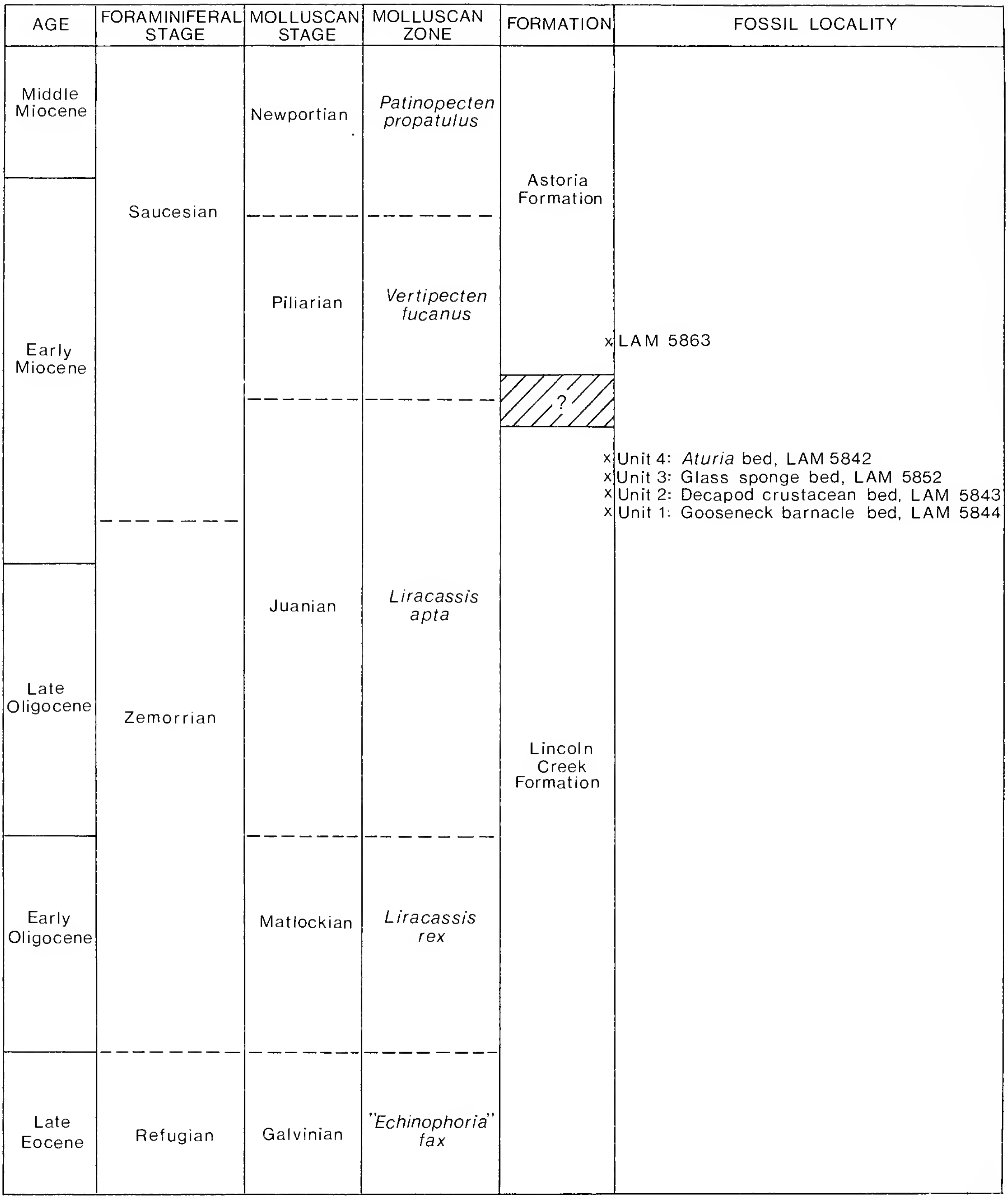

Figure 3. Stratigraphic position of fossil localities in the Lincoln Creek Formation and adjacent formations in southwestern Washington.

species in common with the Juanian than with the Pillarian, which may indicate that it is closer in age to the Juanian or lived at depths more commonly represented in the Juanian.

The mollusks from the upper part of the Lincoln Creek Formation are similar enough to the molluscan fauna from the upper part of the Pysht Formation of the Twin River Group, exposed along the Strait of Juan de Fuca, to suggest a partial correlation of those formations. Addicott (1976b:

Figure 4. View looking southwest toward Knappton monument at upper left and past fossil localities along the coast at the right. [m = monument; f = fossil localities.]

442) considered the molluscan fauna in the upper part of the Pysht Formation to belong to the *Liracassis apta* Molluscan Zone. Although *L. apta* was not collected from the Pysht Formation, Addicott believed that this was due to that unit's relatively shallow-water depositional environment rather than to the organism's extinction. On the basis of foraminiferal evidence, Addicott assigned the upper part of the Pysht Formation to the Saucesian. "*Bathybembix*" *hickmanae* n. sp., *Bruclarkia yaquinana,* and *Megasurcula* sp. cf. *M. wynoocheensis* suggest correlation of the upper part of the Lincoln Creek Formation with the upper part of the Pysht Formation.

Musashia (*Nipponomelon*) *shikamai* n. sp. and *Bruclarkia yaquinana,* from the upper part of the Lincoln Creek Formation at Knappton, were previously reported from strata no older than the Clallam Formation (Addicott, 1976c:14–15) of early Miocene age, equivalent to the Pillarian Molluscan Stage. The occurrence of these species in the upper part of the Lincoln Creek Formation extends their range

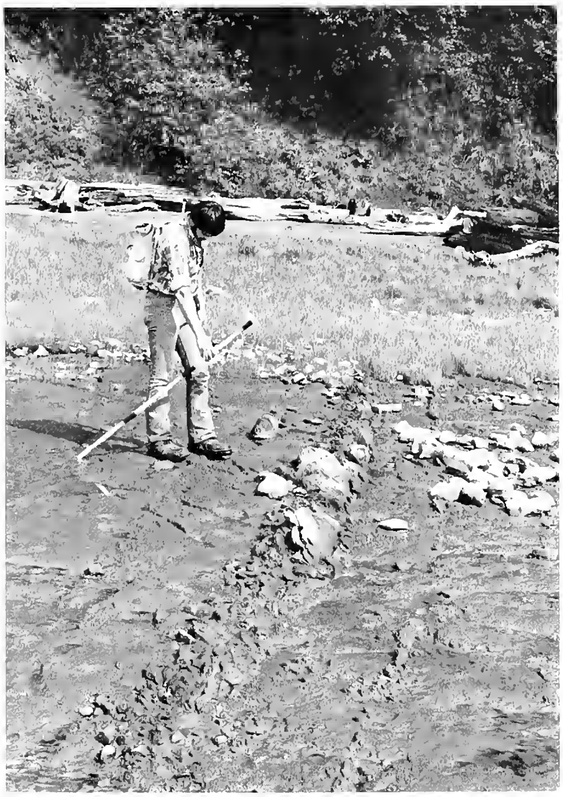

Figure 6. Tidal exposure of upper part of the Lincoln Creek Formation on the Columbia River terrace.

Figure 5. Landslide exposure of upper part of the Lincoln Creek Formation along the Columbia River.

Figure 7. Concretionary layer in upper part of the Lincoln Creek Formation exposed in a landslide block along the Columbia River.

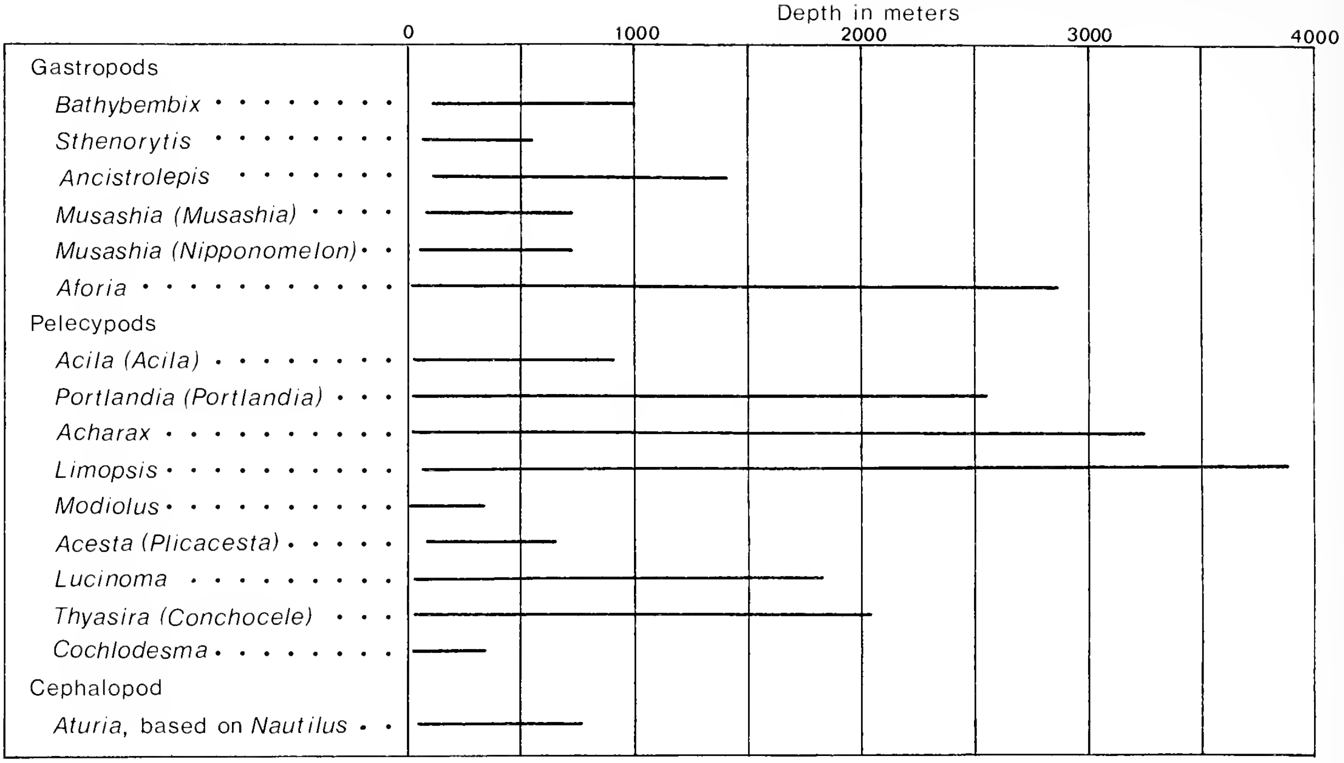

Figure 8. Depth range of living species of genera of fossils found in concretions in the *Aturia* bed near the top of the Lincoln Creek Formation, at Knappton, Washington. The overlapping ranges indicate a depth for the assemblage of about 100 to 350 meters, equivalent to the outer continental shelf or the upper continental slope.

downward into the upper part of the Juanian Molluscan Stage. This further refines the Juanian Molluscan Stage and indicates an interval in the earliest part of the Saucesian when a single molluscan province may have extended from southwestern to northwestern Washington.

The generic composition of the Knappton fauna ("*Bathybembix*," *Liracassis, Ancistrolepis,* and *Musashia*) is similar to other assemblages of mollusks collected from the Lincoln Creek Formation and its correlative units, and the conditions of deposition seem also to be similar.

Musashia (*Nipponomelon*) *weaveri* survived throughout the entire Oligocene. *Musashia* (*N.*) *shikamai* n. sp., also present in the Clallam Formation (Addicott, 1976c, pl. 3, fig. 27) and in the upper part of the Poul Creek Formation, replaced *M. weaveri* in the upper part of the Lincoln Creek Formation.

Liracassis durhami Kanno, which occurs with *Liracassis apta* at Knappton (Moore, 1984), was present during the upper part of the Juanian Stage, then became locally extinct, but survived through the Pillarian Stage in the upper part of the Poul Creek Formation in the Gulf of Alaska. Although common in the collections from Knappton, *L. durhami* is rare in other exposures of the Lincoln Creek Formation.

Ancistrolepis clarki teglandae occurs in the Oligocene part of the Juanian Stage and was preceded by *A. clarki clarki* in the Matlockian Stage. *Ancistrolepis jimgoederti* n. sp. occurs in the upper part of the Lincoln Creek at Knappton, in the lower Miocene part of the Juanian Stage.

The uppermost part of the Lincoln Creek Formation at Knappton is assigned to the earliest Miocene on the basis of its molluscan fauna. Two fossil localities of Goedert, units 3 and 4 are of early Miocene age; units 1 and 2 may be of late Oligocene age. The upper part of the Lincoln Creek Formation at Knappton is correlative with the upper part (lower Miocene) of the Pysht Formation. The placement of the upper part of the Lincoln Creek Formation in the lower Miocene corroborates the assignment of the upper part of the Juanian Stage to the lower Miocene (Addicott, 1976b:442).

PALEOECOLOGY

The Lincoln Creek Formation in southwestern Washington represents the accumulation of sediment in a relatively stable basin environment that shallowed to the southeast. The molluscan fauna of the lowermost Miocene part of the Lincoln Creek Formation at Knappton lived at dephs between 100 and 350 m (Fig. 8).

The mollusk-bearing concretions are highly bioturbated with numerous burrows. Preserved fecal pellets occur as small spherical ooids within the body chambers of gastropods, elongate pelloids within the septal chambers of the cephalopod *Aturia* (Figs. 156, 157), and both types scattered throughout the concretions. Seventeen phyla are represented in the fauna, and they indicate a healthy community of organisms living in water of normal salinity. The abundance of *Aturia* suggests that the water temperature may have been as high as 16°C with shallow embayments nearby with temperatures as high as 24°C for egg laying (Cochram, Rye, and Landman, 1981:477). The abundance of preserved organic material suggests that the sediment below the level of bioturbation was dysaerobic, reduced in oxygen (0.1–0.5 ml/liter), and that regular sedimentation gradually buried the organic material without destroying it or the organisms that lived there.

Zullo (1982 and written commun., 1982) described *Solidobalanus* (*Hesperibalanus*) aff. *S.* (*H.*) *sookensis* (Cornwall) from the upper part of the Lincoln Creek Formation at Knappton. Although this archeobalanid barnacle is representative of a sessile-benthic group usually found at subtidal to inner-shelf depths, the basal plates of the Knappton specimens suggest attachment to shells or wood, which could have been transported to the site of deposition.

Rigby and Jenkins (1983) described and assigned sponges from the upper part of the Lincoln Creek Formation to the genera *Aphrocallistes* and *Eurete;* the distribution of living species of both genera suggests that they lived at a depth of approximately 300 to 350 m.

The foraminifers in the upper part of the Lincoln Creek Formation in the Grays River quadrangle, just east of Knappton, indicate water depths of 300 to 900 m (Rau *in* Wolfe and McKee, 1972:42).

James C. Ingle, Jr. (written commun., 1982) examined thin sections made from the centers of mollusk-bearing concretions. He concluded: "All of the evidence in your thin sections suggests deposition occurred on a continental slope or marginal basin associated with impingement of the oxygen minimum layer producing anaerobic or dysaerobic conditions . . . . The core of this oxygen depleted water mass commonly occurs at a depth between 200 and 600 m off California today and the foraminifera identified in your thin sections support this depth range (*Globulimina, Epistominella, Bolivina, Uvigerina*). There is evidence of redeposition of some of the material from shallower environments with neritic-littoral echinoderm spines and thick walled porcelaneous foraminifera present in several samples. In addition, the rare glauconite fragments were likely redeposited from the adjacent shelf-edge or outer neritic area."

A sample of sediment from the head of the active landslide at the west end of the major fossil-bearing concretion locality (LAM 5842) and samples from a measured section stratigraphically below have yielded Zemmorian age foraminiferal assemblages and suggest, as a conservative estimate, that the water depth was midslope, 1000 m or possibly deeper (Kristin McDougall, written commun., 1982; James C. Ingle, Jr., written commun., 1983).

Bruce J. Welton, studying the fish remains from Knappton, has found bones, scales, and teeth to be abundant at all the localities and bony-fish otoliths to be common in almost all samples. Preliminary identifications show that the fish include seven genera of sharks representing six families, and one family of bony fish, in addition to numerous unidentified otoliths and isolated bones. According to Welton (written commun., 1982),

> Ecologically, the sharks are represented by two epipelagic genera (*Cetorhinus* and *Eugomphodus*) and five genera (*Centrophorus, Chlamydoselachus, Notorynchus, Scymnodon,* and *Pristiophorus*) with closely related living species which are predominantly benthic and deep water forms. Several taxa are broad ranging bathymetrically (*Notorhynchus* and *Pristiophorus*) but collectively the assemblage is taxonomically right for deep water. A precise depth would be difficult to substantiate but all forms would be expected to occur together at a depth of 600 to 1500 ft [180 to 460 m].
>
> Silicified otoliths are usually poorly preserved, however, the majority (98%) are of mesopelagic lanternfishes (Family Myctophidae). Many compare favorably to the genus *Diaphus.* The extant *D. theta* occurs today in the N. Pacific from N. Baja California to the Gulf of Alaska and Japan, at depths from surface (over deep water) to 2600 ft [790 m].
>
> If one considers only the present day bathymetric distribution of the genera of sharks and bony fishes known to occur at Knappton, the assemblage from all four localities would have to be characterized as a mix of epipelagic and deep water benthic sharks and mesopelagic teleosts. A bottom depth of 600 to 1500 ft [180 to 460 m] would not be unreasonable.
>
> Although the sample is small, the absence of other selachian taxa (e.g. *Heterodontus, Squatina, Squalus, Triakis, Mustelus, Galeorhinus,* and assorted skates and rays) strongly dictates against both a shallow water (shelf) origin of the fauna or resedimentation of a shallow water assemblage into deeper water by turbidites or related processes.

From LAM Vertebrate Locality 4510 (=LAM Invertebrate Locality 5842) Welton has identified *Scymnodon* sp., cf. *Diaphus* sp., and Myctophidae with a combined modern bathymetric distribution of 300 to 800 m.

Because *Aturia* is 20 times as abundant as any other mollusk in the fauna, particular attention should be paid to its inferred ecologic requirements. *Nautilus,* the structurally similar closest living relative of *Aturia,* implodes at a water depth of 785 m (Kanie et al., 1980), which presumably sets a maximum living depth for *Aturia* and the associated megafauna and microfauna. *Nautilus* eggs are probably laid in shallow water, 100 m or less. After hatching, the young descend to 250 to 350 m (Hamada, Obata, and Okutani, 1980: 47). The first seven septa in *Nautilus* have shown low $\delta^{18}O$ values, indicating *Nautilus* hatched in warm, shallow water, about 24°C (Cochram, Rye, and Landman, 1981:477). The eighth and later septa have higher $\delta^{18}O$ values, suggesting that the juvenile *Nautilus* subsequently migrates to deeper, colder water, about 16°C. Indirect evidence for the need of shallow warm water for egg laying and hatching of *Aturia* lies in the present distribution of *Nautilus* in the south Pacific

Other authors:	This report:
Musashia (*Musashia*) n. sp. Armentrout in MS (1973)	*Musashia* (*Musashia*) n. sp. a
Musashia (*Musashia*) sp. of Allison and Marincovich (1981, pl. 3, figs. 8, 14)	*Musashia* (*Musashia*?) sp. b
Musashia (*Musashia*) sp. of Allison and Marincovich (1981, pl. 3, figs. 12, 13)	*Musashia* (*Musashia*?) n. sp. c
Musashia (*Musashia*) sp. of Allison and Marincovich (1981, pl. 3, figs. 16, 17)	*Musashia* (*Nipponomelon*?) n. sp.?
Miopleiona sp. A Durham (1944:178; UCMP 35421, 35422)	*Musashia* (*Musashia*) n. sp. a
Miopleiona sp. B Durham (1944:178; UCMP 35423)	*Musashia* sp.
Miopleiona weaveri Tegland (1933:127–128, pl. 11, figs. 1–5)	*Musashia* (*Nipponomelon*) *weaveri* (Tegland)
Miopleiona scowensis Durham (1944:177–178, pl. 17, fig. 15)	*Musashia* (*Nipponomelon*) *weaveri* (Tegland)
Psephaea (*Miopleiona*) cf. *P.* (*M.*) *weaveri* (Tegland) of Addicott (1970, pl. 13, figs. 15, 19)	*Musashia* (*Nipponomelon*) *weaveri* (Tegland)
Psephaea (*Miopleiona*) *indurata* (Conrad) of Moore (1963:43–44, pl. 7, figs. 1, 2, 3–9, 11; pl. 8, figs. 1–4, 5)	*Musashia* (*Miopleiona*) *indurata* (Conrad)
Miopleiona oregonensis Dall (1909:35–36, pl. 18, figs. 3, 7)	*Musashia* (*Nipponomelon*) *oregonensis* (Dall)
Miopleiona sp. Clark (1918, pl. 23, fig. 13; UCMP 11244	*Musashia* (*Nipponomelon*?) sp.
Psephaea (*Miopleiona*) *weaveri* (Tegland) of Addicott (1970, pl. 13, fig. 17)	*Musashia* (*Nipponomelon*) *weaveri* (Tegland)
Miopleiona indurata (Conrad) of Clark (1918:185; UCMP 12030)	*Musashia* (*Nipponomelon*?) sp. cf. *M.* (*N.*) *weaveri* (Tegland)
Psephaea corrugata Clark (1932:831, pl. 21, figs. 5, 11)	*Musashia* (*Neopsephaea*) *corrugata* (Clark)
Miopleiona sp. Loel and Corey (1932:241; UCMP 12136)	*Musashia* (*Nipponomelon*) *shikamai* n. sp.
Psephaea (*Miopleiona*) cf. *P.* (*M.*) *indurata* (Conrad) of Addicott (1970, pl. 13, figs. 6, 8)	*Musashia* (*Nipponomelon*) *shikamai* n. sp.
Musashia indurata (Conrad) of Addicott (1976c, pl. 3, fig. 27)	*Musashia* (*Nipponomelon*) *shikamai* n. sp.
Musashia n. sp. of Addicott (1976a, pl. 4, fig. 18)	*Musashia* (*Nipponomelon*) n. sp.?
Rostellaria indurata Conrad (1849:727–728, pl. 19, fig. 12)	*Musashia* (*Miopleiona*) *indurata* (Conrad)
Miopleiona indurata (Conrad) of Weaver (1942:491, pl. 94, figs. 5, 8, 13)	*Musashia* (*Miopleiona*) *indurata* (Conrad)

Figure 9. Allocation of Eastern Pacific Tertiary volutids assigned to the genus *Musashia*.

and in the fact that *Aturia* became extinct in the eastern Pacific at the close of the early Miocene. A combination of cooling and marine regression may have eliminated suitable sites for reproduction. *Aturia* also probably inhabited a shelf or slope environment where it could have come into shallow warm water for nocturnal feeding and reproduction and easily returned to deeper water for resting and escape from predators.

A depth between 100 and 350 m for the organisms preserved in the concretions is indicated on the basis of all the mollusks including the most abundant element of the fauna, *Aturia*. Foraminifers from nearby sediment at the modern landslide at Knappton indicate a greater depth (about 1000 m). If the difference is real, a possible explanation is that an early Miocene submarine landslide transported the *Aturia*-bearing sediment into deeper water before lithification.

Other fossil remains present in the biota but not yet studied in detail include radiolarians, coelenterates, echinoderms, bryozoans, brachiopods, decapods, polychaetes, trace fossils, marine mammals (cetaceans), birds, seeds, and wood.

The pelecypods are mostly infaunal at shallow subbottom depths; the spantagoid echinoids and marine worms also are infaunal, perhaps to depths as much as 6 cm. The gastropods are mostly epifaunal, although the cassids may have plowed through the sediment in search of their echinoid prey. The sponges, coral, and crabs were also mostly epifaunal.

Temperature data obtained from living or closely related molluscan species are somewhat ambiguous. Whereas mollusks such as *Ancistrolepis, Aforia, Portlandia, Acharax, Acesta* (*Plicacesta*), *Acesta* (*Acesta*), and *Lucinoma* suggest temperatures between 5 and 8°C, *Aturia* may have required a temperature of at least 16°C.

MOLLUSCAN PALEONTOLOGY

The molluscan fauna consists of 33 taxa and many of these have been treated by Tegland (1931, 1933), Durham (1944), and Addicott (1970, 1976b, 1976c). Taxonomic notes rather than formal systematic descriptions are used for all but new species to avoid redundancy. Newly described species are treated more formally.

The following taxa are included, and, unless otherwise indicated, all are from LAM Locality 5842 (Unit IV) and are illustrated at natural size.

Gastropods:
- "*Bathybembix*" *hickmanae* n. sp.
- *Epitonium* (*Nitidiscala*?) sp.
- *Sthenorytis* sp.
- Unidentified naticids
- *Liracassis durhami* Kanno
- *Liracassis apta* (Tegland)
- Buccinid?
- *Bruclarkia yaquinana* (Anderson and Martin)
- *Ancistrolepis jimgoederti* n. sp.

- *Priscofusus*? sp. cf. *P. geniculus* (Conrad)
- *Musashia* (*Musashia*) n. sp.
- *Musashia* (*Nipponomelon*) *shikamai* n. sp.
- *Musashia* (*Miopleiona*) n. sp.
- *Aforia wardi* (Tegland)
- *Turricula*? sp.
- *Megasurcula*? sp. cf. *M. wynoocheensis* (Weaver)
- *Microglyphus* n. sp.?

Pelecypods:
- *Acila* (*Acila*) *gettysburgensis* (Reagan)
- *Portlandia* (*Portlandia*) *chehalisensis* (Arnold)
- *Acharax dalli* (Clark)
- *Limopsis nitens* (Conrad)
- *Modiolus addicotti* n. sp.
- *Acesta* (*Acesta*) *twinensis* (Durham)
- *Acesta* (*Plicacesta*) *wilsoni* n. sp.
- *Crassostrea*? sp.
- *Lucinoma hannibali* (Clark)
- *Thyasira* (*Conchocele*) *disjuncta* (Gabb)
- *Nemocardium*? sp. cf. *N. lorenzanum* (Arnold)
- *Macoma* sp. cf. *M. twinensis* Clark
- *Cochlodesma bainbridgensis* Clark
- Teredinid

Scaphopod:
- *Dentalium* (*Fissidentalium*?) sp. cf. *D. porterensis* Weaver

Cephalopods:
- *Aturia angustatata* (Conrad)
- Sepiid?

ABBREVIATIONS

CAS: California Academy of Sciences, San Francisco.

LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, California.

LACMP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, California.

LAM: Natural History Museum of Los Angeles County, California.

CAS/SU: Stanford University, Stanford, California. (The Stanford University collections are now housed at the California Academy of Sciences.)

SU: Stanford University, Stanford, California.

UC: University of California, Berkeley.

UCMP: University of California, Museum of Paleontology, Berkeley.

USGS: U.S. Geological Survey, Washington, D.C., Cenozoic locality register.

USGS M: U.S. Geological Survey, Menlo Park, California, Cenozoic locality register.

USNM: National Museum of Natural History, Washington, D.C.

UW: University of Washington, Seattle, Washington.

GASTROPODS

Trochidae

The genus *Bathybembix* is used here in a broad sense following Hickman (1980:16) who is currently undertaking a detailed revision of the large tuberculate trochid gastropods allied to *Bathybembix.* The Pacific Northwest fossil species, *Turcicula columbiana* Dall (1909:99–100, pl. 3, figs. 2, 11) and *T. washingtoniana* Dall (1909:99–100, pl. 17, figs. 1, 2; pl. 18, fig. 4) were considered by Rehder (1955:225) to "belong to *Bathybembix,* or are more closely related to that genus than to any other." Noda (1975:60) believed that "*Turcicula*" *columbiana* and "*T.*" *washingtoniana* differ sufficiently to warrant a new subgeneric name. Certainly "*T.*" *washingtoniana* needs more careful scrutiny in terms of generic or subgeneric allocation. Other Pacific coast fossil species that have been assigned to *Turcicula* or to *Bathybembix* are: *Turcicula arnoldi* Durham (1944:153–154, pl. 15, fig. 10), *Turcicula sanctacruzana* Arnold (1908:373, pl. 33, fig. 4), *Turcicula turbonata* Clark (1932:826, pl. 20, fig. 11), and *Bathybembix nitor* Hickman (1980:17–18, pl. 2, figs. 1, 2). In addition, Armentrout (1973), in his study of the Lincoln Creek Formation in Washington, recognized three new species which he assigned to *Bathybembix.*

"*Bathybembix*" *hickmanae* n. sp.

Figures 10–12, 18

Bathybembix aff. *B. arnoldi* (Durham). Addicott, 1976b, figs. 6u, w.

"*Bathybembix*" *hickmanae* is a thin-shelled, moderately large trochid with five whorls. The body whorl is characterized by two spiral cords separated by an almost vertical angulation. The whorls of the spire also have two spiral cords, one at the suture separated from the cord above by the same type of vertical angulation. The outer shell layer is preserved only in small patches, but the spirals may have been keeled and tuberculate on the shoulder of the body whorl and the spire whorls; the rest of the shell may have been smooth. The available specimens are poorly preserved and no nacreous shell material is apparent on any of shell patches preserved, whereas nacreous shell material is commonly preserved on both "*Bathybembix*" *columbiana* and "*Bathybembix*" *washingtoniana.*

HOLOTYPE. LACMIP 6623, height 42 mm, width 35 mm; paratypes LACMIP 6621, height 41 mm, width 35 mm; LAM 6622, height 28 mm.

TYPE LOCALITY. LAM 5842.

"*Bathybembix*" *hickmanae* somewhat resembles "*B.*" *arnoldi* (Durham) and "*B.*" *sanctacruzana* (Arnold) in outline but differs in having both a steeper and longer slope between the spirals and the suture on the body whorl. In addition, "*B.*" *hickmanae* has the anterior spiral on the spire whorls at the suture, whereas "*B.*" *arnoldi* and "*B.*" *sanctacruzana* have a space between the anterior spiral and the suture. The vertical angulation between spirals on the body whorl and the higher spire in proportion to width separate "*B.*" *hickmanae* from "*B.*" *washingtoniana* (Dall). In addition, "*B.*" *washingtoniana* has a strong keel on the periphery of the body whorl. The vertical angulation between spirals on the body whorl distinguishes "*B.*" *hickmanae* from "*B.*" *turbonata* (Clark). "*Bathybembix*" *columbiana* (Dall, 1909:100, pl. 3, figs. 2, 11) has a higher spire and larger nodes than

"*B.*" *hickmanae.* "*Bathybembix*" *hickmanae* differs from "*Bathybembix*" *nitor* (Hickman) in having a quadrate rather than an ovate aperture.

Traditionally, the species assigned to *Bathybembix* have been assumed to indicate deep, often bathyal depths. The bathymetric distribution of living species in Japan, assigned to *Turcicula, Bathybembix, Ginebis,* and *Convexia,* is 100 to 1000 m (Noda, 1975:58, fig. 3).

This species is named in honor of Carole S. Hickman.

Epitoniidae

Epitonium (*Nitidiscala*?) sp.

Figures 13, 14, 16

A latex impression of the mold of a specimen preserved in a concretion is illustrated along with the original external and internal molds. It is a thick-shelled epitoniid with seven whorls preserved each of which probably bore 14 or 15 thick axial ribs (seven are exposed). No spiral sculpture is preserved.

The rounded whorls, deep sutures, slim high spire, and lack of spiral sculpture between the axial ribs suggest *Nitidiscala.*

This species somewhat resembles *Epitonium* (*Cirsotrema*) *saundersi* Tegland (1933:133, pl. 13, figs. 7–9; Durham, 1937: 491–492, pl. 57, fig. 21) which occurs in the *Liracassis rex* Molluscan Zone (Durham, 1944:158). *Epitonium saundersi,* however, has spiral sculpture and less rounded but wider whorls than *E.* (*N.*?) sp.

Sthenorytis sp.

Figures 15, 19, 20

Sthenorytis sp. may have had five, or possibly more, rapidly enlarging well-rounded whorls, including a very large body whorl set off from the axis at an angle of about 40°, as is typical of *Sthenorytis.* The suture presumably is deep, and the body whorl may have had 16 varices. The varices are rather evenly spaced, triangular in cross section, sharp edged, and project about 4 mm beyond the shell.

The only described species resembling *S.* sp. is *Sthenorytis ventricosum* (Clark, 1918:164, pl. 23, fig. 14) from the San Ramon Sandstone, California. It has a smaller body whorl (31 mm wide) than *S.* sp. (36 mm wide) and is 45 mm high compared to about 55 mm for *S.* sp. The varices number about 12 and are rounded on *S. ventricosum; S.* sp. has about 16 varices that are triangular and sharp-edged.

Three Pacific coast Tertiary species are assigned to *Sthenorytis: S.*? *crescentense* (Durham, 1937), *S. ventricosum* (Clark, 1918), and *S. stearnsi* (Dall, 1892). The geologic range of these species is Eocene to Pliocene and the geographic range is northwestern Washington to southern California.

Sthenorytis lives today no farther north than the Gulf of California and Cape San Lucas; it lives in warm water in the Pacific and the Atlantic and is usually found on sandy bottoms (Durham, 1937:499). Woodring (1959:184) reported *S. pernobilis* (Fischer and Bernardi) from Cape Hatteras to the Lesser Antilles at depths of 134 to 220 m, Keen (1971:434, 436) recorded *S. dianae* (Hinds) from Baja California Sur in 82 to 145 m and *S. turbinum* (Dall) from the Gulf of California to the Galapagos Islands in 82 to 550 m, and Clench and Turner (1950:225–226) recorded *S. pernobilis* (Fischer and Bernardi) from North Carolina to the Lesser Antilles at 134 to 284 m.

Naticidae

Unidentified naticid

Figure 17

Naticids that may represent *Polinices* (*Euspira*) are represented by three specimens, none with the umbilical area well enough preserved for positive identifications.

Cassididae

Two species of *Liracassis, L. durhami* and *L. apta,* were found in the upper part of the Lincoln Creek Formation.

Liracassis durhami Kanno

Figures 21–23, 25, 26

Liracassis durhami Kanno, 1971:112–113, pl. 13, figs. 14a–b.

Liracassis durhami Kanno has nodes on the shoulder that usually form oblique ridges to the suture (Figs. 21–23, 25), but may be separated from the suture by a narrow unsculptured band or confined to two spiral straps. Secondary spirals are absent on the body whorl except for one specimen which

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Figures 10-23. "*Bathybembix*" *hickmanae* n. sp., *Epitonium* (*Nitidiscala*?) sp., *Sthenorytis* sp., unidentified naticid, and *Liracassis durhami* Kanno.

Figures 10-12, 18. "*Bathybembix*" *hickmanae* n. sp. **10.** Paratype LACMIP 6621, height 41 mm, width 35 mm. Showing cross section of spiral cords. **11.** Paratype LACMIP 6622, height 28 mm. Showing nodes on shoulders of spire and body whorl, ×1.5. **12, 18.** Holotype LACMIP 6623, height 42 mm, width 35 mm. Showing patches of preserved shell.

Figures 13, 14, 16. *Epitonium* (*Nitidiscala*?) sp. **13.** Latex impression of specimen shown in Figure 16, ×1.5. **14.** Internal mold, height 25 mm, width 10 mm. LACMIP 6624a. **16.** External mold from which latex impression was taken shown in Figure 13, ×2.0; height 26 mm, width 10 mm. LACMIP 6624.

Figures 15, 19, 20. *Sthenorytis* sp. **15.** View looking down upon spire, ×1.5; height 55 mm. LACMIP 6625a. **19.** View of base of same specimen in Figure 15 showing triangular cross section of varices, ×1.5. LACMIP 6625b. **20.** Portion of body whorl of specimen shown in Figure 19, width 37 mm.

Figure 17. Unidentified naticid, ×1.5; height 23 mm, width 20 mm. LACMIP 6626.

Figures 21-23. *Liracassis durhami* Kanno. **21.** Showing one secondary rib in interspace, ×1.5; width 46 mm. LACMIP 6627. **22.** Showing ridges on shoulder of body whorl; height 57 mm, width 46 mm. LACMIP 6628. **23.** Showing spire; height 63 mm, width 48 mm. LACMIP 6493.

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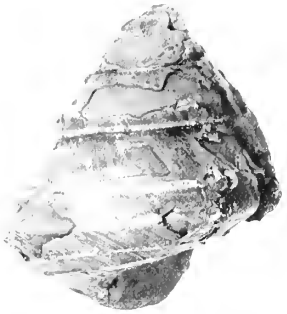

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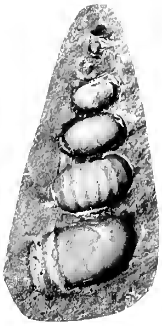

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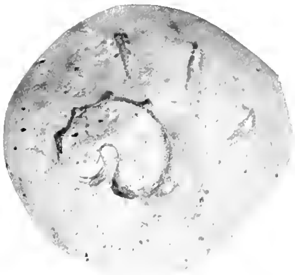

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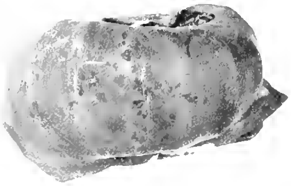

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has a single intercalary in one interspace (Fig. 26). *Liracassis durhami* always has a rounded body whorl without nodes below the shoulder; this character distinguishes it from *Liracassis rex* (Tegland, 1931:413–415, pl. 60, fig. 12; pl. 61, figs. 1–4; pl. 62, figs. 1–6), depicted in Figure 32 and the tabulate form of *L. apta* (Figs. 27, 31, 33, 39, 42). From the round form of *L. apta* (Figs. 24, 28, 30, 47), *L. durhami* is distinguished by its more concave body-whorl shoulder, ridgelike nodes on the shoulder, and the absence of intercalaries on the body whorl. *Liracassis durhami* always has nodes on the shoulder of the body whorl, whereas the round form of *L. apta* may not. *Liracassis petrosa* (Moore, 1963, pl. 10, figs, 7, 17) differs from *L. durhami* in having intercalaries between primary spirals on the body whorl and nodes that are more fluted on the periphery of the body-whorl shoulder, forming less oblique and generally smaller ridges on the shoulder.

Liracassis durhami ranges from the northeastern Gulf of Alaska to southwestern Washington; it occurs in the upper part of the Poul Creek Formation and the lower part of the Yakataga Formation, Alaska, as well as in the upper part of the Lineoln Creek Formation, Washington. In the lower part of the Yakataga Formation in Alaska, *L. durhami* is associated with Pillarian mollusks (Scott McCoy, pers. commun., 1980). In Washington, *L. durhami* ranges from the upper Galvinian Stage through the Juanian Stage. The infrequent occurrence of *L. durhami* compared to *L. apta* in the upper part of the Lincoln Creek Formation may indicate that southwestern Washington was at the southern limit of its range. *Liracassis apta* is restricted to the Juanian, but has a greater geographic range than *L. durhami,* having been found as far south as California (Ham, 1952:8).

Liracassis apta (Tegland)

Figures 24, 27–31, 33, 39, 42, 46, 47

Galeodea apta Tegland, 1931:415–417, pl. 63, figs. 1–10.

Liracassis apta is common in the upper part of the Lincoln Creek Formation. The largest specimens of *L. apta* usually have round shoulders (Figs. 28, 30), but it is not uncommon to find large specimens with tabulate shoulders nor is it unusual to find small specimens with round shoulders. The largest specimens of the round-shouldered form almost never have nodes on either the shoulder or the rest of the body whorl. The tabulate form always has nodes on the shoulder of the body whorl and may have them on spiral cords anterior to the shoulder. Of the *Liracassis* species studied (Moore, 1984), *L. apta* is the only one showing the wide range of variation first noted by Tegland (1931:401, 406), who distinguished three varieties. Tegland's varieties 1 and 2 fit into the tabulate form and variety 3 into the round-shouldered form. *Liracassis apta* has intercalaries in the interspaces between primary spiral cords (Fig. 24) as do *L. rex,* from the type section of the Blakeley Formation of Weaver (1912), Washington, and *L. petrosa,* from the Astoria Formation, Oregon, but *L. durhami* is distinguished by having smooth spaces between the primary spirals. *Liracassis rex* always has nodes on the concave shoulder of its body whorl; these nodes are not confined to the shoulder but continue adapically as ridges to the suture, whereas in *L. apta* the nodes, if present, are confined to the shoulder periphery. *Liracassis rex* always has at least one, and commonly more than one, row of nodes below the shoulder; *L. apta* never has more than one row and commonly has none at all. The nodes on the periphery of the shoulder of *L. petrosa* are fluted, whereas they are rounded in *L. apta. Liracassis apta* is restricted to the Juanian Stage, and its geographic range is from California to the western Gulf of Alaska.

Studies of living cassids have shown that these carnivores eat only echinoids, and that different species within each cassid genus prefer certain distantly related genera of echinoids. That different echinoids can serve as food for closely related cassids makes clear how two different species of *Liracassis,* such as *L. durhami* and *L. apta,* could live in the same biologic community, but in different niches.

Buccinidae?

Unidentified buccinid

Figure 36

A single specimen of a poorly preserved gastropod may be a buccinid. Although many gastropod families can be eliminated from consideration on the basis of outline, sculpture, suture, aperture, or siphonal canal, the specimen is not identified with complete confidence as a buccinid. The evenly rounded whorls, slightly impressed suture, elongate-oval aperture, seeming lack of columellar plaits, a probably short, straight siphonal canal, and cancellate sculpture suggest buccinid genera such as *Cymatophos* or *Antillophos.*

Neptuneidae

Bruclarkia yaquinana (Anderson and Martin)

Figures 41, 44

Agasoma yaquinana Anderson and Martin, 1914:75, pl. 4, figs. 5a–b.

Figures 24-33. *Liracassis apta* (Tegland), *Liracassis durhami* Kanno, and *Liracassis rex* (Tegland).

Figures 24, 27-31, 33. *Liracassis apta* (Tegland). **24.** Round form without body-whorl nodes; height 44 mm, width 37 mm. LACMIP 6495. **27.** Tabulate form; height 55 mm. LACMIP 6629. **28.** Round form; height 85 mm, width 62 mm. LACMIP 6630. **29.** Showing round body whorl and tabulate spire; height 63 mm, width 49 mm. LACMIP 6631. **30.** Round form; height 63 mm. LACMIP 6632. **31.** Tabulate form with nodes on body whorl; height 47 mm, width 42 mm. LACMIP 6633. **33.** Tabulate form with beads on body whorl; height 40 mm, width 33 mm. LACMIP 6634.

Figures 25, 26. *Liracassis durhami* Kanno. **25.** Showing smooth interspaces and ridges on shoulder; height 43 mm, width 39 mm. LACMIP 6496. **26.** Showing straplike spiral cords; height 70 mm, width 66 mm. LACMIP 6494.

Figure 32. *Liracassis rex* (Tegland). Showing nodes on body whorl of holotype UCMP 32067; height 75 mm, width 64 mm. Blakeley Formation, Restoration Point, Seattle, Washington.


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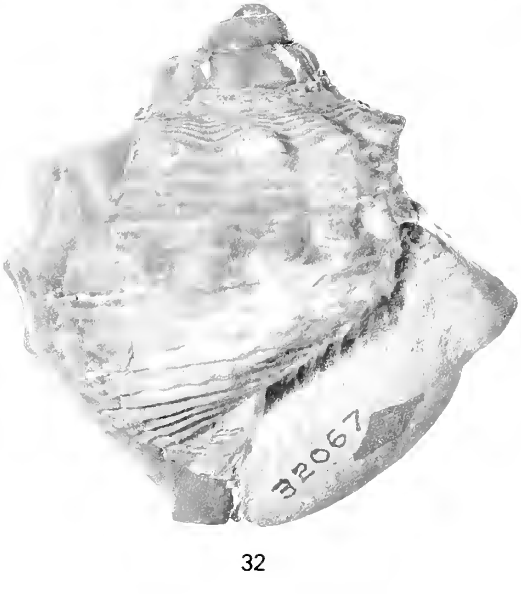

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Bruclarkia yaquinana is represented by a single incompletely preserved specimen (Figs. 41, 44). As noted by Addicott (1970:90–91; 1976c:23), *B. yaquinana* is characterized by four or five coarsely noded spiral cords on the body whorl. *Bruclarkia oregonensis* (Conrad, 1848:433, fig. 13; Moore, 1963: pl. 3, figs. 2, 3, 8, 11, 13) has finer spiral seulpture and is a larger, more rounded species. In the San Joaquin Valley, California, the stratigraphic occurrence of *B. yaquinana* (basal part of the Jewett Sand) and *B. oregonensis* (Olcese Sand) is mutually exclusive (Addicott, 1970:91). In the Clallam Formation of northwestern Washington, *B. oregonensis* occurs almost exclusively at the top of the formation, and *B. yaquinana* at and near the base (Addicott, 1976c:23–24).

Ancistrolepis jimgoederti n. sp.

Figures 34, 35, 37, 38, 40, 43, 45, 56, 58, 59

The shell of *Ancistrolepis jimgoederti* is large and thin with eight or nine subtabulate whorls that bear T-shaped spiral cords that are strongly undercut and, on the holotype (Figs. 35, 37, 38), preserve three secondary spiral cords. The interspaces on the body whorl bear secondary spiral cords and one specimen has four moderately prominent and three very fine secondary cords preserved in one interspace. On this same specimen, fine vertical striations are preserved in one interspace, perhaps reflecting the periostracum. The specimen with the most whorls preserved (eight) is 68 mm in height (incomplete), and the specimen with the largest body whorl has a maximum width of 36 mm. The largest T-shaped spiral cord preserved projects 3.2 mm beyond the shell body. The T-shaped spirals are preserved only in concretionary matrix (Fig. 58) from which they were subsequently exposed by preparation (Figs. 34, 35, 37, 38, 40). The body of the shell is so thin that the spiral cords exfoliate easily from the shell, leaving preserved a completely erroneous shell outline (Figs. 43, 45). The T-shaped spirals are now replaced by sparry calcite, but do not seem to have been hollow folds of the shell, as in the genus *Ecphora* from the Miocene of the eastern United States (Vokes, 1957, pl. 25, fig. 2).

HOLOTYPE. LACMIP 6636, height 55 mm, width 35 mm; paratypes LACMIP 6635, height 40 mm, width 29 mm; LACMIP 6637, height 67 mm, width 35 mm; LACMIP 6638, height 65 mm, width 35 mm; LACMIP 6646, width 35 mm; and LACMIP 6647, height 70 mm.

TYPE LOCALITY. LAM 5842.

Species, such as *Ancistrolepis clarki* (Tegland, 1933:131–132, pl. 12, fig. 14), *A. landesi* (Tegland, 1933:132–133, pl. 13, figs. 1–4), and *A. clarki teglandae* (Durham, 1944:177, pl. 17, fig. 2), may also have had T-shaped spirals that were removed by exfoliation. The concretionary fragments remaining with the holotype of *A. clarki teglandae*, and the specimen itself (Figs. 52, 54), show no indication of T-shaped spirals, but some specimens of *A. jimgoederti* also show no indication of these spirals (Fig. 43).

Grant and Gale (1931:657) noted the similarity in spiral sculpture between *Ancistrolepis* and *Beringius* and suggested that perhaps *Ancistrolepis* should be considered a section or synonym of *Beringius* (Dall, 1887:304; type species *Chrysodomus crebicostatus* Dall). Clifford M. Nelson, U.S. Geological Survey, kindly called my attention to the fact that the whorl proportions, aperture, and fasciole of *A. jimgoederti* do not fit *Neptunea* in the strict sense, and that the speeies is more closely related to *Ancistrolepis*. Species from the eastern Pacific Tertiary that have been assigned to *Ancistrolepis* are: *Ancistrolepis rearensis* (Clark, 1932), *Ancistrolepis macneili* Kanno (1971), *Ancistrolepis clarki clarki* Tegland (1933), *Ancistrolepis clarki teglandae* Durham (1944), *Ancistrolepis landesi* Tegland (1933), and *Ancistrolepis packardi* Durham (1944).

The spiral ribs on the penultimate whorl of *Ancistrolepis rearensis* (Clark, 1932:831, pl. 20, figs. 14, 15) are described as having a fairly prominent collar and thus would resemble those on *A. jimgoederti. Ancistrolepis rearensis* has convex whorls rather than subtabulate ones and lacks the concavity just below the suture, present on *A. jimgoederti.* Kanno (1971: 118) placed *A. clarki teglandae* into synonymy with *A. rearensis* without discussion, and Addicott (1976c:23) cited it as a junior synonym. *Ancistrolepis clarki teglandae* (Figs. 52, 54) has a round body whorl and a shorter, wider spire than *A. jimgoederti. Ancistrolepis macneili* Kanno (1971:119, pl. 14, fig. 7) is much more inflated and has a shorter spire in proportion to the body whorl than does *A. jimgoederti*. The body whorl of *A. clarki clarki* is evenly rounded to the suture; the body whorl of *A. jimgoederti* is deeply concave between the suture and the first spiral cord and the whorls of the spire are more tabulate. *Ancistrolepis clarki clarki* is also wider and has fewer whorls (six or seven) than *A. jimgoederti. Ancistrolepis landesi* has a high spire, similar to *A. jimgoederti*, but the body whorl is convex to the suture rather than concave just below the suture. In addition, the primary spiral cords on the body whorl of *A. landesi* are grouped together

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Figures 34–47. *Ancistrolepis jimgoederti* n. sp., unidentified buccinid, *Liracassis apta* (Tegland), and *Bruclarkia yaquinana* (Anderson and Martin).

Figures 34, 35, 37, 38, 40, 43, 45. *Ancistrolepis jimgoederti* n. sp. **34.** Paratype LACMIP 6635. Showing secondary spirals, ×1.5; height 40 mm, width 29 mm. **35, 37, 38.** Holotype LACMIP 6636; height 55 mm, width 35 mm. Figures 35 and 37 show primary spirals sculptured by secondaries. Figure 38 is the same specimen tipped to display undercut spiral cords. **40.** Same specimen as Figure 34. Showing angular spiral cord, ×1.5. **43.** Paratype LACMIP 6637. Showing cast from which shell has exfoliated; height 67 mm, width 35 mm. **45.** Showing spiral cords in concretion; height 65 mm, width 35 mm. Paratype LACMIP 6638.

Figure 36. Unidentified buccinid, ×2.0; height 28 mm, width 13 mm. USGS Loc. M 7891, USNM 363986.

Figures 39, 42, 46, 47. *Liracassis apta* (Tegland). **39.** Tabulate form with body whorl nodes; height 45 mm, width 35 mm. LACMIP 6497. **42.** Tabulate form showing nodes and intercalaries; height 49 mm. LACMIP 6639. **46, 47.** Rear and apertural view of round form; height 68 mm, width 45 mm. LACMIP 6640.

Figures 41, 44. *Bruclarkia yaquinana* (Anderson and Martin). Views of aperture and side showing configuration and sculpture, ×1.5; height 30 mm, width 22 mm. LACMIP 6641.


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on the middle of the body whorl whereas they are equally spaced from the suture on *A. jimgoederti.* The entire shell of *A. landesi* bears fine, evenly spaced secondary spiral sculpture. The one specimen of *A. jimgoederti* that has the secondary spiral sculpture preserved (Figs. 34, 37, 40) shows the spirals to be of unequal strength and spacing. The living species *Ancistrolepis grammatus* (Dall, 1907:158; 1925:3, pl. 30, fig. 8) has T-shaped spiral cords on a thin shell with subtabulate whorls. The body whorl, however, has nine T-shaped spirals of almost equal width compared to five on *A. jimgoederti* and the spire whorls have five rather than three or four spirals. The siphonal canal of *A. jimgoederti* is probably slightly longer and more strongly recurved than on *A. grammatus* and also bears finer spiral sculpture.

Weaver (1942:427) assigned *Ancistrolepis clarki clarki* to *Neptunea,* and renamed it *N. teglandae,* as *N. clarki* was a homonym of *Neptunea clarki* (Meek). The reassignment of *A. clarki clarki* to *Ancistrolepis* makes this action by Weaver no longer necessary.

Ancistrolepis landesi and *A. clarki clarki* occur in the type Blakeley Formation in the *Liracassis rex* Molluscan Zone. *Ancistrolepis clarki teglandae* occurs in the upper part of the Pysht Formation of the Twin River Group in the *Liracassis apta* Molluscan Zone. *Ancistrolepis rearensis* was originally collected from the upper part of the Poul Creek Formation in the *Liracassis apta* Molluscan Zone and the geographic and stratigraphic ranges were subsequently extended by Addicott (1976c:23) to the Clallam Formation, Washington, in the *Vertipecten fucanus* Molluscan Zone. *Ancistrolepis jimgoederti* was collected from the upper part of the Lincoln Creek Formation, in the upper (Saucesian) part of the *Liracassis apta* Molluscan Zone.

Chrysodomus eucosimium Dall (1891:187–188), the genotype of *Ancistrolepis,* was collected off the coast of Unalaska in the Bering Sea. *Ancistrolepis grammatus* was collected from Tsugaru Strait, Japan, at a depth of 550 m where the surface temperature averages about 18°C.

This species is named in honor of James L. Goedert.

Fusinidae

Priscofusus? sp. cf. *P. geniculus* (Conrad)

Figures 50, 53, 55, 60, 61

Priscofusus? sp. cf. *P. geniculus* (Conrad) is represented by three specimens; two free of matrix (Figs. 50, 53, 55, 61) and the third preserved in a concretion with the shell missing on most of the specimen, but replaced by sparry calcite where still embedded (Fig. 60). *Priscofusus geniculus* (Conrad, 1849: 728, pl. 20, fig. 3) has been described and illustrated by Moore (1963:40–41, pl. 6, figs. 13, 15–18) and by Addicott (1970: 101–102, pl. 12, figs. 21, 22, 26, 28–30) and occurs in the Astoria Formation, Oregon, and the Jewett Sand, California. The *Priscofusus* reported from the Clallam Formation (Addicott, 1976c:24, pl. 2, fig. 12) and the Nye Mudstone (Moore, 1963:41, pl. 6, figs. 12, 19) may represent a new species.

Volutidae

Neogene volutids of the eastern Pacific Tertiary have in recent years commonly been assigned to the genus *Musashia* (Hayashi, 1960) and the subgenus *Musashia* or *Miopleiona* (Dall, 1907). A new species of *Miopleiona* from the Eugene Formation in Oregon (Howe, 1922) extends the geologic range of that subgenus into the late Eocene or early Oligocene.

Nipponomelon (Shikama, 1967), a subgenus previously reported from the Miocene to Holocene in Japan, is used here for most of the northeastern Pacific volutids, thus extending the geographic range of the subgenus across the Pacific and the geologic range into the Oligocene.

Musashia (*Musashia*) has a smooth shell or only thin axial ribs; axial ribs, if present, may be only on the posterior portion of the whorls (Fig. 70); the suture is slightly impressed. *Musashia* (*Nipponomelon*) has thin axial ribs, a slightly impressed suture, and only rarely a sutural collar (Figs. 66, 68). *Musashia* (*Miopleiona*) has very thick keel-like ribs markedly curved near the suture, which is deeply impressed and channeled (Figs. 51, 57, 64, 67). Shikama (1967) thought that *Miopleiona* was intermediate between the subgenera *Musashia* and *Nipponomelon* and was uncertain as to its proper assignment, although he placed it in the genus *Musashia.* On the basis of the suture and the thick axial ribs, *Miopleiona* could perhaps be elevated to generic rank. The type species of *Miopleiona* is *Musashia* (*Miopleiona*) *indurata* (Conrad, 1849). The markedly curved axial ribs and deeply channeled suture of *M.* (*M.*) *indurata* set it apart from all other described species of volutids, but the undescribed new species from the Eugene Formation, Oregon (Howe, 1922), also has a deeply channeled suture (Fig. 48) and is here assigned to *Miopleiona.* The suture is so deeply channeled on *Miopleiona* that even internal molds can be identified as belonging in the subgenus.

Figures 48-61. *Musashia* (*Miopleiona*) n. sp., *Musashia* (*Nipponomelon*) *shikamai* n. sp., *Priscofusus*? sp. cf. *P. geniculus* (Conrad), *Musashia* (*Nipponomelon*) *indurata* (Conrad), *Ancistrolepis clarki teglandae* Durham, and *Ancistrolepis jimgoederti* n. sp.

Figure 48. *Musashia* (*Miopleiona*) n. sp. Plaster cast of a specimen from the Eugene Formation, Oregon; height 95 mm. CAS/SU 2358.

Figure 49. *Musashia* (*Nipponomelon*) *shikamai* n. sp. Paratype. Latex impression showing fine spiral sculpture, height 82 mm. LACMIP 6642.

Figures 50, 53, 55, 60, 61. *Priscofusus*? sp. cf. *P. geniculus* (Conrad). **50, 53.** Internal mold showing traces of axial ribs, ×1.5; height 21 mm, width 18 mm. LACMIP 6643. **55, 61.** Almost complete internal mold showing spire outline and axial ribs; height 26 mm, width 15 mm. LACMIP 6644. **60.** Showing siphonal canal; height 51 mm, width 18 mm. LACMP 6645.

Figures 51, 57. *Musashia* (*Nipponomelon*) *indurata* (Conrad). Showing twisted axial ribs and deeply impressed suture, ×0.8; height 125 mm, width 59 mm. From the Astoria Formation, Lincoln County, Oregon. CAS 037058.

Figures 52, 54. *Ancistrolepis clarki teglandae* Durham. Latex impression of holotype external molds, UCMP 35417, showing spiral sculpture; height 48 mm.

Figures 56, 58, 59. *Ancistrolepis jimgoederti* n. sp. **56, 59.** Paratype LACMIP 6646. Showing siphonal canal, ×1.5; width 35 mm. **58.** Paratype LACMP 6647. Showing T-shaped cross section of spiral ribs preserved in concretion, ×2.0; height 70 mm.

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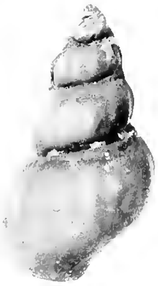

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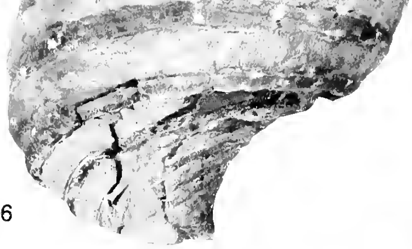

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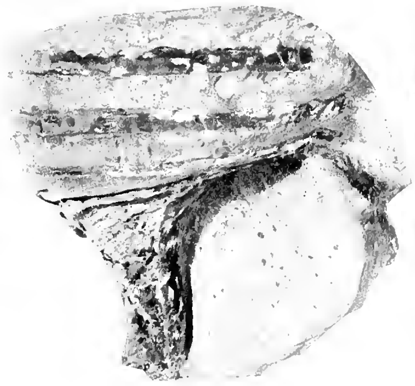

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Armentrout (1973) reported an undescribed species of volutid from the Lincoln Creek Formation and assigned it to *Musashia* (*Musashia*), an assignment with which I concur. Although several species of *Musashia* (*Musashia*) have been described from the Cenozoic of Japan, Armentrout's material documents the occurrence of the subgenus in western North America. It has a smooth shell, a slightly impressed suture that is markedly inclined, and a spire that is short in relation to the length of the body whorl (Figs. 62, 65, 76, 80, 87).

Subgeneric characters used by Shikama (1967) to differentiate volutids, such as the character of the protoconch and the number of initial and last columellar plaits, are useful for the allocation of living species, but are difficult to use with incompletely preserved fossils. The character of the suture and axial ribs serve best to distinguish fossil forms both subgenerically and specifically. On the basis of thin axial ribs and a slightly impressed suture, I assign most of the eastern Pacific Tertiary volutids to the subgenus *Nipponomelon* (Fig. 68). My allocation of eastern Pacific Tertiary species is shown in Figure 9.

Hayashi (1960:2) in his description of the genus *Musashia* noted that sexual dimorphism is very pronounced and that the large convex shells may be female. It is well to bear this in mind when looking at closely related eastern Pacific Tertiary species. In the Knappton fauna, however, slim forms are more common that convex forms, which would lead to the presumably false conclusion that males were more abundant than females.

The oldest recorded occurrence I have found for *Musashia* is *Musashia* (*Nipponomelon*?) *caucasica* (Korobkov, 1949: 694–695, text figs. 1, 2; 1955:205–206, pl. 4, figs. 6, 6a) from the middle Eocene in the Caucasus of the U.S.S.R. The oldest record of *Miopleiona* is *Musashia* (*Miopleiona*) n. sp. from the Eugene Formation, Oregon, of late Eocene to middle Oligocene age. The oldest record of *Nipponomelon* in the eastern Pacific is in the lower Oligocene part of the Lincoln Creek Formation, Washington. *Musashia* and *Nipponomelon* may have originated in the western Pacific; *Miopleiona* is indigenous to Alaska, Washington, Oregon, and California, and did not invade the western Pacific.

Musashia (*Musashia*) n. sp.

Figures 62, 65, 76, 80, 87

Miopleiona sp. A Durham, 1944:178.

Musashia (*Musashia*) *evelynae* Armentrout, 1973, in MS: 338–339, pl. 5, figs. 25, 27.

Musashia (*Musashia*) n. sp. has a slim shell with a very low spire compared to the body-whorl height. The suture is very slightly impressed and markedly inclined. The shell is smooth, without axial ribs, and only growth lines are preserved. The aperture is elongate oval, the siphonal fasciole probably straight and with a rather thick posterior callus and with two columellar plaits, the anteriormost one bladelike.

Musashia (*Musashia*) n. sp. is the only species assigned to this subenus in the eastern Pacific. The type species of *Musashia* is *M.* (*M.*) *hirasei* (Sowerby) (Figs. 69, 70). The only other described species at all similar to *M.* n. sp. is *Musashia* (*Musashia*?) *nagaoi* Shikama (1967:111–112, pl. 13, figs. 9–12) from the late Oligocene and early Miocene in Japan. Shikama (1967:112) considered *M. nagaoi* to be unique among Japanese fulgorids because it lacks axial ribs and radial striations; this is equally true for *M.* n. sp. in the eastern Pacific. *Musashia nagaoi* has a much more inflated body whorl than *M.* n. sp. and the suture of *M. nagaoi* is not as steeply inclined. *Musashia* (*Musashia*) n. sp. is being described by J. M. Armentrout.

Musashia (*Nipponomelon*) *shikamai* n. sp.

Figures 49, 63, 72, 74, 75, 77, 78, 82, 83, 88, 89

Psephaea (*Miopleiona*) cf. *P.* (*M.*) *indurata* (Conrad). Addicott, 1970:105, pl. 13, fig. 8; not pl. 13, fig. 6 (=*M. indurata*).

Musashia indurata (Conrad, 1849). Addicott, 1976c:25, pl. 3, fig. 27. Not *Rostellaria indurata* Conrad, 1849.

Musashia (*Nipponomelon*) *shikamai* is large, slender, and high spired with about nine whorls. The shell bears narrow axial ribs that are closely spaced and usually twisted near the suture. On large specimens the axial ribs disappear toward the anterior end. Narrow axial folds between the ribs presumably represent growth lines; the entire shell is sculptured by closely spaced subrounded spiral cords. The suture is slightly impressed and no subsutural band is preserved. The number of axial ribs ranges from 16 to 19, with 18 or 19 being the most common. The protoconch is not preserved. The aperture is assumed to be elongate oval. The siphonal fasciole is not preserved but may have been straight and long.

HOLOTYPE. LACMIP 6652, height 135 mm, width 52 mm; paratypes LACMIP 6642, height 87 mm; LACMIP 6648, height 73 mm, width 32 mm; LACMIP 6649, height 41 mm, width 20 mm; LACMIP 6650, height 90 mm, width 34 mm; LACMIP 6654, height 67 mm, width 25 mm; LAC-

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Figures 62–70. *Musashia* (*Musashia*) n. sp., *Musashia* (*Nipponomelon*) *shikamai* n. sp., *Musashia* (*Miopleiona*) *indurata* (Conrad), *Musashia* (*Nipponomelon*) *prevostiana magna* (Kuroda and Habe), and *Musashia* (*Musashia*) *hirasei* (Sowerby).

Figures 62, 65. *Musashia* (*Musashia*) n. sp. U W 16444a; height 57 mm, width 25 mm. **62.** Showing smooth shell. **65.** Showing columnar plaits.

Figure 63. *Musashia* (*Nipponomelon*) *shikamai* n. sp. Paratype LACMIP 6648. Showing narrow axial ribs; height 73 mm, width 32 mm.

Figures 64, 67. *Musashia* (*Miopleiona*) *indurata* (Conrad). Showing wide axial ribs and deeply impressed suture; height 66 mm, width 35 mm. USNM 363987.

Figures 66, 68. *Musashia* (*Nipponomelon*) *prevostiana magna* (Kuroda and Habe). CAS 028423; height 170 mm, width 60 mm. **66.** Looking down on apex to show suture. **68.** View of aperture.

Figures 69, 70. *Musashia* (*Musashia*) *hirasei* (Sowerby). CAS 028422; height 165 mm, width 56 mm. **69.** Looking down on apex to show suture. **70.** View of aperture.

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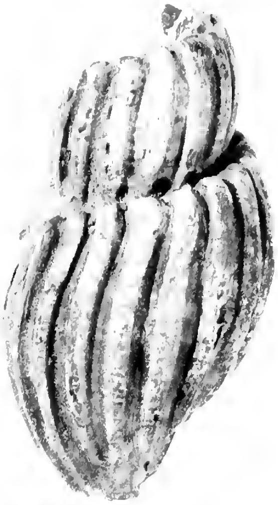

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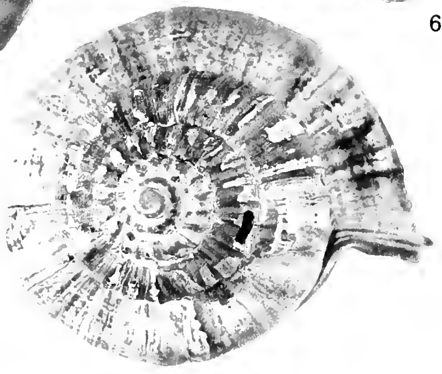

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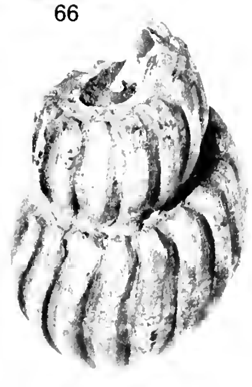

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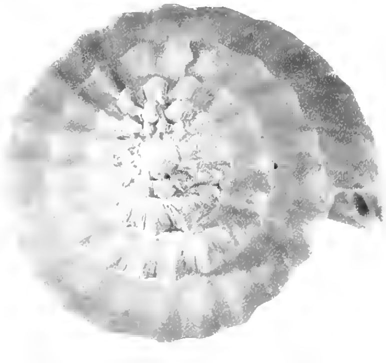

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MIP 6655, height 104 mm, width 36 mm; and LACMIP 6651, height 67 mm, width 26 mm.

TYPE LOCALITY. LAM 5842.

The species closely similar to *M.* (*N.*) *shikamai* are *M.* (*N.*) *weaveri* (Tegland, 1933) and *M.* (*N.*) *miensis* (Araki, 1960). *Musashia weaveri* (Figs. 71, 81, 94) has a slimmer shell with fewer (11 to 14) and wider axial ribs and a slightly angulated shoulder rather than a smoothly rounded one as in *M. shikamai. Musashia miensis* is slimmer and more elongate in outline, the axial ribs are not twisted near the suture, and the preserved radial sculpture is not as well developed as in *M. shikamai.*

Musashia n. sp. of Addicott (1976a:108, pl. 4, fig. 18) is similar to *M. shikamai* but has a few more axial ribs and a concave area below the suture. The latter character, however, could reflect sexual dimorphism.

Musashia (*Miopleiona*) *indurata* (Conrad, 1849) is distinguished from *M. shikamai* by its deeply impressed, channeled suture and by its strongly twisted keel-like axial ribs.

Musashia indurata (Conrad) of Addicott (1976c:25, pl. 3, fig. 27) does not have the deeply impressed, channeled suture and wide, keel-like axial ribs of *M.* (*Mioleiona*) *indurata* and is here assigned to *M. shikamai.*

On the basis of the incomplete holotype of *Miopleiona scowensis* Durham (1944:177–178, pl. 17, fig. 15), I am unable to find any characters to distinguish it from *M. weaveri* and believe it should be synonymized with that species.

Musashia (*Neopsephaea*) *corrugata* (Clark, 1932:831–832, pl. 21, figs. 4, 5, 11; Addicott et al., 1971, figs. 2y, aa–bb), from the Poul Creek Formation, Alaska (Figs. 73, 90, 92, 93, 95) is slimmer than *M. shikamai* and has a more sharply inclined suture and fewer axial ribs that are thicker and more widely spaced than in *M. shikamai.*

Musashia (*Musashia*) sp. of Allison and Marincovich (1981, pl. 3, figs. 12, 13; not pl. 3, figs. 8, 14, 16, 17) has a much wider body whorl in proportion to spire height and fewer (about 14) axial ribs than *M. shikamai.* The specimen figured by Allison and Marincovich (1981, pl. 3, figs. 8, 14), although poorly preserved, probably belongs in the subgenus *Musashia.*

Figures 71-77. *Musashia* (*Nipponomelon*) *weaveri* (Tegland), *Musashia* (*Nipponomelon*) *shikamai* n. sp., *Musashia* (*Neopsephaea*) *corrugata* (Clark), and *Musashia* (*Musashia*) n. sp.

Figures 71. *Musashia* (*Nipponomelon*) *weaveri* (Tegland). Showing spacing of axial ribs and spiral sculpture; height 125 mm, width 40 mm. UC locality A1806, Blakeley Formation of Weaver (1912), Bainbridge Island, Washington. UCMP 35420.

Figures 72, 74, 75, 77. *Musashia* (*Nipponomelon*) *shikamai* n. sp. **72.** Showing inflation of body whorl ×0.8; height 135 mm, width 52 mm. Holotype LACMIP 6652. **74.** Showing spiral sculpture ×2.0; height 41 mm, width 20 mm. Paratype LACMIP 6649. **75.** Showing deflection of ribs near suture; height 90 mm, width 34 mm. Paratype LACMP 6650. **77.** Showing spacing of ribs and spiral sculpture. Paratype LACMIP 6651.

Figure 73. *Musashia* (*Neopsephaea*) *corrugata* (Clark). Showing inclined suture and sculpture; height 120 mm, width 33 mm. Upper part of the Poul Creek Formation, Yakataga Reef, Alaska. USNM 363988.

Figure 76. *Musashia* (*Musashia*) n. sp. Showing outline of shell and inclined suture ×1.5; height 52 mm, width 20 mm. LAM Loc. 5843; LACMIP 6653.

Figures 78-86. *Musashia* (*Nipponomelon*) *shikamai* n. sp., *Musashia*? sp., *Musashia* (*Musashia*) n. sp., *Musashia* (*Nipponomelon*) *weaveri* (Tegland), and *Musashia* (*Nipponomelon*) *prevostiana magna* (Kuroda and Habe).

Figures 78, 82, 83. *Musashia* (*Nipponomelon*) *shikamai* n. sp. **78.** Paratype LACMIP 6654. Showing inclined suture ×1.5; height 67 mm, width 25 mm. **82.** Showing narrow, closely spaced axial ribs; height 73 mm, width 32 mm. Paratype LACMIP 6648, shown in Figure 63. **83.** Paratype LACMIP 6655. Showing siphonal canal and spiral sculpture; height 104 mm, width 36 mm.

Figure 79. *Musashia*? sp. Immature? specimen ×1.5; height 24 mm, width 10 mm. LACMIP 6656.

Figure 80. *Musashia* (*Musashia*) n. sp. Showing smooth shell and inclined suture; height 57 mm, width 22 mm. UW 16444.

Figures 81, 84, 86. *Musashia* (*Nipponomelon*) *weaveri* (Tegland). **81.** Showing widely spaced axial ribs and spiral sculpture ×1.5; height 40 mm, width 23 mm. USNM 363989. **84, 86.** From the basal part of the Jewett Sand, California. USNM 650185; height 73 mm, width 30 mm.

Figure 85. *Musashia* (*Nipponomelon*) *prevostiana magna* (Kuroda and Habe). Rear view showing narrow, closely spaced axial ribs and suture; height 170 mm, width 60 mm. CAS 028423.

Figures 87-95. *Musashia* (*Musashia*) n. sp., *Musashia* (*Nipponomelon*) *shikamai* n. sp., *Musashia* (*Neopsephaea*) *corrugata* (Clark), and *Musashia* (*Nipponomelon*) *weaveri* (Tegland).

Figure 87. *Musashia* (*Musashia*) n. sp. Showing smooth shell and inclined suture ×1.5; height 62 mm, width 19 mm. USNM 363992. USGS Loc. 25764, Lincoln Creek Formation, Grisdale Quadrangle, Washington.

Figure 88, 89. *Musashia* (*Nipponomelon*) *shikamai* n. sp. **88.** USGS Loc. M4050, Clallam Formation, Washington. Hypotype (Addicott, 1976c, pl. 3, fig. 27) USNM 216000; height 74 mm, width 34 mm. **89.** UCMP Loc. 3229, Monterey Group of Wagner and Schilling (1923). Hypotype (Addicott, 1970, pl. 13, fig. 6) UCMP 12136, a latex impression ×1.5; height 52 mm, width 21 mm.

Figures 90, 92, 93, 95. *Musashia* (*Neopsephaea*) *corrugata* (Clark). **90.** Paratype UCMP 12399; height 55 mm, width 30 mm. Poul Creek Formation, Alaska. **92, 95.** Holotype UCMP 12399; height 85 mm, width 29 mm. Poul Creek Formation, Alaska. **93.** Showing spire and aperture of specimen from Yakataga Reef, Alaska; height 120 mm, width 33 mm. USNM 363988. Same specimen shown in Figure 73.

Figures 91, 94. *Musashia* (*Nipponomelon*) *weaveri* (Tegland). **91.** View looking down on apex showing suture, ×1.5; height 40 mm, width 23 mm. Same specimen shown in Figure 81. USGS Loc. 4093, USNM 363989. **94.** Showing outline, axial ribs, and spiral sculpture; height 125 mm, width 40 mm. Same specimen shown in Figure 71. UCMP Locality A1806, Blakeley Formation of Weaver (1912), Bainbridge Island, Washington. UCMP 35420.

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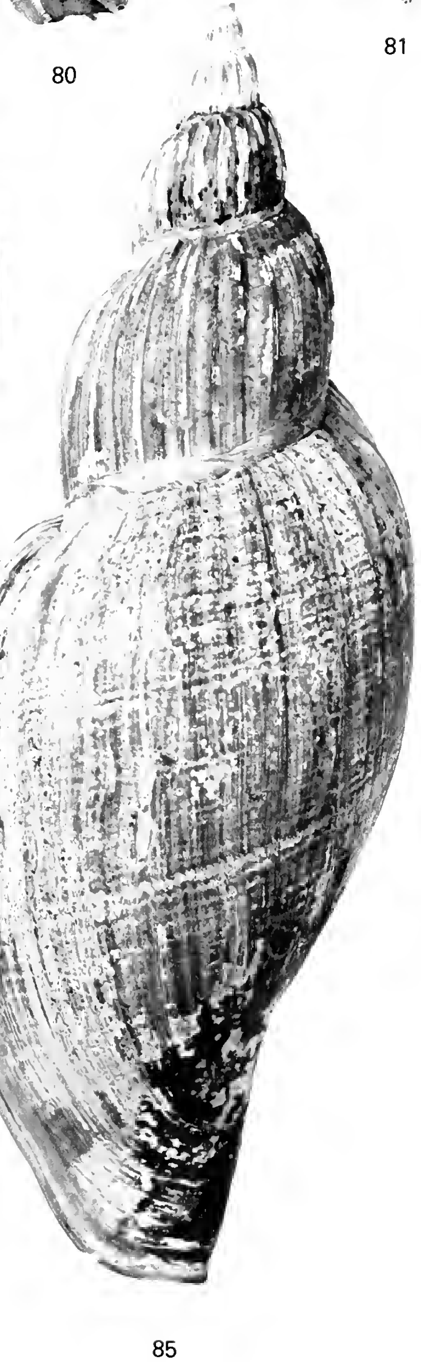
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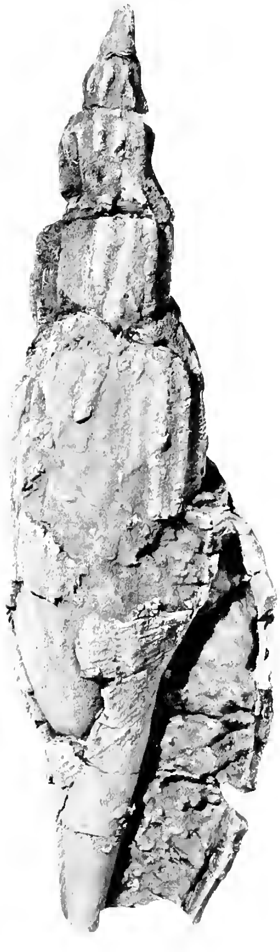

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Musashia (*Musashia*) n. sp., described above, differs from *M. shikamai* by having a smooth shell without axial ribs or radial threads, a much larger body whorl in proportion to height, and a strongly inclined suture.

In outline and axial sculpture, *M. shikamai* resembles *Musashia* (*Nipponomelon*) *elegantula* Shikama (1967) from the early Pliocene, Japan, but differs from that species by not having a subsutural band.

The early whorls of a few specimens of *M. shikamai* from the upper part of the Lincoln Creek Formation at Knappton, Washington, are filled with barite.

OCCURRENCE ELSEWHERE. Upper part of the Poul Creek Formation, Alaska, upper part of the Pysht Formation of the Twin River Group and the Clallam Formation, northwestern Washington, the Nye Mudstone, Oregon (Howe, 1922:138, pl. 10, fig. 3 as *Miopleiona clatsopensis* Howe, n. sp.), and the Freeman-Jewett Silt of Matthews (1955) and the Vaqueros Formation, southern California.

Musashia (*Miopleiona*) n. sp.

Figure 48

Miopleiona n. sp. Howe, 1922:137.

Musashia (*Miopleiona*) n. sp., collected from the Eugene Formation in Oregon, is a large volutid with a thick shell that bears perhaps as many as 30 narrow, keel-like axial ribs. The suture is deeply impressed, channeled, and inclined. The species is represented by a single plaster cast of a specimen consisting of half of two whorls. The preserved portion is identical in all characters to *Musashia* (*Miopleiona*) *indurata* except that the axial ribs are half as wide and twice as closely spaced as on *M.* (*M.*) n. sp.

There is no doubt in my mind that *M.* (*M.*) n. sp. was collected from the Eugene Formation on the University of Oregon campus. The record is based on a specimen, now missing and presumed lost, collected by Professor Earl L. Packard, a paleontologist of note, and I have no reason to suspect the locality data. The specimen was first mentioned by Howe (1922:137) as "*Miopleiona* n. sp., (very large), lower Oligocene, Eugene," and later by Schenck (1928:11) as *Miopleiona* n. sp. from the Eugene Formation, Oregon. A plaster cast was made of the specimen for Schenck and deposited in the Stanford University collection, now housed at the California Academy of Sciences. Hickman (1969) did not describe any volutids from the Eugene Formation. Presumably the plaster cast was not seen at that time, or the locality description was considered suspect.

Musashia (*Miopleiona*) n. sp. is the oldest known species of *Miopleiona,* as the subgenus is used here. Its occurrence in the Eugene Formation extends its geologic range from the Miocene into the early Oligocene or late Eocene.

The Eugene Formation has been extensively collected, in part because it is exposed in almost all excavations made for buildings on the University of Oregon campus. The single, incomplete specimen of *M.* (*M.*) n. sp. indicates its rareness. Hickman (1969:22) suggested that the Eugene molluscan fauna lived at a depth of 55 m. The molluscan fauna of the upper part of the Lincoln Creek Formation at Knappton probably lived at a depth no shallower than 100 m and the related *Musashia* (*Nipponomelon*) is common in that part of the unit. *Musashia* (*Miopleiona*) *indurata* is usually found in the finer-grained, deeper-water facies of the Astoria Formation. I suggest that the molluscan fauna in the Eugene Formation lived in shallower water than was common for *Miopleiona.*

Turridae

Aforia wardi (Tegland)

Figure 99

Leucosyrinx clallamensis wardi Tegland, 1933:124, pl. 10, figs. 5–8.

Aforia wardi is of medium size and pagodaform, with nine strongly angulated whorls and a U-shaped sinus on the shoulder (Fig. 99). The shell is smooth above the angulations but sculptured by fine spiral threads below, and these spirals extend down the siphonal canal on the body whorl. *Aforia campbelli* (Durham, 1944:183, pl. 14, fig. 4) differs in having the whorl angulation closer to the suture, and the angulation is rounded rather than bladelike. Javidpour (1973) discussed the phylogeny of eastern Pacific Tertiary species of *Aforia.* The correlation diagram (Javidpour, 1973:198, fig. 17) is misleading in that *Aforia campbelli* is shown in the upper Oligocene part of the Lincoln Creek Formation, whereas it should have been placed in the middle Oligocene part of the unit as stated in the text (Javidpour, 1973:196, 199–200). *Aforia* was placed in the subfamily Turriculinae by McLean (1971:119), following Powell (1942).

Living species of *Aforia* in the eastern Pacific have been recorded from depths of 6 to 2870 m (Abbott, 1974:265) and in the western Pacific from depths of 55 to 90 m (Kira, 1962: 102). Powell (1969:411–414) said that *Aforia* prefers cold water ranging from −0.6° to +5.4°C and is bipolar, going deeper under equatorial waters.

Based on the illustrations by Powell (1969:411, pl. 322, figs. 1–4; 414, pl. 323, figs. 1–3) of the type species of *Aforia, Pleurotoma circinata* Dall, characters such as apical angle and position of whorl angulation are not useful in distinguishing species. If larger collections of well-preserved specimens of *Aforia* become available, future workers may see fit to synonymize some of the species proposed for eastern Pacific Tertiary *Aforia.*

OCCURRENCE ELSEWHERE. Lower part of the Blakeley Formation in the *Liracassis rex* Molluscan Zone, Washington.

Turricula? sp.

Figure 97

Turricula? sp. is represented by one incompletely preserved specimen on which the siphonal canal is not exposed. The sinus is U-shaped and confined to the shoulder slope. The shell is sculptured by moderately strong spiral cords that are not noded. *Turricula washingtonensis* (Weaver, 1912:78, pl.

3, fig. 31; 1942:533, pl. 98, figs. 16, 17, 22) differs from *Turricula*? sp. in having nodes.

Megasurcula? sp.
cf. *M. wynoocheensis* (Weaver)

Figure 96

Megasurcula? sp. cf. *M. wynoocheensis* (Weaver) is represented by a single poorly preserved and somewhat crushed specimen. *Megasurcula wynoocheensis* (Weaver, 1912:70–71, pl. 11, figs. 87–89, 94) is a middle Miocene and possibly early Miocene species (Addicott, 1976c:27, pl. 3, figs. 16, 17).

Actenoidae

***Microglyphus*? n. sp.?**

Figure 98

Microglyphus? n. sp.? has three or possibly four whorls and a body whorl that is very inflated with the maximum width at the middle of the whorl. The spiral cords, bounded by incised grooves, are not equidimensional. The single specimen is very small (2.1 mm high, 1.9 mm wide) and, although it may be an immature individual, the number of whorls indicates that it probably is a very small species. In addition to its small size, *Microglyphus*? n. sp.? differs from other described Tertiary actenoids in having a more globose body whorl with the maximum inflation at the middle of the whorl.

PELECYPODS

Nuculidae

Acila (*Acila*) *gettysburgensis* (Reagan)

Figures 100–102, 105

Nucula (*Acila*) *gettysburgensis* Reagan, 1909:171, 175, 177, pl. 1, fig. 3.

Acila (*Acila*) *gettysburgensis* is represented by five specimens. *Acila* (*A.*) *gettysburgensis* ranges from the Matlockian through the Pillarian Molluscan Stages.

Nuculanidae

Portlandia (*Portlandia*) *chehalisensis* (Arnold)

Figures 103, 104, 106, 107

Malletia chehalisensis Arnold, 1908:365, pl. 33, fig. 9.

Portlandia (*Portlandia*) *chehalisensis* is represented by seven specimens, some well preserved (Fig. 107) and one double-valved (Figs. 103, 104). One incomplete specimen has concentric *Saccella*-like ridges on the midportion of the shell near the ventral margin (Fig. 106). One single valve is 31.8 mm long, 18.5 mm high, and 7.0 mm thick; perhaps the largest specimen of the species collected. The largest specimen noted by Hickman (1969:31) measured 26 mm in length. *Yoldia reagani* Dall (1922:306) was considered a synonym of *Portlandia chehalisensis* (Hickman, 1969:30).

Living eastern Pacific species of *Portlandia* occur no farther south than latitude 54°N and are found at depths of 10 to 2560 m and temperatures from −2° to +6°C (Bernard, 1983:13).

Solemyidae

Acharax dalli (Clark)

Figures 108–111, 114

Solemya dalli Clark, 1925:73, pl. 9, fig. 3.

Acharax dalli is represented by six specimens, all but one double-valved. Fingerlike projections of the periostracum are partially preserved on some specimens (Fig. 108). *Acharax ventricosa* (Conrad, 1849:723, pl. 17, figs. 7, 8), a species found in the Astoria Formation in Oregon and Washington, is higher in proportion to length than *A. dalli*.

The eastern Pacific Holocene species *Acharax johnsoni* (Dall, 1891) lives at a depth between 800 and 3000 m at temperatures of 1° to 9°C (Bernard, 1983:9). Vokes (1955:536–537) said that living species of *Acharax* are found at depths of 5 to 3180 m and that the controlling factor in their distribution may be water temperature.

Limopsidae

Limopsis nitens (Conrad)

Figures 112, 113, 115, 116

Pectunculus nitens Conrad, 1849:726, pl. 18, figs. 9a–b.

Limopsis nitens occurs as numerous single valves (Figs. 112, 113) and occasional paired valves (Figs. 115, 116). Radial lines of sculptural punctures are preserved on some specimens.

The lithology of the concretions from Knappton and the clustering together of many specimens is similar to the concretion presumably from the Astoria Formation, at Astoria, Oregon, that contains the lectotype of *L. nitens* (Moore, 1963:61–62, pl. 15, figs. 2, 5). Weaver (1942:76) suggested that the lectotype was collected at Knappton, rather than at Astoria, because he had found nodules containing large numbers of *L. nitens* at Knappton and had not found any specimens at Astoria. Howe (1922:70) did not find any specimens of *L. nitens* at Astoria and I found none in the Astoria Formation farther south (Moore, 1963:62). The rock containing the lectotype of *L. nitens* may have come from Knappton, or the upper part of the Lincoln Creek Formation may have been exposed on the Columbia River terrace at Astoria when Dana made his collection in 1841, yet no other mollusks typical of the Lincoln Creek Formation were collected by him.

Most species of *Limopsis* live in deep water (Keen, 1971:54); *Limopsis diegensis* Dall has been collected at depths of 120 to 1500 m and at temperatures between 3° and 27°C (Bernard, 1983:17). The fact that *Limopsis nitens* most commonly occurs in clumps suggests that the species was gregarious.

Mytilidae

***Modiolus addicotti* n. sp.**

Figures 117, 125

Modiolus n. sp.? aff. *M. restorationensis* Van Winkle. Addicott, 1976c:28, pl. 5, fig. 5.

Modiolus addicotti is a rather small *Modiolus* with weakly inflated valves, a markedly thin shell, and a convex dorsal margin. The posterior end is only moderately enlarged, and slightly longer near the ventral margin. The anterior end is small and evenly curved. The umbones are close to the anterior margin. Patches of preserved shell are light brown and iridescent with mostly evenly spaced growth lines but with a few bunched together forming low ridges.

HOLOTYPE. LACMIP 6672, length 47 mm, height 25 mm.

TYPE LOCALITY. LAM 5842.

Modiolus addicotti differs from *Modiolus restorationensis* Van Winkle (1918:82, pl. 4, fig. 5) in having a convex dorsal margin and a narrower posterior end.

Modiolus lives intertidally to 360 m in the eastern Pacific, but most species are found at depths no greater than 50 m (Bernard, 1983:19).

OCCURRENCE ELSEWHERE. Lowermost part of the Clallam Formation, northwestern Washington.

This species is named in honor of Warren O. Addicott.

Limidae

Acesta (*Acesta*) *twinensis* (Durham)

Figures 119, 123, 124

Lima twinensis Durham, 1944:139, pl. 13, fig. 11.

Acesta (*Acesta*) *twinensis* is represented by one incomplete double-valved specimen and four incomplete single valves all of which are preserved intact with their original inflation. The anterior ears are small and well defined by a deep concave groove along the anterior margin (Fig. 124). The anterior margin is straight, not concave, and joins the ventral margin without an abrupt break in alignment. The posterior ears are large and indistinctly delineated (Figs. 119, 124). The shells are large (maximum estimated height 140 mm), thin, and smooth in the center but with rounded ribs of varying widths at the shell margins (Fig. 124). The shells are inflated, and the largest specimen suggests a thickness of 25 mm (one valve). Portions of the brown translucent outer shell layer are preserved on most specimens, but this shell layer tends to stay attached to the enclosing rock when the specimens are broken away.

Acesta twinensis is distinguished by its sharply truncated anterior margin, which differentiates it from *Acesta robertsae* (Durham, 1944), an early Oligocene species that has a more rounded anterior margin.

Acesta (*Acesta*) *oregonensis* Clark (1925:84, pl. 14, figs. 3, 4), a species from the upper Eocene and lower Oligocene Keasey Formation, Oregon, has an arcuate anterior margin.

Acesta twinensis ranges from the Matlockian through the Juanian Molluscan Stages. Living species of *Acesta* (*Acesta*) are found in the eastern Pacific at depths between 600 and 2200 m and at temperatures of 1° to 8°C (Bernard, 1983:22). One species has been collected in the western Pacific near Japan at a depth of 185 m.

OCCURRENCE ELSEWHERE. Blakeley Formation, Washington.

***Acesta* (*Plicacesta*) *wilsoni* n. sp.**

Figures 118, 132, 134

Acesta (*Plicacesta*) *wilsoni* is of moderate size and subovate in outline, with a thicker shell than *Acesta* (*Acesta*) and radial ribs of varying widths and spacing that are rounded and most prominent on the middle portion of the shell but that persist to the shell margins. Beaks small; anterior auricle presumed small and delineated; posterior auricle large and not delin-

Figures 96-117. *Megasurcula*? sp. cf. *wynoocheensis* (Weaver), *Turricula*? n. sp.?, *Microglyphus*? n. sp.?, *Aforia wardi* (Tegland), *Acila* (*Acila*) *gettysburgensis* (Reagan), *Portlandia* (*Portlandia*) *chehalisensis* (Arnold), *Acharax dalli* (Clark), *Limopsis nitens* (Conrad), and *Modiolus addicotti* n. sp.

Figure 96. *Megasurcula*? sp. cf. *wynoocheensis* (Weaver). Rear view, × 1.5; height 32 mm, width 20 mm. USGS Loc. 7891, USNM 363990.

Figure 97. *Turricula*? n. sp.? Showing spiral sculpture, × 2.0; height 15 mm, width 10 mm. LACMIP 6657.

Figure 98. *Microglyphus*? n. sp.? Showing outline and spiral sculpture, × 5.0; height 2.7 mm, width 2.4 mm. LACMIP 6658.

Figure 99. *Aforia wardi* (Tegland). Showing pagodaform outline, × 1.5; height 28 mm, width 14 mm. LACMIP 6659.

Figures 100-102, 105. *Acila* (*Acila*) *gettysburgensis* (Reagan). **100.** Showing primary bifurcation, × 2; length 13 mm, height 11 mm. LACMIP 6660. **101.** Showing sulcus × 1.5; height 17 mm. LACMIP 6661. **102.** Showing secondary bifurcation, × 2. LACMIP 6662. **105.** Showing outline and bifurcation, × 1.5; length 25 mm, height 20 mm. LACMIP 6663.

Figures 103, 104, 106, 107. *Portlandia* (*Portlandia*) *chehalisensis* (Arnold). **103, 104.** Double-valved specimen showing sculpture and lunule, × 1.5; length 21 mm, height 12 mm, width 8 mm (both valves). LACMIP 6664. **106.** Showing *Saccella*-like sculpture, × 2; length 22 mm, height 13 mm. LACMIP 6665. **107.** Showing outline and sculpture, × 1.5; length 32 mm, height 18 mm. LACMIP 6666.

Figures 108-111, 114. *Acharax dalli* (Clark). **108, 114.** Showing extensions of fingerlike periostracum and dorsal side; length 28 mm, height 24 mm, width 16 mm (both valves). LACMIP 6667. **109, 110.** Showing sculpture of double-valved specimen, × 1.5; length 45 mm, height 20 mm, width 11 mm (both valves). LACMIP 6668. **111.** Showing sculpture × 1.5; length 35 mm, height 13 mm. LACMIP 6669.

Figures 112, 113, 115, 116. *Limopsis nitens* (Conrad). **112.** Showing outline, × 3; 10 mm long, 7 mm high. LACMIP 6670. **113.** Showing radial punctae, × 3; length 9 mm, height 7 mm. LACMIP 6671. **115, 116.** Double-valved specimen showing thickness of valves, × 5; length 8 mm, height 6 mm, width 5 mm (both valves). USGS Loc. 7891, USNM 363991.

Figure 117. *Modiolus addicotti* n. sp. Holotype LACMIP 6672. Showing outline of valve; length 47 mm, height 25 mm.


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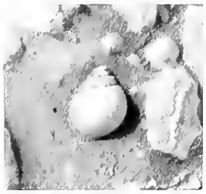
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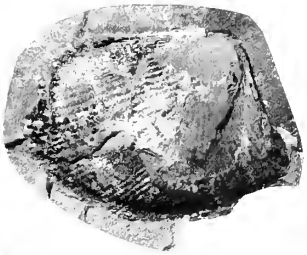
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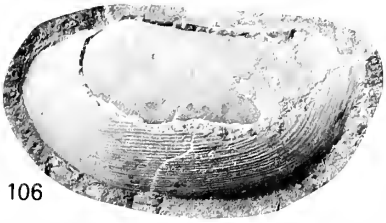
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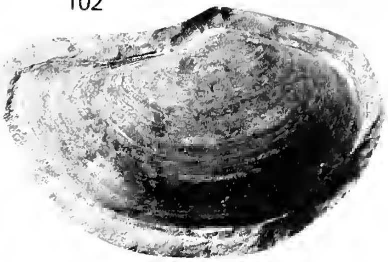
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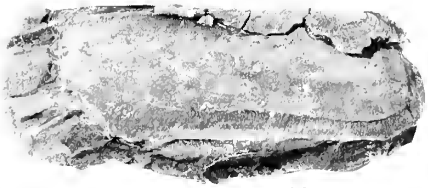
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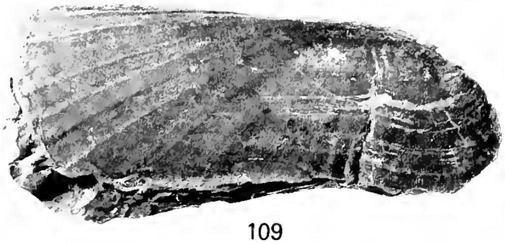
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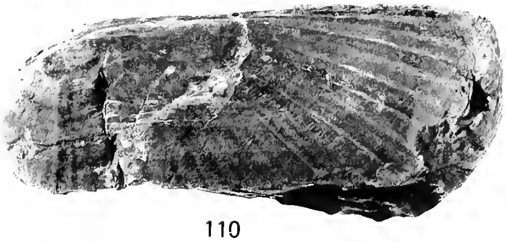
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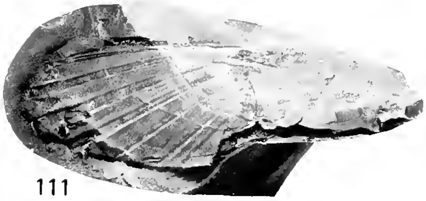
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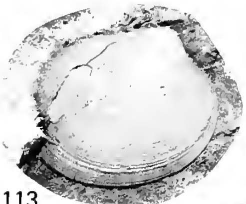
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eated. No concentric sculpture is preserved. The holotype (incomplete) is 60 mm high and 50 mm wide and the thickness of one valve is 13 mm (Figs. 118, 132). The paratype (incomplete) is 63 mm high and 40 mm wide and the thickness of one valve is 11 mm (Fig. 134).

HOLOTYPE. LACMIP 6673, length 51 mm, height 61 mm, width 10 mm (one valve); paratype LAM 6686, length 41 mm, height 61 mm.

TYPE LOCALITY. LAM 5842.

Acesta wilsoni is smaller than *Acesta* (*Plicacesta*) *oakvillensis* (Clark, 1925:84, pl. 15, figs. 1, 3) and has fewer ribs and a more rounded anterior margin. A topotype specimen, earlier illustrated by Weaver (1942, pl. 21, fig. 1), is figured for comparison (Fig. 126). *Acesta* cf. *A. oakvillensis* Clark of Addicott (1976b, figs. 6a, c) has narrower ribs that are more widely and evenly spaced than on *A. wilsoni* and may be a new species.

Acesta wilsoni and *A. oakvillensis* are the only Tertiary species of *Plicacesta* known in North America. *Acesta* n. sp. of Addicott (1976b, figs. 6x, z, ab) may also be a *Plicacesta.*

The Holocene species *Acesta* (*Plicacesta*) *sphoni* (Hertlein, 1963) was collected at latitude 33°N at a depth between 455 and 550 m and a temperature between 4° and 9°C. *Acesta* (*Plicacesta*) *smithi* (Sowerby) occurs off Honshu, Japan, at depths between 90 and 185 m (Kira, 1962:145).

This species is named in honor of Edward C. Wilson.

Ostreidae

Crassostrea? sp.

Figure 127

Crassostrea? sp. is represented by a single double-valved specimen preserved in a concretion and broken upon removal from the matrix. Indigenous Holocene species of *Crassostrea* live intertidally to a depth of 7 m in the eastern Pacific (Bernard, 1983:23).

Lucinidae

Lucinoma hannibali (Clark)

Figures 120–122

Phacoides (*Lucinoma*) *hannibali* Clark, 1925:89, pl. 22, figs. 2, 4.

Lucinoma hannibali is represented by six double-valved specimens (Figs. 120–122) from the upper part of the Lincoln Creek Formation, one with the shell replaced by barite. The specimens range in height from 27 mm to 52 mm. *Lucinoma acutilineata* (Conrad, 1849:725, pl. 18, figs. 2, 2a, 2b) has a shorter more concave dorsal margin than *L. hannibali.* Variation has been noted (Moore, 1963:70) in the spacing of concentric lamellae within single lots of the Holocene species *Lucinoma annulata* (Reeve, 1850) and by Addicott (1976c: 30) in the Oligocene to Miocene species *L. acutilineata,* yet specimens of *L. hannibali* from the upper part of the Lincoln Creek Formation have concentric lamellae rather consistently less densely spaced (Figs. 120–122) than the lamellae on *L. acutilineata* from the lower part of the Astoria Formation. *Lucinoma acutilineata* has been found in the Eugene Formation (upper Eocene to middle Oligocene) in Oregon (Hickman, 1969:38, 42) and in the lower and middle Miocene Astoria Formation (Moore, 1963:70–71, pl. 15, figs. 7–10, 12) in Oregon and Washington. If *L. hannibali* and *L. acutilineata* are distinct species, and I believe that they are, *L. acutilineata* may have preferred somewhat shallower water (50 m or less) than *L. hannibali,* and the two species coexisted at different depths. *Lucinoma annulata* lives today from latitude 33° to 47°N at depths of 25 to 750 m and *L. aequizonata* (Stearns, 1891) lives from latitude 34° to 37°N at depths of 400 to 650 m (Bernard, 1983:29). *Lucinoma hannibali* has a wider escutcheon and less concave dorsal margin than *L. columbiana* (Clark and Arnold, 1923:144–145, pl. 25, figs. 2a–b) from the Sooke Formation, Vancouver Island, and the Blakeley Formation of Weaver (1912). *Lucinoma hannibali* ranges from the Matlockian through the Juanian Molluscan Stages.

Thyasiridae

Thyasira (*Conchocele*) *disjuncta* (Gabb)

Figures 136, 138, 142

Conchocele disjuncta Gabb, 1866:28; 1869:99, pl. 7, figs. 48a–b.

Thyasira (*Conchocele*) *disjuncta* is larger, more quadrate, and has a more truncated anterior end than *Thyasira bisecta* (Conrad, 1849:724, pl. 17, figs. 10, 10a) from the Astoria Formation in Oregon (Moore, 1963:72, pl. 23, figs. 8, 14, 15). *Thyasira disjuncta* occurs in the Clallam Formation (Addicott, 1976c:30, pl. 6, fig. 7) and is living today (Bernard, 1983:29). The presence of two internal casts (Figs. 136, 138) and one specimen with the outer shell preserved (Fig. 142)

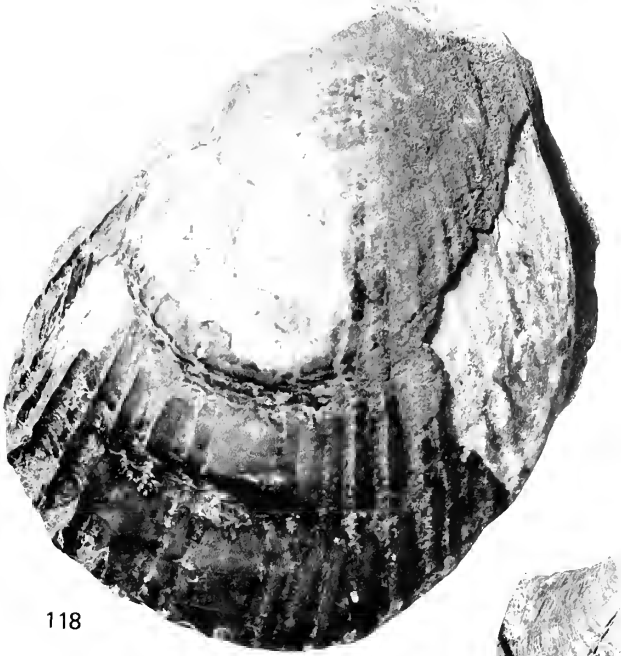
Figures 118–125. *Acesta* (*Plicacesta*) *wilsoni* n. sp., *Acesta* (*Acesta*) *twinensis* (Durham), *Lucinoma hannibali* (Clark), and *Modiolus addicotti* n. sp.

Figure 118. *Acesta* (*Plicacesta*) *wilsoni* n. sp. showing outline and radial ribs, ×1.5; length 51 mm, height 61 mm, width 10 mm (one valve). Holotype LACMP 6673.

Figures 119, 123, 124. *Acesta* (*Acesta*) *twinensis* (Durham). **119, 123.** Showing posterior ears. **119.** Length 74 mm, height 93 mm, width 22 mm (one valve). LACMP 6675. **123.** Length 92 mm, height 75 mm. LACMP 6674. **124.** Showing anterior ear and axial ribs, ×1.5; length 60 mm, height 70 mm. LACMP 6676.

Figures 120–122. *Lucinoma hannibali* (Clark). **120.** Showing profile of lunule; length 29 mm, height 27 mm, width 11 mm (both valves). LACMP 6677. **121.** Showing sulcus; length 39 mm, height 34 mm, width 16 mm (both valves). LACMP 6678. **122.** Showing concentric sculpture; length 40 mm, height 37 mm, width 27 mm (both valves). LACMP 6679.

Figure 125. *Modiolus addicotti* n. sp. Holotype LACMP 6672. Tipped to show configuration of double-valved specimen, ×1.5; length 47 mm, height 25 mm. Same specimen shown in Figure 117.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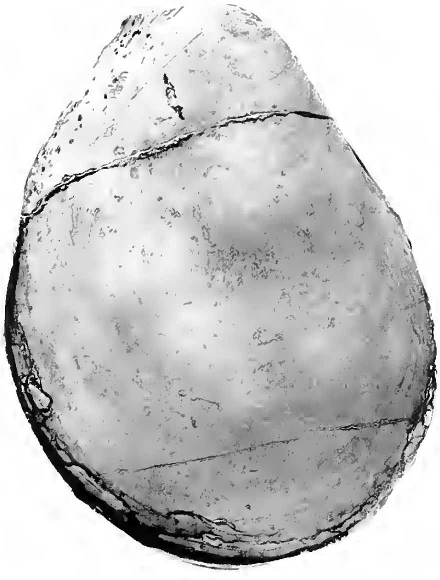
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in the upper part of the Lincoln Creek Formation extends the range of the species downward into the upper part of the Juanian Molluscan Stage. *Thyasira disjuncta* lives today from latitude 48° to 54°N at depths of 100 to 750 m and at temperatures between 0° and 7°C. *Thyasira bisecta* lives from latitude 43° to 57°N at depths between 50 and 300 m and temperatures between −1° and +11°C (Bernard, 1983:29). The occurrence of *T. disjuncta* in the Lincoln Creek Formation and of *T. bisecta* in the Astoria Formation is related to depth of water; the Astoria Formation represents a shallower-water facies than the Lincoln Creek Formation.

Cardiidae

Nemocardium? sp. cf. *N. lorenzanum* (Arnold)

Figure 130

Nemocardium? sp. cf. *N. lorenzanum* (Arnold, 1908:366, pl. 33, fig. 6) is represented by two poorly preserved single valves; one is illustrated (Fig. 130).

Tellinidae

Macoma sp. cf. *M. twinensis* Clark

Figure 128

Macoma sp. cf. *M. twinensis* Clark is represented by a single valve that does not have the hinge exposed (Fig. 128). In size, outline, and position of umbo, the specimen resembles *M. twinensis* Clark (1925:96, pl. 12, fig. 7), which ranges from late Oligocene to early Miocene.

Periplomatidae

Cochlodesma bainbridgensis Clark

Figures 139, 141

Cochlodesma bainbridgensis Clark, 1925:86, pl. 13, figs. 3, 4.

Cochlodesma bainbridgensis Clark has a thin, internally nacreous, fragile shell, that is sculptured with concentric undulations (Figs. 139, 141). Five specimens and one possible juvenile (Fig. 131) were collected from the upper part of the Lincoln Creek Formation. As noted by Moore (1976:53, pl. 16, figs. 4, 6–11), the variation in outline is great and not useful in the discrimination of fossil species. Holocene species of the closely related genus *Periploma* live intertidally to a depth of 380 m (Bernard, 1983:64).

Teredinidae

Figures 172, 177, 179

Teredinid burrows are preserved in wood and the tubes are filled with quartz (Fig. 172) or with sediment (Figs. 177, 179). No pallets are preserved, enabling generic differentiation, but

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Figures 126–134. *Acesta* (*Plicacesta*) *oakvillensis* (Clark), *Crassostrea*? sp., *Macoma* sp. cf. *M. twinensis* Clark, *Flabellum* sp., *Nemocardium*? sp. cf. *N. lorenzanum* (Arnold), *Cochlodesma*? sp., *Lima* (*Plicacesta*) *wilsoni* n. sp., and *Aturia angustata* (Conrad).

Figure 126. *Acesta* (*Plicacesta*) *oakvillensis* (Clark). Showing closely spaced axial ribs; length 79 mm, height 95 mm. UC Loc. A368, lower part of the Lincoln Creek Formation, Grays Harbor County, Washington. UCMP 32405.

Figure 127. *Crassostrea*? sp. Showing configuration; length 70 mm, height 102 mm. LACMP 6680.

Figure 128. *Macoma* sp. cf. *M. twinensis* Clark. Showing outline and concentric lines, ×1.5; length 15 mm, height 10 mm. LACMP 6681.

Figure 129. *Flabellum* sp. ×1.5; height 22 mm. LACMP 6682.

Figure 130. *Nemocardium*? sp. cf. *N. lorenzanum* (Arnold). Showing configuration and radial ribs, ×1.5; height 20 mm. LACMP 6683.

Figure 131. *Cochlodesma*? sp. Showing outline, ×2; length 11 mm, height 8 mm. LACMP 6684.

Figures 132, 134. *Lima* (*Plicacesta*) *wilsoni* n. sp. **132.** Showing outline and radial ribs, ×1.5; length 51 mm, height 61 mm, width 10 mm (one valve). Holotype LACMP 6673. **134.** Showing radial ribs ×1.5; length 41 mm, height 61 mm. Paratype LACMP 6686.

Figure 133. *Aturia angustata* (Conrad). Immature specimen, ×1.5; height 24 mm. LACMP 6687.

Figures 135–145. *Aturia angustata* (Conrad), *Thyasira* (*Conchochele*) *disjuncta* (Gabb), and *Cochlodesma bainbridgensis* Clark.

Figures 135, 137, 140, 143–145. *Aturia angustata* (Conrad). **135.** Showing outer shell and growth lines, ×0.7; height 150 mm. LACMP 6688. **137.** Cross section showing funnel-shaped septal structures; height 29 mm. LACMP 6689. **140.** Cross section showing septal structures; height 37 mm. LACMP 6690. **143.** Apertural view of broken specimen showing siphuncular orifices; height 90 mm. LACMP 6691. **144.** Cross section showing septal structures; height 60 mm. LAM Loc. 5843, LACMP 6692. **145.** Side view showing sutures; height 65 mm, width 27 mm (maximum diameter). Same specimen shown in Figure 150. LACMP 6693.

Figures 136, 138, 142. *Thyasira* (*Conchochele*) *disjuncta* (Gabb). **136.** Showing sulcus and configuration; length 70 mm, height 67 mm. LACMP 6694. **138.** Showing sulcus and configuration; length 52 mm, height 43 mm. LACMP 6695. **142.** Showing outer shell and concentric lines, ×1.5; length 37 mm, height 32 mm. LACMP 6696.

Figures 139, 141. *Cochlodesma bainbridgensis* Clark. **139.** Showing concentric undulations, ×1.5; length 34 mm, height 27 mm. LACMP 6697. **141.** Showing outline, ×1.5; length 30 mm, height 25 mm. LACMP 6698.

Figures 146–154. *Aturia angustata* (Conrad) and a crab claw.

Figures 146, 147, 149, 150, 152–154. *Aturia angustata* (Conrad). **146.** Thin section showing radiating calcite within phragmocone chamber in crossed-polarized light, ×70. LACMP 6699. **147.** Showing suture, ×0.8; height 95 mm. LAM Loc. 5287, LACMP 6700. **149.** Showing silicified siphuncular neck and orifice; height 43 mm. LACMP 6701. **150.** Showing sutures; height 65 mm, width 27 mm (maximum diameter). Same specimen shown in Figure 145. LACMP 6693. **152.** Broken specimen showing siphuncular orifice and neck; height 114 mm. LACMP 6702. **153.** Cross section showing funnel-shaped siphuncular necks, ×2.0; length 45 mm. LACMP 6703. **154.** Broken specimen showing siphuncular orifice; height 75 mm. LACMP 6704.

Figures 148, 151. Crab claw; length 40 mm. LACMP 6705.

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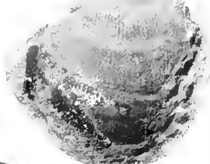

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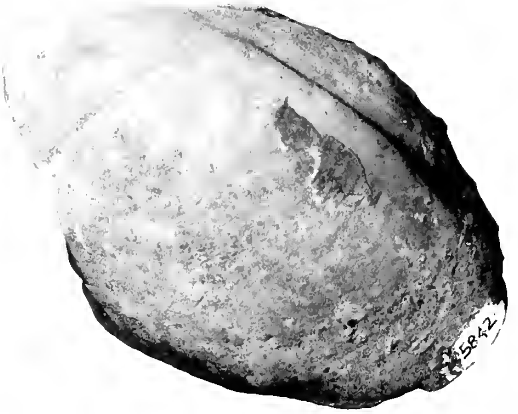

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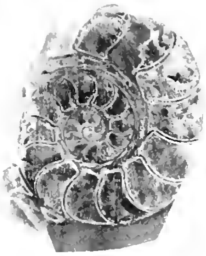

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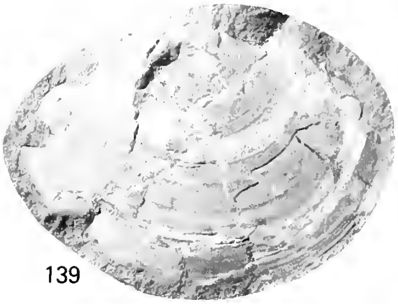

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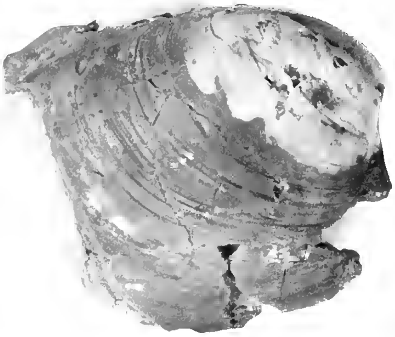

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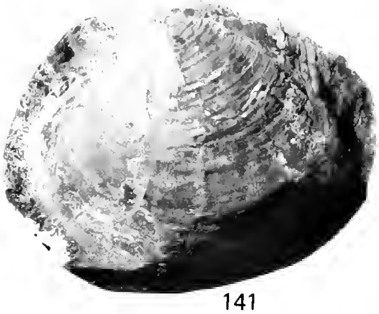

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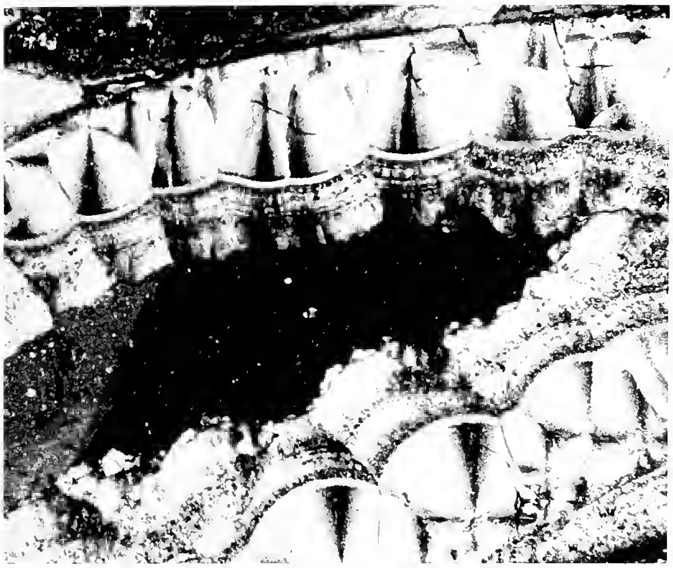
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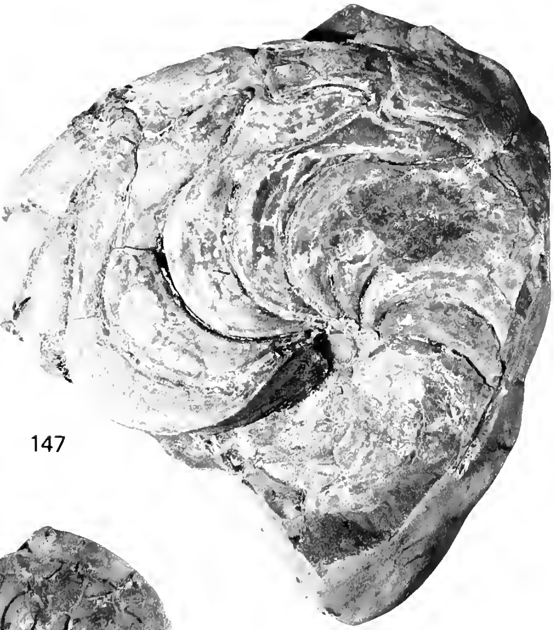
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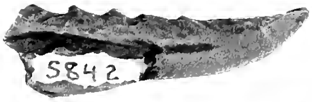

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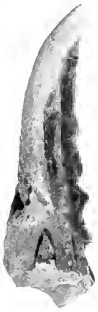
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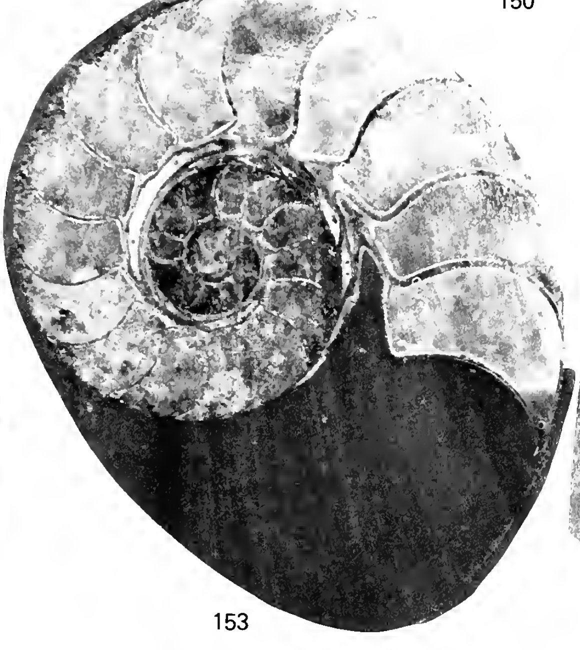
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on the basis of the size and configuration of the burrows, two different genera may be present.

SCAPHOPOD

Dentaliidae

Dentalium (*Fissidentalium*?) sp. cf. *D. porterensis* (Weaver)

Dentalium (*Fissidentalium*?) sp. cf. *D. porterensis* (Weaver, 1912:79, pl. 13, fig. 113) is circular in cross section, slightly tapered, and has perhaps 32 (16 exposed on one half) fine radial riblets crossed by strong concentric threads that produce a basket-weave sculpture. The preservation does not permit comparison with other ribbed Tertiary dentaliids.

CEPHALOPODS

Aturidae

Aturia angustata (Conrad)

Figures 133, 135, 137, 140, 143–145, 146, 147, 149, 150, 152–154, 155–159

Nautilus angustatus Conrad, 1848:728, pl. 20, figs. 5, 6.

Aturia angustata has been described in detail by Schenck (1931:457–462) and Miller (1947:85–88), and the type specimen figured and discussed by Moore (1963:85–86, pl. 31, figs. 1, 5).

A total of 180 specimens of *A. angustata* is in the Knappton collections, making this cephalopod by far the most abundant mollusk collected. Taking into account a possible bias in favor of collecting *Aturia*, this is still a large number. Kummel (1956:330–331) called attention to the rarity of post-Triassic nautiloids saying that no large collection representing a population had ever been assembled from a single horizon and locality. Stenzel (*in* Ladd, 1957:893) noted that there are in excess of 1000 mollusks representing other classes for every nautiloid shell and that the proportion may actually surpass 10,000 to 1.

The shell of the preserved portion of the living chamber is commonly slightly broken but more frequently is intact. The outer shell layer is dark brown and the entire shell or venter is thin, thinner than that of the living *Nautilus*. Faint, closely spaced growth lines can be seen on some specimens (Fig. 135). The lateral lobes are tongue-shaped and ascending on young specimens (Figs. 133, 145, 150), but not on more mature specimens (Fig. 147).

The specimens are believed to range in size from 30 to 180 mm in greatest diameter. The smallest specimens (25 mm) are not complete and so were probably 5 to 10 mm larger, and the largest specimen measures 170 mm but is incomplete and has an estimated size of 180 mm. The largest number of specimens sufficiently complete to make size measurement meaningful (22%) are 90 mm in greatest diameter. Presumably, this means that many of the specimens had not reached maturity before death. About 24% of the specimens are 100 to 180 mm in maximum diameter and are assumed to have been mature. The specimens are not crushed, and none shows any indication that it imploded as a result of having been transported to great depths.

The suture is simple with a broad flattened ventral saddle, a narrow pointed lateral lobe on the umbilical slope and dorsal area, and a broad saddle on the dorsal area divided by a deep, narrow lobe (Figs. 145, 147, 150). The siphuncle is moderate in size, subdorsal and marginal in position (Figs. 137, 140, 143, 144, 149, 152, 154, 155, 157), and located near the apex in the adapical flexure of the septa. The siphuncular tube consists of a series of cone-in-cone necks, or long funnel-shaped connecting rings (Fig. 157) without the long gaps between the necks that are present in *Nautilus*.

The phragmocone chambers may be filled with sediment (Fig. 154) but are more commonly partially filled with calcite or completely filled with calcite, barite, quartz, or combinations of these minerals (Fig. 153). A phragmocone chamber of one specimen is filled with glauconite. Some of the specimens have empty phragmocone chambers except for a calcite buttress, and these chambers may be followed or preceded by sediment-filled chambers, indicating that the sediment did not enter through the siphuncular tube but entered through a puncture in the shell. The body chamber, of course, is always filled with sediment.

Most of the shells of *Aturia angustata* are preserved in concretions as almost complete specimens, but some are fragments that may have weathered out of concretions or not have been so preserved. The specimens that show a sequence of mineralization, which is currently being studied in detail, begin with a buttressing of the shell walls with as many as nine layers of radial calcite (Fig. 146), followed by the dissolution of the aragonitic shell, and then the filling of the shell cavities and the remaining chamber voids with calcite, barite, and/or quartz in that sequence.

Sepiidae?

A trace fossil that may represent the cuttlebone of a sepiid is illustrated (Fig. 178).

FOSSILS OTHER THAN MOLLUSKS

SPONGES

Two sponges have been described by J.K. Rigby and D.E. Jenkins (1983) from the upper part of the Lineoln Creek Formation: *Aphrocallistes polytretos* (Fig. 180) and *Eurete*

Figures 155–159. *Aturia angustata* (Conrad). **155.** Broken specimen showing siphuncular orifices, ×3; height 80 mm. LACMP 6706. **156.** Showing phragmocone chambers filled with wood fragments and sediment. LACMP 6707. **157.** Silicified specimen etched in dilute hydrochloric acid to show cone-in-cone, funnel-shaped septal necks, ×1.5; 47 mm greatest diameter. LACMP 6708. **158.** Fecal pellets probably formed by a marine worm in phragmocone chamber, ×3. LACMP 6709. **159.** Fecal pellets in phragmocone chamber, ×5. LACMP 6710.

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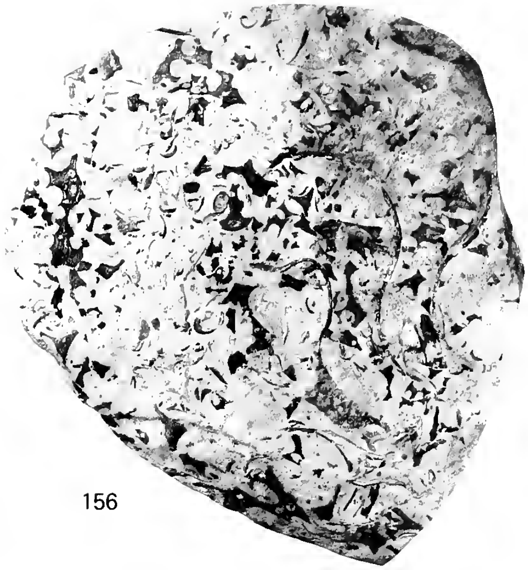

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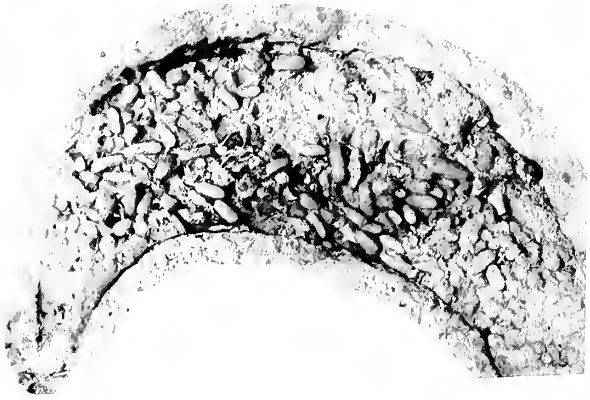

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goederti. In addition, hexactinellid root tuffs were identified that may represent a third sponge. Although the sponges are most common stratigraphically just below the major mollusk locality, they also occur within it. *Aphrocallistes* lives at depths of 100 to 1700 m (Schulze, 1887) and *Eurete* between 220 and 715 m, with the majority of species living at depths between 300 and 360 m (Rigby and Jenkins, 1983).

CORALS

Dendrophyllia hannibali Nomland (1916:67, pl. 6, figs. 1–3) was found in one concretion that also contains abundant fish debris and a small patch of the siliceous sponge, *Eurete goederti* Rigby and Jenkins (1983). The specimens are poorly exposed and recrystallized (Fig. 175), but some show septa (Fig. 176).

Dendrophyllia hannibali was described by Nomland (1916: 67) as colonial, branching, and forming several vertical series that unite when coming in contact. It has deep nearly round calices with about 42 to 48 septa. The maximum number of preserved septa counted on the specimens described by Nomland is about 20, but recrystallization is believed to have destroyed many of the septa.

Dendrophyllia is a scleractinian, ahermatypic (nonreef-building; capable of living in cold deep water) coral. According to Wells (1956:F362, F435), "the greatest development of ahermatypic corals occurs near and down the edges of continental slopes and the equivalent bathymetric zone around oceanic islands in depths from 175 to about 800 m . . . in temperatures of 4° to 21°C." *Dendrophyllia* is cosmopolitan in its modern distribution and is known from the Eocene through the Holocene at depths ranging from 0 to 1370 m.

Flabellum sp. (Fig. 129) has also been collected.

BRACHIOPOD

Laqueus? sp. cf. *L. vancouverensis* Davidson is poorly preserved and only three (or possibly four) specimens have been collected. The outer shell is smooth (Figs. 166, 168, 169), or may possibly on some specimens be finely ribbed (Fig. 167), and the inner fibrous layer is punctate. The specimens resemble *L. vancouverensis* (Davidson, 1887:113, pl. 18, figs. 10–13b) more than any other described species. Gradational variation in sculpture between subspecies of the terebratellids (Hertlein and Grant, 1944:132) seems to be sufficient to perhaps allow for both smooth-shelled and finely ribbed forms in one species.

ECHINOIDS

Most of the echinoids (Figs. 160–162, 164, 170) are tests of a spatangoid (heart urchin) that was probably buried in living position since so many of its spines are attached (Porter M. Kier, written commun., 1980). The species probably lived in a burrow at a depth of one to several centimeters within the sediment. All the tests are broken, perhaps by the weight of the overburden as the attached spines suggest the specimens were not transported. The echinoids have not been found in the center of spherical concretions typical of the rest of the fauna.

A single specimen thought to be a madreporite, a sievelike structure that provides access to the water-vascular system (Fig. 163), was also collected.

LOCALITIES

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

5787. From landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, NW ¼ sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle (1973 edition), on the Columbia River, Washington. (General locality that includes 5842, 5843, 5844, and 5852.)

5802. From a limestone quarry in the siltstones of Cliff Point unit (Wells, 1979) in the bluff on the south side of Bear River, 2.3 km northeast of Goulter Ranch, on the section line between secs. 20 and 21, T. 10 N., R. 10 W., Chinook

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Figures 160–170. Spatangoid echinoids and a brachiopod.

Figures 160–162, 164, 170. Spatangoid echinoids. **160.** Showing test outline and spines, ×6.0; 8 mm greatest diameter of test. LACMP 6491. **161.** Showing ambulacral area and spines, ×3.0. LACMP 6710. **162.** Showing test outline and attached spines, ×3.0; 20 mm greatest diameter of test. LACMP 6492. **164.** Showing broken test with preserved ambulacral areas, ×2.0; 52 mm greatest diameter of test. LACMP 6711. **170.** Showing outline of several tests with associated wood fragments. LACMP 6712.

Figure 163. Madreporite? of spatangoid echinoid, ×12.0; 2.4 mm greatest diameter. LACMP 6713.

Figures 165–169. *Laqueus*? sp. cf. *L. vancouverensis* Davidson. **165.** View of apex, ×1.5. LACMP 6714. **166.** Showing configuration and narrow axial ribs; length 23 mm, width 23 mm. LACMP 6715. **167.** Showing radial ribs, ×1.5; width 23 mm. LACMP 6716. **168.** Showing configuration; height 17 mm. LACMP 6717. **169.** Showing configuration and smooth shell; length 35 mm, width 34 mm. Same specimen shown in Figure 165. LACMP 6714.

Figures 171–180. Teredinid bores, crab claw, *Dendrophyllia hannibali* Nomland, a trace fossil, and *Aphrocallistes polytretos* Rigby and Jenkins.

Figures 171, 172, 177, 179. Teredinid-bored wood. **171.** View of bored wood within *Aturia.* Same specimen shown in Figure 156, ×3.0. LACMP 6707. **177, 179.** Teredinid tubes in wood. LACMP 6716. **177.** Cross-sectional view. **179.** Longitudinal view, ×0.8.

Figures 173, 174. Crab claw showing nodes, ×1.5; length 35 mm. USNM 363992.

Figures 175, 176. *Dendrophyllia hannibali* Nomland. **175.** Showing configuration, ×1.5. LACMP 6719. **176.** Showing septa, ×3.0. LACMP 6720.

Figure 178. Trace fossil, possibly cuttlebone of sepiid, ×1.5; length 45 mm. LACMP 6721.

Figure 180. *Aphrocallistes polytretos* Rigby and Jenkins. Showing irregular branching growth. LACMP 6722.

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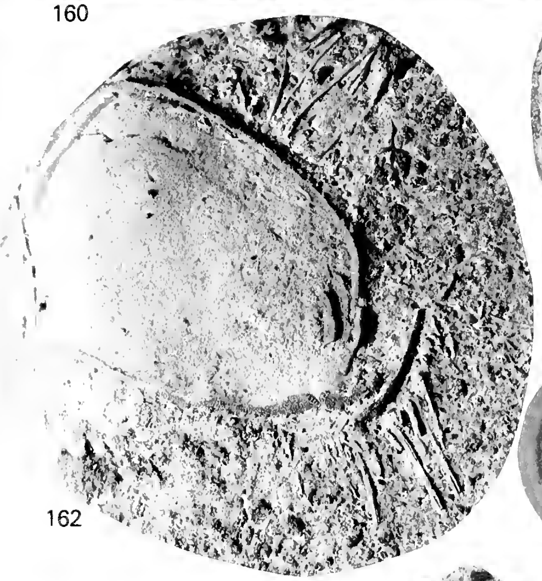

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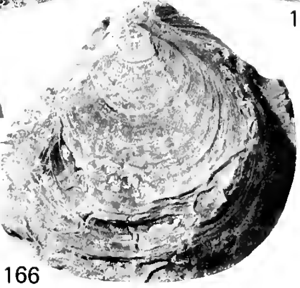

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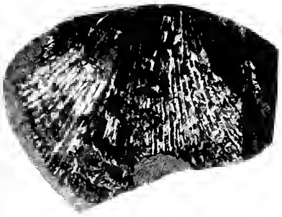

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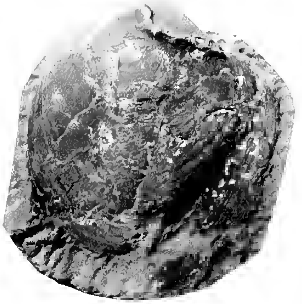

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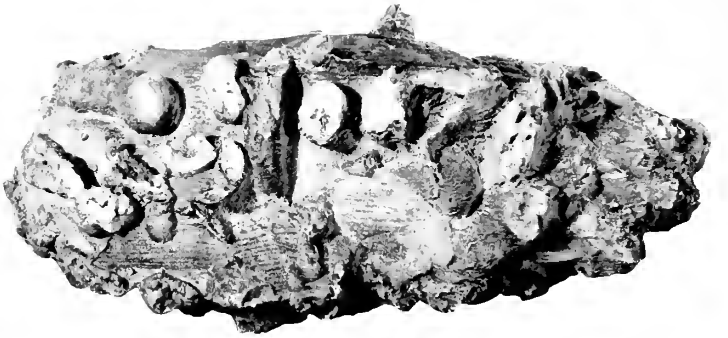

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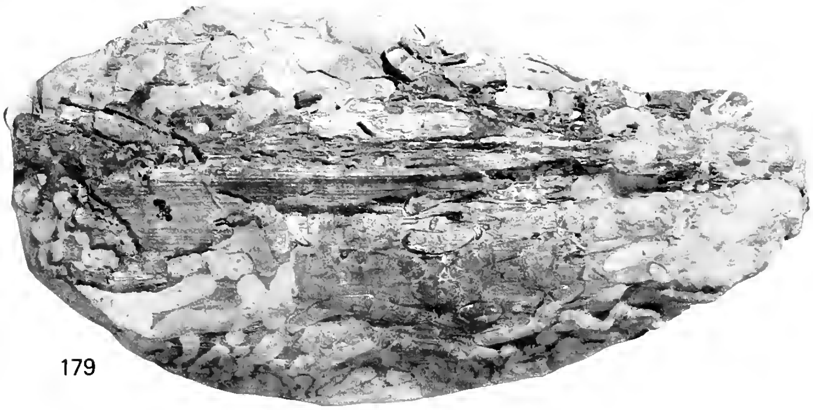

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7½-minute quadrangle, about 15 km northwest of Knappton, Pacific County, Washington.

5842. From landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, in the center of the N ½, N ½ sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, on the Columbia River, Washington.

5843. From landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, 305 m south and 430 m east of NW cor. sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, on the Columbia River, Washington.

5844. From landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, 122 m east and 520 m south of NW cor. sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, on the Columbia River, Washington.

5852. From landslide block in upper part of the Lincoln Creek Formation between Knappton and Grays Point, NE ¼, NW ¼ sec. 9, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, on the Columbia River, Washington.

5863. From the Astoria Formation between Knappton and Grays Point, SE ¼, NW ¼ sec. 10, T. 9 N., R. 9 W., Knappton 7½-minute quadrangle, on the Columbia River, Washington.

U.S. GEOLOGICAL SURVEY, MENLO PARK, CALIFORNIA

M7891. The same locality as LAM 5842, but collected by E.J. Moore.

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LITERATURE CITED

Abbott, R.T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold, New York. 663 pp., 24 pls.

Addicott, W.O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. United States Geological Survey Professional Paper 642:1–174, 21 pls., 11 figs., 9 tables.

———. 1976a. Neogene molluscan stages of Oregon and Washington. Neogene Symposium, Pacific Section, Society of Economic Paleontologists and Mineralogists Meeting, San Francisco, California. Pages 95–115, 5 pls., 6 figs., 1 table.

———. 1976b. New molluscan assemblages from the upper member of the Twin River Formation, western Washington: significance in Neogene chronostratigraphy. United States Geological Survey, Journal of Research 4(4):437–447, 6 figs., 2 tables.

———. 1976c. Molluscan paleontology of the lower Miocene Clallam Formation, northwestern Washington. United States Geological Survey Professional Paper 976: 1–44, 9 pls., 10 figs., 7 tables.

Addicott, W.O., Saburo Kanno, Kenji Sakamoto, and J.W. Miller. 1971. Clark's Tertiary molluscan types from the Yakataga district Gulf of Alaska. United States Geological Survey Professional Paper 750-C:18–33, 6 figs.

Allison, R.C. 1978. Late Oligocene through Pleistocene molluscan faunas in the Gulf of Alaska region. The Veliger 21(2):171–188, 2 figs., 2 tables.

Allison, R.C., and Louie Marincovich. 1981. A late Oligocene or earliest Miocene molluscan fauna from Sitkinak Island, Alaska. United States Geological Survey Professional Paper 1233:1–11, 3 pls., 3 figs., 6 tables.

Anderson, F.M., and Bruce Martin. 1914. Neocene record in the Temblor Basin, California, and Neocene deposits of the San Juan district, San Luis Obispo County. California Academy of Sciences Proceedings ser. 4, 3:15–112, pls. 1–10.

Araki, Yoshio. 1960. Geology, paleontology and sedimentary structures (including Problematica) of the Tertiary formations developed in the environs of Tsu City, Mie Prefecture, Japan. Liberal Arts Department, Mie University Bulletin, Special Volume 1:1–118, 11 pls.

Armentrout, J.M. 1973. Molluscan paleontology and stratigraphy of the Lincoln Creek Formation, late Eocene-Oligocene, southwestern Washington. University of Washington, Seattle, Ph.D. dissertation. 479 pp., 15 pls.

———. 1975. Molluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. Paleogene symposium and selected technical papers. Pacific Sections American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, Society of Economic Geologists, 1975, Annual Meeting, Long Beach, California. Pages 14–18.

———. 1977. Cenozoic molluscan stages of Oregon and Washington. Geological Society of America, Abstracts with Programs 9(7):882–883.

Arnold, Ralph. 1908. Description of new Cretaceous and Tertiary fossils from the Santa Cruz Mountains, California. United States National Museum, Proceedings 34(1617):345–390, pls. 31–37.

Bernard, F.R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean, Bering Strait to Cape Horn. Canadian Special Publication of Fisheries and Aquatic Sciences 60:102.

Clark, B.L. 1918. The San Lorenzo series of middle California. University of California Publications, Department of Geology, Bulletin 11(2):45–234, pls. 3–24.

———. 1925. Pelecypoda from the marine Oligocene of western North America. University of California Publications, Department of Geological Sciences, Bulletin 15(4):69–136, pls. 8–22.

———. 1932. Fauna of the Poul and Yakataga Formations (upper Oligocene) of southern Alaska. Geological Society of America, Bulletin 43(3):797–846, pls. 14–21.

Clark, B.L., and Ralph Arnold. 1923. Fauna of the Sooke Formation, Vancouver Island, with description of a new coral by T. Wayland Vaughan. University of California Publications, Department of Geological Sciences, Bulletin 14(5):123–234, pls. 15–42.

Clench, W.J., and R.D. Turner. 1950. The genera *Sthenorytis, Cirsotrema, Acirsa, Opalia,* and *Amaea* in the western Atlantic. Johnsonia 2(29):221–248.

Cochram, J.K., D.M. Rye, and N.H. Landman. 1981. Growth rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. Paleobiology 7:469–480.

Conrad, T.A. 1848. Fossil shells from Tertiary deposits on Columbia River, near Astoria. American Journal of Science, ser. 2, 5:432–433, 14 figs.

———. 1849. Fossils from northwestern America. *In* Dana, J. D., United States Exploring Expedition . . . 1838–1842, under the command of Charles Wilkes 10:722–728 (appendix), atlas pls. 17–21. (Text reprinted in Dall, 1909:152–156.)

Dall, W.H. 1887. Supplementary notes on some species of mollusks of the Bering Sea and vicinity. United States National Museum, Proceedings 9(571):297–309, pls. 3, 4.

———. 1891. Scientific results of explorations by the United States Fish Commission Steamer "Albatross" (20). On some new or interesting west American shells obtained from the dredgings of the United States Fish Commission Steamer "Albatross" in 1888, and from other sources. United States National Museum, Proceedings 14(849):173–191, pls. 5–7.

———. 1892. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex beds of Tampa and the Pliocene beds of the Caloosahatchie River. Wagner Free Institute of Science, Transactions 3(2): 201–473, pls. 13–22.

———. 1907. Descriptions of new species of shells, chiefly Buccinidae, from the dredgings of the U.S.S. "Albatross" during 1906, in the northwestern Pacific, Bering, Okhotsk, and Japanese Seas. Smithsonian Miscellaneous Collections 50(2)1727:139–173.

———. 1909. Contributions to the Tertiary paleontology of the Pacific Coast, I. The Miocene of Astoria and Coos Bay, Oregon. United States Geological Survey, Professional Paper 59:1–278, 23 pls.

———. 1922. Fossils of the Olympic Peninsula [Washington]. American Journal of Science ser. 5, 4:305–314.

———. 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum: United States National Museum, Proceedings 66:1–41, art. 17, no. 2554, pls. 1–36.

Davidson, Thomas. 1887. A monograph of recent Brachiopoda. Transactions of the Linnean Society of London, Zoology, ser. 2, 4(2):1–248.

Durham, J.W. 1937. Gastropods of the family Epitoniidae from Mesozoic and Cenoizoic rocks of the west coast of North America, including one new species by F. E. Turner and one by R. A. Bramkamp. Journal of Paleontology 11(6):479–512, pls. 56, 57.

———. 1944. Megafaunal zones of the Oligocene of northwestern Washington. University of California Publications, Department of Geological Sciences, Bulletin 27(5): 101–212, pls. 13–18, figs. 1–7.

Gabb, W.M. 1866. Tertiary invertebrate fossils. California Geological Survey, Palaeontology 2(1) pt. 2:1–38, pls. 1–13.

———. 1869. Tertiary invertebrate fossils. California Geological Survey, Paleontology, Cretaceous and Tertiary fossils 2(1):65–124, part 3.

Grant, U.S., IV, and H.R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California. San Diego Society Natural History, Memoir 1:1–1036, 32 pls., 15 figs., 3 tables.

Ham, C.K. 1952. Geology of Las Trampas Ridge, Berkeley Hills, California. California Division of Mines, Special Report 22:1–26, 20 pls.

Hamada, Takashi, Ikuo Obata, and Takashi Okutani. 1980. *Nautilus macromphalus* in captivity. Takai University Press, Tokyo, Japan. 80 pp.

Hayashi, Tadaichi. 1960. On a new subgenus and a new species of *Fulgoraria* from Japan. Venus, Japanese Journal of Malacology 21(1):1–4, 1 pl.

Hertlein, L.G. 1963. A new species of giant *Lima* from off southern California (Mollusca: Pelecypoda). California Academy of Sciences, Occasional Paper 40:1–6, 3 figs.

Hertlein, L.G., and U.S. Grant, IV. 1944. The Cenozoic Brachiopoda of western North America. University of California, Los Angeles, Publications in Mathematical and Physical Sciences 3:1–236, 21 pls., 34 figs.

Hickman, C.S. 1969. The Oligocene marine molluscan fauna of the Eugene Formation in Oregon. University of Oregon, Natural History Museum, Bulletin 16:1–112, 14 pls.

———. 1980. Paleogene marine gastropods of the Keasey Formation in Oregon. Bulletins of American Paleontology 78(310):1–112, 10 pls., 5 figs.

Howe, H.V.W. 1922. The Miocene of Clatsop and Lincoln Counties, Oregon. Stanford University, California, Ph.D. dissertation. 286 pp., 14 pls., 1 map.

Javidpour, Mahdokt. 1973. Some records on west American Cenozoic gastropods of the genus *Aforia.* The Veliger 15(3):196–205, 1 pl., 2 figs.

Kanie, Yasumitsu, Yoshio Fukuda, Hideaki Nakayama, Kunihiro Seki, and Mutsuo Hattori. 1980. Implosion of living *Nautilus* under increased pressure. Paleobiology 6(1):44–47, 3 figs.

Kanno, Saburo. 1971. Tertiary molluscan fauna from the Yakataga district and adjacent areas of southern Alaska. Palaeontological Society of Japan, Special Papers 16: 1–154, 18 pls., 20 figs.

Keen, A.M. 1971. Sea shells of tropical west America, 2nd ed. Stanford University Press, Stanford, California. 1064 pp., 3305 figs.

Kira, Tetsuaki. 1962. Shells of the western Pacific in color.

Hoikusha Publishing Company, Osaka, Japan. 224 pp., 72 pls. (English edition).

Korobkov, I.A. 1949. O nakhozhdenii roda *Psephaea* Crosse v sredneeotsenovykh otlozheniakh severnogo Kavkaza [On the occurrence of *Psephaea* Crosse in middle Eocene sediments of the northern Caucasus]. Akademia Nauk SSSR, Doklady 66(4):693–695, 2 figs.

———. 1955. Mollyuski srednego eotsena severnogo Kavkaza i usloviya ikh obitaniya. Leningradskii Gosudarstvennyi Universitet, Uchenye Zapiski, Seriya Geologicheskikh Nauk; Uchenye Zapiski, no. 189, pp. 158–230. Seriya Geologo-Pochvennykh Nauk; Vestnik 6, Seriya Geologii i Geografii.

Kummel, Bernard. 1956. Post-Triassic nautiloid genera. Harvard University Museum of Comparative Zoology, Bulletin 114(7):324–494, 28 pls., 35 figs.

Ladd, H.S., editor. 1957. Treatise on marine ecology and paleoecology. 2, paleoecology. Geological Society of America, Memoir 67(2):1–1077.

Loel, Wayne, and W.H. Corey. 1932. The Vaqueros Formation, Lower Miocene of California; [part] 1, paleontology. University of California Publications, Department of Geological Sciences, Bulletin 22(3):31–286, pls. 4–65.

Marincovich, Louie. 1979 [1980]. Miocene mollusks of the Topsy Formation, Lituya District, Gulf of Alaska Tertiary province, Alaska. United States Geological Survey, Professional Paper 1125-C:1–13, 30 figs.

Matthews, J.F. 1955. Edison Groves area of Edison oil field. California Oil Fields 41(2):11–14, 1 pl.

McLean, J.H. 1971. A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. The Veliger 14(1): 114–130, 4 pls., 1 table.

Miller, A.K. 1947. Tertiary nautiloids of the Americas. Geological Society of America, Memoir 23:1–234, 100 pls., 30 figs., 1 table.

Moore, E.J. 1963 [1964]. Miocene mollusks from the Astoria Formation in Oregon. United States Geological Survey, Professional Paper 419:1–109, 32 pls., 9 figs., 3 tables.

———. 1976. Oligocene marine mollusks from the Pittsburg Bluff Formation in Oregon. United States Geological Survey, Professional Paper 922:1–66, 17 pls., 5 tables.

———. 1984. Middle Tertiary molluscan zones of the Pacific northwest. Journal of Paleontology 58(3):718–737, 10 figs.

Noda, Hiroshi. 1975. Turciculid Gastropoda of Japan. Science Reports of Tohuku University, Sendai, Ser. 2 (Geology) 45(2):51–82, pls. 9–12, 3 figs., 2 tables.

Nomland, J.O. 1916. Corals from the Cretaceous and Tertiary of California and Oregon. University of California Publications, Department of Geology, Bulletin 9(5):59–76, pls. 3–6.

Powell, A.W.B. 1942. The New Zealand Recent and fossil Mollusca of the family Turridae, with general notes on turrid nomenclature and systematics. Auckland Institute and Museum Records 2:1–188, 14 pls., 6 figs.

———. 1969. The family Turridae in the Indo-Pacific, part 2, the subfamily Turriculinae. Indo-Pacific Mollusca 2(10):215–415, pls. 188–324.

Reagan, A.B. 1909. Some notes on the Olympic Peninsula, Washington. Kansas Academy of Sciences, Transactions 22:131–238, 6 pls.

Reeve, Lovell. 1850. Conchologia iconica: or illustrations of the shells of molluscous animals, 6 [1849–1851]. London.

Rehder, H.A. 1955. The genus *Turcicula* Dall. Malacological Society, Proceedings 31:222–225, 1 pl.

Rigby, J.K., and D.E. Jenkins. 1983. The Tertiary sponges *Aphrocallistes* and *Eurete* from western Washington and Oregon. Natural History Museum of Los Angeles County, Contributions in Science 344:1–13, 23 figs.

Schenck, H.G. 1928. Stratigraphic relations of western Oregon Oligocene Formations. University of California Publications, Department of Geological Sciences, Bulletin 18(1):1–50, 18 text figs.

———. 1931. Cephalopods of the genus *Aturia* from western North America. University of California Publications, Department of Geological Sciences, Bulletin 19(19): 435–490, pls. 66–78.

Schulze, F.E. 1887. Report on the Hexactinellida collected by H.M.S. *Challenger* during the years 1873–76. Report of Scientific Results of the Voyage of the H.M.S. *Challenger*, Zoology 21:1–513.

Shikama, Tokio. 1967. System and evolution of Japanese fulgorarid Gastropoda. Science Reports of the Yokohama National University, section II, 13:23–132, 17 pls., 26 figs., 41 tables.

Stearns, R.E.C. 1891. Scientific results of explorations by the United States Fish Commission steamer Albatross, no. 17. Descriptions of new west American land, freshwater, and marine shells, with notes and comments. United States National Museum, Proceedings 13:205–225, pls. 15–17.

Tegland, N.M. 1931. Gastropod genus *Galeodea* in the Oligocene of Washington. University of California Publications, Department of Geological Sciences, Bulletin 19(18):387–444, pls. 59–65.

———. 1933. The fauna of the type Blakeley upper Oligocene of Washington. University of California Publications, Department of Geological Sciences, Bulletin 23(3):81–174, pls. 2–15.

Van Winkle, K.E. 1918. Paleontology of the Oligocene of the Chehalis Valley, Washington. Washington University (Seattle) Publications in Geology 1(2):69–97, pls. 6–7.

Vokes, H.E. 1955. Notes on the Tertiary and Recent Solemyacidae. Journal of Paleontology 29(3):534–545.

———. 1957. Miocene fossils of Maryland. Maryland Department of Geology, Mines, and Water Resources, Bulletin 20:1–85.

Weaver, C.E. 1912. A preliminary report on the Tertiary paleontology of western Washington. Washington Geological Survey, Bulletin 15:1–80, pls. 1–15.

———. 1942. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington [Seattle], Publication in Geology 5(1–3):1–789, 104 pls. [1943]

Wells, J.W. 1956. Scleractinia. *In* Moore, R. C., ed., Treatise on invertebrate paleontology, Coelenterata, part F. Geological Society of America and University of Kansas Press, Lawrence. Pages F328–F444, figs. 222–243.

Wells, R.E. 1979. Geologic map of the Cape Disappointment-Naselle River area, Pacific County, Washington. United States Geological Survey, Open-File Report 79-389, 1:48,000.

Wolfe, E.W., and E.H. McKee. 1972. Sedimentary and igneous rocks of the Grays River Quadrangle, Washington. United States Geological Survey, Bulletin 1335:1–70.

Woodring, W.P. 1959. Geology and paleontology of Canal Zone and adjoining parts of Panama; description of Tertiary mollusks (Gastropods: Vermetidae to Thaididae). United States Geological Survey, Professional Paper 306-B:147–239, pls. 24–37.

Zullo, V.A. 1982. *Arcoscapellum* Hoek and *Solidobalanus* Hoek (Cirripedia, Thoracica) from the Paleogene of Pacific County, Washington, with a description of a new species of *Arcoscapellum.* Natural History Museum of Los Angeles County, Contributions in Science 336:1–9, 18 figs.

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FISHES OF THE GENUS *NANSENIA* (MICROSTOMATIDAE) WITH DESCRIPTIONS OF SEVEN NEW SPECIES

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Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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FISHES OF THE GENUS *NANSENIA* (MICROSTOMATIDAE) WITH DESCRIPTIONS OF SEVEN NEW SPECIES

Kouichi Kawaguchi[1] and John L. Butler[2]

ABSTRACT. The microstomatid fishes of the genus *Nansenia* are reviewed on a worldwide basis and 13 valid species are recognized. Of the 10 nominal taxa six species are recognized: *N. candida* (with *N. sanrikuensis* as a possible synonym), *N. groenlandica, N. atlantica, N. oblita, N. crassa,* and *N. ardesiaca* (with *N. tanakai, N. schmitti, N. macrolepis,* and *N. robusta* as synonyms). Seven new species are described based on specimens collected from the Atlantic, Pacific, and Antarctic oceans. Original descriptions are presented for *N. ahlstromi, N. antarctica, N. pelagica, N. megalopa, N. longicauda, N. tenera,* and *N. tenuicauda.* The species of *Nansenia* are separated into two groups based on the number of branchiostegal rays, either three or four; species of each group are distinguished on the basis of the differences in vertebral and gill raker counts, predorsal length in percent of standard length, and proportional size of the caudal peduncle. A key is presented.

Five species, *N. atlantica, N. oblita, N. megalopa, N. tenera,* and *N. tenuicauda* occur only in the Atlantic; three, *N. ahlstromi, N. candida,* and *N. crassa,* are limited to the Pacific. *Nansenia ardesiaca* is widespread in the slope waters of southeast Asian seas, extending northward to off southern Japan and westward to off South Africa. *Nansenia groenlandica* occurs in the subarctic Atlantic and subantarctic eastern Pacific. Antarctic waters are inhabited by a circumpolar species, *N. antarctica. Nansenia pelagica* and *N. longicauda* are found in both the Atlantic and Pacific oceans; the latter species restricted to the Northern Hemisphere. Distributional patterns of *Nansenia* are discussed in relation to those of other midwater fishes.

Six species exhibit allometric growth of head length, predorsal length, and eye diameter. Allometry may be an adaptation to mesopelagic and benthopelagic habitats.

INTRODUCTION

Fishes of the microstomatid genus *Nansenia* are distributed widely in the world ocean. They are found in oceanic and coastal waters from the subarctic to the subantarctic. Collections from both midwater and bottom trawls suggest that these fishes inhabit the epi- and mesopelagic zones and also the benthopelagic zone of continental or insular slopes. In areas of high productivity examples of *Nansenia* often exceed 200–300 mm in standard length and are sometimes captured in large numbers.

Notwithstanding the considerable numbers of adults and juveniles taken with trawls and larvae collected in plankton nets, the species are poorly known. Cohen (1958) examined specimens of six of seven nominal species that had been referred to *Nansenia* and concluded that the paucity of material precluded a critical revision. Since 1958 no comprehensive taxonomic work has been done on the genus, although four additional species have been described (Blache and Rossignol, 1962; Lavenberg, 1965; Abe, 1976; Kanayama and Amaoka, 1983). In general, specimens of *Nansenia* are soft-bodied, poorly ossified and hence often collected in poor condition. As a result the nominal species are inadequately known and a considerable number of species remain undescribed. Some species are distributed worldwide, but in previous works geographical variation and clines were not considered, and specimens from new localities were named as new species. The degree of ossification is different, both among species and growth stages, which, combined with the lack of a complete size series for all species, makes comparative osteology difficult. For all these reasons it is not possible at this time to present a comprehensive definition of the genus.

The present study is a preliminary one that aims to diagnose each species, both previously described and ones described in this paper with the objective of contributing information that will lead to a clearer definition of *Nansenia* and to the osteology, phylogeny, zoogeography, early life history, and ecology of each species.

METHODS AND MATERIALS

Measurements were taken with dividers and recorded to the nearest 0.1 mm. Unless otherwise indicated, definitions follow Hubbs and Lagler (1964) and include the following: standard length (SL); length of head (HL); depth of body (BD)—vertical through origin of base of dorsal fin; least depth of caudal peduncle (CPD); caudal peduncle length (CPL); diameter of eye (ED)—horizontal distance between opposite

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[1] Ocean Research Institute, University of Tokyo.

[2] Southwest Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla.

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margins of socket; snout length (Sn); interorbital length (Intor); width of body (BW)—width just behind the head; predorsal length (Pre D); preanal length (Pre A); preventral length (PreV)—distance from tip of snout to structural base of outermost ventral fin ray. Size of specimen is recorded in standard length, with standard deviation and range in parentheses. Center of body is the midpoint of standard length. If allometric growth is indicated for a species, data are presented for different size groups.

Numbers of vertebrae and median fin rays were counted from radiographs. The ultimate double rays of the anal and dorsal fins were counted as one. The short spine sometimes found at the base of the outermost pelvic fin ray was not counted. In other counts, all elements were included. The upturned ural centra were counted as one. Teeth were counted on both sides of the upper and lower jaws. Frequency distributions of gill raker and vertebrae counts are shown with the number of specimens in parentheses following each count.

In the materials section of each species, catalogue numbers are followed by the number of specimens and their size range in parentheses. The station number is preceded by the cruise number unless other wise indicated. The sampling depth is indicated by m and the length of wire out by mwo. The following institutional abbreviations are used.

UBC	Institute of Fisheries, University of British Colombia, Vancouver, Canada.
CAS	California Academy of Sciences, San Francisco, USA.
FMNH	Field Museum of Natural History, Chicago, USA.
ISH	Institute für Seefischerei, Hamburg, West Germany.
KU	Kochi University, Japan.
KYO	Department of Fisheries, Kyoto University, Japan.
LACM	Natural History Museum of Los Angeles County, USA.
OSU	School of Oceanography, Oregon State University, Corvallis, USA.
SIO	Scripps Institution of Oceanography, University of California, La Jolla, USA.
SWFC	Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, USA.
UF	Florida State Museum, University of Florida, Gainesville, USA.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.
ZMUC	Zoologiske Museum, University of Copenhagen, Denmark.

Genus *Nansenia* Jordan and Evermann, 1896

Nansenia Jordan and Evermann, 1896:528 (type species by monotypy, *Microstomus grönlandicus* Reinhardt, 1839; cf. Follet and Cohen, 1958).

Bathymacrops Gilchrist, 1922:531 (type species by monotypy, *Bathymacrops macrolepis* Gilchrist, 1922).

Euproserpa (subgenus) Fowler, 1934:256 (type species by original designation, *Microstoma schmitti* Fowler, 1934).

The definition of the genus *Nansenia* adopted here basically follows Chapman (1942, 1943, 1948) and Cohen (1964). The placement of the genus *Nansenia* in the family Microstomidae follows Ahlstrom et al., 1984. Body slender, subcylindrical or slightly compressed. Dorsal adipose fin present on the last quarter of body. Predorsal length less than 61 percent of SL. Snout shorter than half of eye, which is directed laterally and is not tubular. Branchiostegals three or four. Anal fin rays 8–10 (rarely 11). Pectoral fins inserted on sides of the body. Parietals large and meeting on the midline. No teeth on premaxillary or maxillary. Teeth present on palatines, head of vomer and dentaries.

REMARKS. The difference between *Nansenia* and *Bathylagus* (presently placed in a separate family, Bathylagidae) is not clear, despite efforts to discover adequate diagnostic characters. Characters concerned with the swimbladder, the otoliths, and morphology of the larvae, which may be diagnostic, are not always known for all members of both genera at different growth stages. Their value for distinguishing the two genera remains to be confirmed.

The arrangement of the parietals, which have been reported to meet broadly on the midline in *Nansenia,* but not meeting in *Bathylagus* (Chapman, 1942, 1943, 1948; Cohen, 1964), is probably diagnostic if it is partly modified to pa-

Table 1. Counts and measurements used in the key to the species with three branchiostegal rays and distributional information.

Species	Vertebrae	Gill rakers	Predorsal distance (% SL)	Ratio CPL/CPD[1]	Distribution
N. ahlstromi	35–36	40	50.5–55.8	1.0–1.3	Subtropical Eastern Pacific, 20°N–35°N
N. candida	44–47	26–31	49.4–57.6	1.8–2.2	Subarctic Pacific, 30°N–55°N
N. groenlandica	42–45	37–45	43.7–45.6	2.8–4.0	Subarctic Atlantic, 40°N–70°N; Eastern South Atlantic
N. antarctica	49–50	35–41	45.9–47.7	2.0–2.5* 2.5–3.0**	Southern oceans, 40°S–60°S

[1] Caudal peduncle length to caudal peduncle depth.

* <110 mm SL.

** >110 mm SL.

Table 2. Counts and measurements used in the key to the species with four branchiostegal rays and distributional information.

Species	Vertebrae	Gill rakers	Predorsal length (% SL)	Caudal peduncle length (% SL)	Caudal peduncle length (% SL)	Ratio CPL/CPD[1]	Distribution
N. pelagica	38–39	36–41	50.4–57.8	11.5–13.3	8.1–11.3	1.1–1.5	Tropical and Subtropical Atlantic and Pacific
N. atlantica	41–42	30–36	51.9–56.9	11.3–12.2	8.2–8.6	1.4–1.5	Tropical Atlantic
N. oblita	42–45	30–36	55.0–56.1	9.3–12.2	8.2–9.6	1.1–1.2	Mediterranean and Eastern North Atlantic
N. crassa	43–46	35–37	49.0–60.2	13.0–15.2	6.3–7.7	1.7–2.2	Eastern Tropical and Subtropical Pacific
N. megalopa	44–45	21–23	42.1–44.2	15.6–17.6	5.2–5.7	2.8–3.2	Tropical Atlantic
N. longicauda	47–50	23–27	41.8–46.0	15.4–18.6	4.3–5.6	3.0–4.1	North Atlantic and North Pacific, 20°N–40°N
N. tenera	42–43	43–46	43.4–45.8	12.6–15.0	6.2–6.5	1.9–2.4	Subpolar and Temperate Atlantic
N. ardesiaca	46–48	27–35	45.7–48.5	13.0–15.0	6.1–7.5	1.7–2.3	Off Japan, Southeast Asia and East Africa
N. tenuicauda	46	38–42	44.0–45.8	13.5–13.9	4.4–5.0	2.7–3.1	South Atlantic

[1] Caudal peduncle length to caudal peduncle depth.

rietals of *Bathylagus* not meeting or meeting at a point in the anteriormost part on midline. Branchiostegal counts are three or four in *Nansenia,* but mostly two in *Bathylagus.* However at least one undescribed bathylagid examined during the present study had exceptionally three branchiostegals. Anal fin ray counts are also useful in separating the two genera: 8–10 (rarely 11) in *Nansenia* and 12–28 (rarely 11) in *Bathylagus.* Better diagnostic characters for the genus *Nansenia* must await a revision of the family Bathylagidae.

KEY TO SPECIES

The species of *Nansenia* are separated into two groups based on branchiostegal counts of three or four. Four species have three branchiostegals and nine have four.

Counts and measurements used in the keys and distributional data are presented for all species in Tables 1 and 2 and Figures 21 and 22. After identification is made with the key, specimens should be checked against the information in the tables and also against the detailed descriptions of each species. The number of branchiostegal rays of *Nansenia* is stable within species, but careful examination under a dissecting microscope is necessary to recognize the innermost small ray (Fig. 1).

KEY TO SPECIES OF *NANSENIA* WITH THREE BRANCHIOSTEGAL RAYS

1a. Ratio of caudal peduncle length to caudal peduncle depth less than 1.5; vertebrae 35–36 .... *ahlstromi*
1b. Ratio of caudal peduncle length to caudal peduncle depth greater than 1.5; vertebrae 40–42 2
2a. Gill rakers on first arch 25–31; predorsal length more than 49 percent of SL .... *candida*
2b. Gill rakers on first arch 35–45, predorsal length less than 49 percent of SL in specimens larger than 50 mm SL 3
3a. Vertebrae 42 (eastern South Pacific), 43–45 (Atlantic) .... *groenlandica*
3b. Vertebrae 49–50 .... *antarctica*

KEY TO SPECIES OF *NANSENIA* WITH FOUR BRANCHIOSTEGAL RAYS

1a. Vertebrae 38–39 .... *pelagica*
1b. Vertebrae 41–50 2
2a. Predorsal length 49 or more percent of SL 3
2b. Predorsal length less than 49 percent of SL 5
3a. Length of caudal peduncle more than 12.5 percent of SL and depth of caudal peduncle less than 8 percent of SL with CPL/CPD ratio more than 1.6 .... *crassa*
3b. Length of caudal peduncle less than 12.5 percent of SL and depth of caudal peduncle more than 8 percent of SL with CPL/CPD ratio less than 1.6 4
4a. Proximal part of adipose fin densely pigmented; vertebrae 41–42; gill raker count 30–36 .... *atlantica*
4b. Proximal part of adipose fin not pigmented; vertebrae 42–45; gill raker count 28–30 .... *oblita*
5a. Length of caudal peduncle more than 15.2 percent of SL and depth of caudal peduncle less than 6 percent of SL; gill rakers 21–27 6
5b. Length of caudal peduncle less than 15.2 percent of SL and depth of caudal peduncle more than 6 percent of SL except in *N. tenuicauda* 7

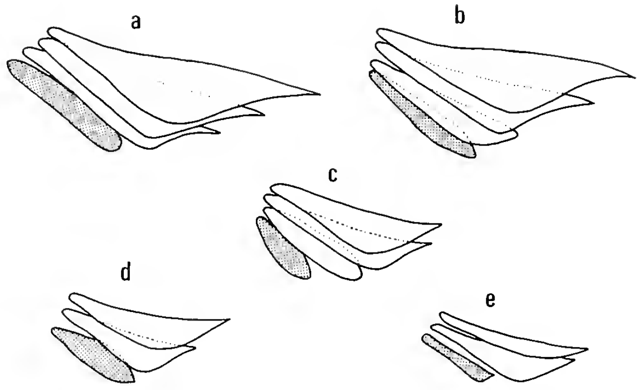

Figure 1. Typical patterns of branchiostegal rays of *Nansenia*. a. *N. ardesiaca, N. ahlstromi, N. crassa,* and *N. megalopa;* b. *N. pelagica* and *N. atlantica;* c. *N. tenera* and *N. longicauda;* d. *N. antarctica;* e. *N. groenlandica.*

6a. Vertebrae 44–45; gill rakers 21–23 .... *megalopa*
6b. Vertebrae 47–50; gill rakers 23–27 ...... *longicauda*
7a. Vertebrae 42–43; gill rakers 43–46 .... *tenera*
7b. Vertebrae 46–48; gill rakers 27–42 8
8a. Gill rakers 27–35; CPL/CPD ratio less than 2.5 .... *ardesiaca*
8b. Gill rakers 38–42; CPL/CPD ratio more than 2.5 .... *tenuicauda*

SPECIES WITH THREE BRANCHIOSTEGAL RAYS

Nansenia ahlstromi new species

Figures 2, 21

HOLOTYPE. SIO 57-87 (1, ca. 95 mm, slightly damaged mature female), R/V *Spencer F. Baird,* 29°15'N, 126°07'W, 2240–0730, 14–15 May 1955, 10 ft.—IKMT, 0–754 m.

PARATYPES. SIO 63-425 (1, 38.7), R/V *Horizon,* 27°46'N, 129°14.9'W, 0534–1006, 2 Apr. 1962, 10 ft.—IKMT, 4500 mwo; LACM 43546-1 (1, 32.0), R/V *David Starr Jordan,* 24°00'N, 145°00'W, 2348–0021, 21–22 May 1972, 6 ft.—IKMT 600 mwo; SWFC 7210-24.139 (1, 58.5 decomposed), R/V *David Starr Jordan,* 24°00'N, 139°00'W, 0040–0159, 29 Oct. 1972, 50 ft. universal MWT, 0–494 m.

DIAGNOSIS. Differs from other *Nansenia* in having three branchiostegal rays and 35–36 vertebrae, the least of any known species.

DESCRIPTION. Counts and measurements are based on three juvenile specimens, 32.0–58.5 mm SL. Only the vertebrae were counted for the damaged adult specimen, ca. 95 mm SL. D 8–9; A 7–8; P 12; V 9–11; gill rakers 12 + 28 in two specimens and 11 + 29 in one, total 40; branchiostegal rays three; vertebrae 35 in one specimen, 36 in three specimens. Pyloric caeca not counted due to paucity of specimens. About 30 conical teeth irregularly arranged on head of vomer; about 100 compressed teeth closely set on dentaries in holotype.

Head relatively large compared with body, reflecting the reduced number of vertebrae. Eye large, diameter 2.3–2.9 times in head length in three specimens, 38.7–ca. 95 mm SL. Head length and eye diameter indicate remarkable allometric growth (Fig. 4). Supraorbital bone damaged and lost in the holotype. Pectoral fin base low, its upper end above ventral margin of body about one-third of the distance between ventral margin and lateral line. Origin of dorsal fin base behind center of body. Ventral fin base below or just behind posterior end of dorsal fin base in the three juveniles, 32.0–58.5 mm SL, but well behind dorsal fin base in the holotype. Adipose fin base over posterior half of the anal fin base.

Tip of lower jaw, anterior part of gular area, and base of adipose fin darkly pigmented in the 38.7-mm SL specimen (SIO 63-425). The same pigment pattern is present in the holotype.

SIZE. The holotype of ca. 95 mm is an adult bearing eggs.

DISTRIBUTION. Restricted to the subtropical eastern North Pacific.

ETYMOLOGY. It is with great pleasure that we name this species *Nansenia ahlstromi* in recognition of the contributions of the late Elbert Halvor Ahlstrom to our knowledge of pelagic fishes.

Nansenia candida Cohen, 1958

Figures 3, 4, 22

Nansenia candida Cohen, 1958:52–54, fig. 1 (orig. descr.) Eastern North Pacific.
?*Nansenia sanrikuensis* Kanayama and Amaoka, 1983:77–79 (orig. descr.) Western North Pacific.

MATERIALS. CAS 51023 (1, alizarin specimen dissected), one of the paratypes, R/V *Hugh M. Smith,* 41°39'N, 139°02'W, 30 May 1956, from the stomach of *Alepisaurus* sp.; OSU 8, 9 (2, 46.4, 80.7), 49°16'N, 132°42'W, 0–60 m; OSU 10, 12 (2, 44.0, 136.9), 41°59.5'N, 126°30.6'W, 0–200 m; OSU 11 (1, 150.5), 44°37.3'N, 125°17.3'W, 1500–500 m; OSU 960 (1, 150.5), 44°37.3'N, 125°38.0'W, 0–200 m; OSU 1132, 1133 (2, 79.0, 72.2), 44°25'N, 129°35'W, 0–75 m; OSU 1166 (1, 32.1), MT-648, 44°16'N, 125°15'W, surface tow, 40 mwo; OSU 1170 (1, 23.5), MT-652, 44°31'N, 125°17'W, 0–1400 m; OSU 1191 (2, 95.8, 99.6), MT-757, 44°38'N, 128°35'W, 0–210 m; OSU 1212 (1, 140.0), 44°39.8'N, 125°00'W, 0–200 m; OSU 1216 (1, 108.2), MT-749, 44°39'N, 125°36'W, 0–200 m; OSU 1217 (1, 60.3), MT-727, 44°39'N, 128°00'W, 0–1000 m; OSU 2003 (1, 179.2), haul 2054, 44°49.7'N, 125°34.0'W, 0–600 m; OSU 2388 (1, 129.1), MT-2398, 44°39'N, 125°29'W, 0–500 m; USNM 197380 (1, 60.5), 20 miles southeast of San Clemente Is., California, spit up by albacore; USNM 195874 (1, 122), sta. BB-76, North Pacific, 0–30 m; USNM 195875 (1, 75.5), sta. BB-176, 48°03'N, 134°20'W; USNM 195876 (1, 156), sta. BB-199, 49°15.6'N, 145°56.7'W, 100 mwo; SIO 66-51-9F (1, 24), 40°35'N, 125°51.5'W; SIO 55-73-9A (1, ca. 64, damaged), 39°01'N, 165°10'W, from *Alepisaurus* stomach; UBC 65-607 (2, 75.5, 81.0) and UBC 65-609 (2, 76.5, 87.5), off Queen Charlotte Sound, B.C., Canada; UBC 65-610 (16, 76.0–88.0) and UBC 65-615 (1, 77.5), off Queen Charlotte Sound; UBC 65-623 (16, 118.0–187.0), 52°11'N, 133°11'W; UBC 65-524 (1, 121.0), 52°13'N, 133°12'W; LACM 34258-1 (2, 63–71),

Figure 2. *Nansenia ahlstromi.* Paratype, SIO 63-425, 38.7 mm SL.

R/V *Alaska,* off San Clemente Is., California; LACM 9006-23 (1, 35), R/V *Velero,* Catalina Basin off California.

DIAGNOSIS. Differs from other *Nansenia* in the following combination of characters, three branchiostegal rays and 26–31 gill rakers on the first arch. Vertebral counts higher (44–47) in *N. candida* than in *N. ahlstromi* (35–36).

DESCRIPTION. D 9–10; A 8–9; P 10–11 (rarely 9); V 9–10 (rarely 11); gill rakers 8–11 + 1 + 17–20, total 26–31 with 26 in one specimen, 27 in five, 28 and 29 in three respectively, 30 in one and 31 in three; branchiostegal rays 3; vertebrae 44–47 with 44 in two specimens, 45 in five, 46 in eight and 47 in two. The above counts are based on 18 specimens, 46.2–179.2 mm SL. Pyloric caeca seven in two specimens, nine in one. About 12–21 conical teeth on head of vomer, about 80–100 teeth on dentaries, resembling a closely spaced picket fence, in three specimens more than 130 mm SL.

Body slender, moderately compressed, with body depth to width ratio 1.5–1.7. Eye diameter 3.0 to 3.4 times in head

Figure 3. *Nansenia candida.* OSU 2003, mature female, 179.2 mm SL.

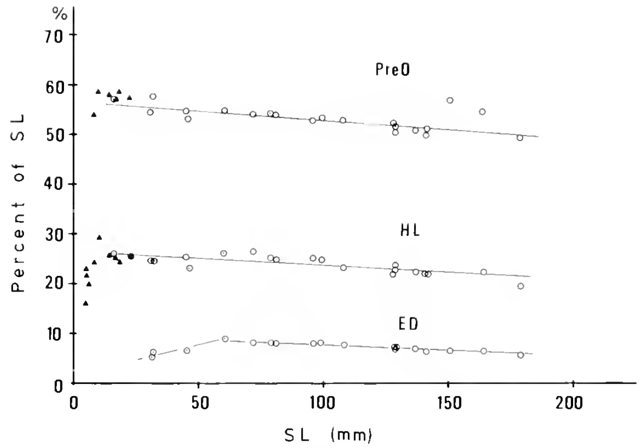

Figure 4. *Nansenia candida.* Predorsal, head lengths, and eye diameter in relation to standard length. Triangles indicate the values for postlarvae and young juveniles smaller than 23 mm SL.

length, viewed laterally, its dorsal margin (supraorbital bone) touching or slightly higher than dorsal margin of head, yellowish iridescent pigment, roughly crescent-shaped, present in the posterior half of iris. Aphakic space developed, its horizontal space nearly equal to width of anteriormost part of iris, and about half the width of its posterior part. Aphakic space less well developed in juveniles smaller than 100 mm SL. Allometric growth in head length, eye diameter and predorsal length is shown in Figure 4.

Upper end of pectoral fin base on midpoint between lateral line and ventral margin of body, or slightly lower; its lower end separated from ventral margin of body by a distance more than length of pectoral fin base. Dorsal fin originating behind center of body. Ventral fin base below posterior part of dorsal fin. Origin of anal fin slightly in advance of adipose fin. Skin around the anterior end of adipose and caudal fin bases densely pigmented. Body color in formalin preserved specimens brown. However, Cohen (1958) noted that in life the entire fish is probably a bright silver.

SIZE. The largest specimen examined, 179.2 mm SL, had mature ovaries.

DISTRIBUTION. *Nansenia candida* has been collected in the subarctic eastern Pacific east of 170°W between 35°N and 55°N and in the California Current region north of 30°N (Fig. 22).

REMARKS. Kanayama and Amaoka (1983) described *Nansenia sanrikuensis* based on two large adult specimens, 206.0 and 238.8 mm SL. This species is closely related to *N. candida,* and both species occur in the subarctic North Pacific. But *N. candida* has been reported only from the eastern part of the Pacific between the latitude of southern California and Canada, and *N. sanrikuensis* was collected in the western Pacific off northern Honshu, Japan. Kanayama and Amaoka (1983) reported that *N. sanrikuensis* differs in having a smaller eye (4.8–5.8 vs. 8.3–9.6 percent of SL), shorter snout (3.5–3.6 vs. 5.1–5.8), lower gill raker counts (25–27 vs. 30) and higher vertebral counts (48–49 vs. 44–47). Their proportional data and gill raker counts for *N. candida* are based on the original description by Cohen (1958) which was taken from three specimens, 54.4–72.4 mm SL,

Figure 5. *Nansenia groenlandica.* ISH 194-59, 112.5 mm SL.

for measurements and five for meristic counts. However, their vertebral counts are based on the present study. Specimens studied by Kanayama and Amaoka (1983) and Cohen (1958) differ greatly in size. In the present study we found considerable allometric growth in eye diameter, snout length, and head length of *N. candida*. We conclude that proportions of snout, eye, and head are invalid for distinguishing the two species. The ranges of gill raker counts are also overlapping between the two (25–27 vs. 26–31) as *N. candida* has a wider range than Cohen (1958) described. At present only vertebral counts (48–49 vs. 44–47) separate these species. Considering the adjacent ranges, the paucity of specimens of *N. sanrikuensis* and the possibility of a geographical cline, the status of *N. sanrikuensis* is questionable.

Nansenia groenlandica (Reinhardt, 1840)

Figures 5, 6, 21

Microstomus grönlandicus Reinhardt, 1840:8 (orig. descr. Fiskenesset, Greenland).

Nansenia groenlandica: Jordan and Evermann, 1896:528; Schmidt, 1918:12, figs. 1–12; Cohen, 1964:24, fig. 8.

MATERIALS. Atlantic: ISH 21/75 (2, 57.0–67.0), FFS *Walther Herwig* sta. 10-I/75, 41°18'N, 27°49'W, 0–117 m; ISH 29/75 (1, 32.5), FFS *Walther Herwig* sta. 14-I/75, 41°26'N, 27°09'W, 0–183 m; ISH 194/59 (1, 112.5), FFS *Anton Dorn* sta. 3257/59, 61°48'N, 13°08'W, 0–1400 m; ISH 314/73 (2, 132.0, damaged), FFS *Walther Herwig* sta. 678/73, 65°09'N, 32°50'W, 0–1100 m; ISH 448/73 (8, 60.5–103.5), FFS *Walther Herwig* sta. 693/73, 57°55'N, 28°23'W, 0–415 m; ISH 473/73 (1, 89.0), FFS *Walther Herwig* sta. 693/73, 56°28'N, 26°44'W, 0–2500 m; ISH 540/73 (3, 80.0–108.0), FFS *Walther Herwig* sta. 696/73, 55°39'N, 25°47'W, 0–2500 m; ISH 540/73 (3, 80.0–108.0), FFS *Walther Herwig* 696/73, 55°39'N, 25°47'W, 0–410 m; ISH 748/73 (1, 57.0), FFS *Walther Herwig* 707/73, 50°03'N, 19°39'W, 0–255 m; USNM 186071 (damaged, head only), M/V *Delaware,* 40°34'N, 64°07'W, from stomach of *Makaira*; USNM 221368 (3, damaged, ca. 63–84), FFS *Walther Herwig* sta. 695/73, 55°43'N, 25°53'W, 0–2600 m. Pacific: LACM 11292 (1, 63.7), R/V *Eltanin* sta. 1972, 39°34'S, 127°18'W, IKMT, 0–4493 m; LACM 10288 (2, damaged, ca. 30), R/V *Eltanin* sta. 190, 34°51'S, 74°04'W, 0–1580 m.

DIAGNOSIS. Differs from other *Nansenia* in having three branchiostegal rays, 42–45 vertebrae (43–45 in the Atlantic, 42 in Pacific specimens), and 37–45 gill rakers on the first arch.

DESCRIPTION. D 9–10; A 8–10; P 11–13; V 11–12 (rarely 10); gill rakers 12–15 + 1 + 23–29, total 37–45 with 37(2), 38(5), 40(1), 41(2), 42(1), 44(2), and 45(1); branchiostegal rays three; vertebrae 42(1) in the South Pacific, 43–45 with 43(8), 44(9), and 45(1) in the North Atlantic. Counts are based on 19 specimens, 48.0 to 132.0 mm SL. Pyloric caeca seven and eight in two specimens; 20–22 conical teeth irregularly arranged on vomer, 50–65 teeth closely set on dentaries in four specimens.

Body slender, body depth–width ratio ranges from 1.0–1.2. Eye large, its diameter 2.5 to 2.8 times in head length. Viewed laterally, about one-third of eye circumferenee protruded above the dorsal margin of the head. White or yellowish tissue developed over posterior half of iris, sometimes covering whole iris. Aphakic space slightly developed anteriorly, its horizontal space nearly equal to half to two-thirds width of the anterior part of iris. Aphakic space less well developed in juveniles smaller than 100 mm SL.

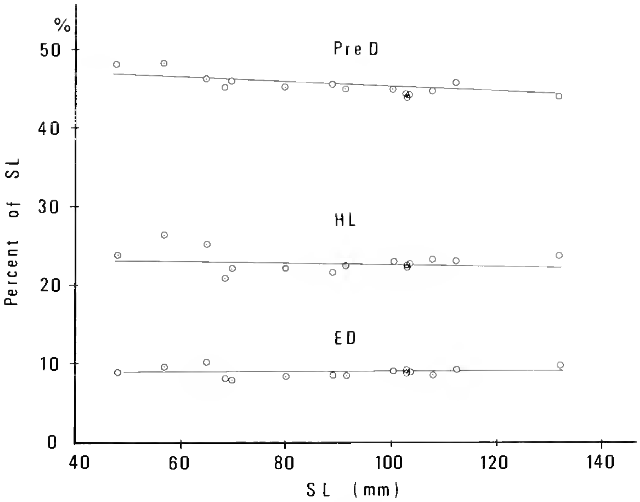

Figure 6. *Nansenia groenlandica.* Predorsal, head lengths, and eye diameter in relation to standard length.

Upper end of pectoral fin base separated from ventral margin of body by one-third of distance between lateral line and ventral margin or slightly higher; its lower end above ventral margin by a space more than the length of pectoral fin base. Dorsal fin originating in front of center of body. Ventral fin base below posterior end of dorsal fin base or just behind it. Adipose fin base above last two anal fin rays. No remarkable inflection in allometric growth for specimens between 48 and 132 mm SL (Fig. 6).

Skin around adipose fin base uniformly pigmented compared to the lateral body surface. Caudal fin base and posterior part of caudal peduncle densely pigmented, sparser in specimens larger than 100 mm SL. Body of preserved specimens usually brown or light brown, some with remains of guanine. The entire body surface of the ISH 194-59 specimen, although all scales had come off, is covered with guanine. This specimen may have been preserved in alchohol.

SIZE. The badly damaged specimen (caudal segment missing) taken from a marlin stomach, USNM 186071, identified as *N. groenlandica* only by its branchiostegal ray count and locality, is a mature male and its standard length can be estimated as about 180 mm based on its head length. The largest four intact specimens, 103.0 to 132.0 mm, collected in September have undeveloped gonads.

DISTRIBUTION. This species occurs widely in the arctic and subarctic waters of the North Atlantic Ocean. The southern limit of its distribution is near 40°N. Present results agree well with the work of Schmidt (1918) in the eastern North Atlantic. Three specimens collected in the subantarctic or

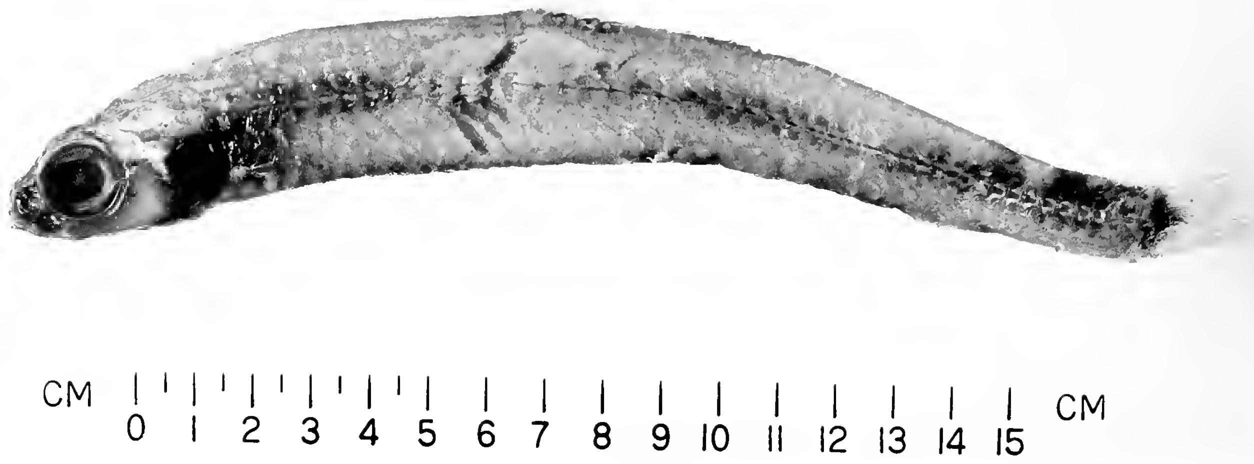

Figure 7. *Nansenia antarctica.* LACM 10875 (one of the three catalogued), 198.9 mm SL, holotype.

transitional waters of the eastern South Pacific show no morphological difference from the Atlantic specimens, but have slightly fewer vertebrae. Mukhacheva (1972) reported a similar distribution pattern for the midwater fish, *Gonostoma bathyphilum,* which is widely distributed in the North Atlantic between 30°N and 60°N, the South Atlantic south of 30°S, and also in the eastern South Pacific south of 30°S.

Nansenia antarctica new species

Figures 7, 8, 21

HOLOTYPE. LACM 10875 (one of three), 198.9 mm SL, R/V *Eltanin* sta. 1204, 55°57′S, 159°23′W, 0560–1035, 10 Aug. 1964, IKMT, 0–4145 m.

PARATYPES. LACM 10875 (two of three) (2, 197.8–207.5), collection data as for holotype. LACM 10658-15 (2, 79.2–225.0), R/V *Eltanin* sta. 858, 64°42′S, 78°34′W, 1905–0030, 17–18 Nov. 1963, IKMT; USNM 247255 (1, 158.6), R/V *Eltanin* cr. 35, sta. 2300, 52°00′S, 124°02′E, 20 Sep. 1968, IKMT, 0–750 m (bottom depth 3914–4362 m).

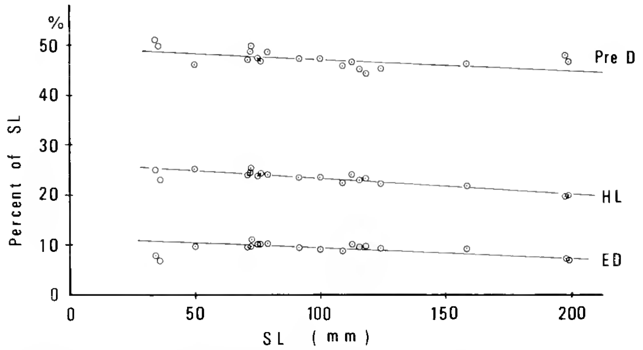

Figure 8. *Nansenia antarctica.* Predorsal, head lengths, and eye diameter in relation to standard length.

OTHER MATERIALS. LACM 11194 (2, 98.9–108.9), R/V *Eltanin* sta. 1661, 61°30′S, 108°26′W, 0134–0430, 26 Apr. 1966, IKMT, 0–5036 m; LACM 11212 (1, 49.9), R/V *Eltanin* sta. 1686, 57°39′S, 115°12′W, 1255–1540, 6 May 1966, IKMT, 0–4286 m; USNM 247254 (7, 31.0–35.0), R/V *Eltanin* cr. 21, sta. 20G, 0–850 m; ISH 688/71 (1, 112.5), FFS *Walther Herwig* sta. 363-III/71, 40°18′S, 39°04′W, 8 Mar. 1971, 0–800 m; ISH 542/71 (1, 118.2), FFS *Walther Herwig* sta. 354-II/71, 39°19′S, 48°09′W, 6 Mar. 1971, 0–ca. 2000 m.

DIAGNOSIS. Differs from other *Nansenia* in having three branchiostegal rays, 47–50 vertebrae, and 35–41 gill rakers.

DESCRIPTION. D 9–10; A 9–10; P 12–14; V 11–12; gill rakers 10–13 + 1 + 23–27, total 35–41 with 35(2), 37(2), 38(2), 39(2), and 41(1); branchiostegals three; vertebrae 49–50 with 49(3) and 50(5). Pyloric caeca seven in one specimen; 27 irregularly arranged conical teeth on head of vomer and about 75 compressed teeth on dentaries on one specimen of 207.5 mm SL.

Body slender, anterior part slightly compressed in specimens larger than 190 mm, subcylindrical in smaller specimens. Caudal peduncle more compressed than anterior part of body. Body depth-width ratio 1.1–1.7. Eye large, diameter 2.4–2.9 times in head length, with its dorsal margin protruding slightly above margin of head. Golden pigment, roughly crescent-shaped, on posterior half of iris. The ratio of width of the posterior part of iris to that of the anterior part is between two and four, whereas the ratio is less than two in other species having three branchiostegal rays. Aphakic space extremely well developed in front of lens (some-

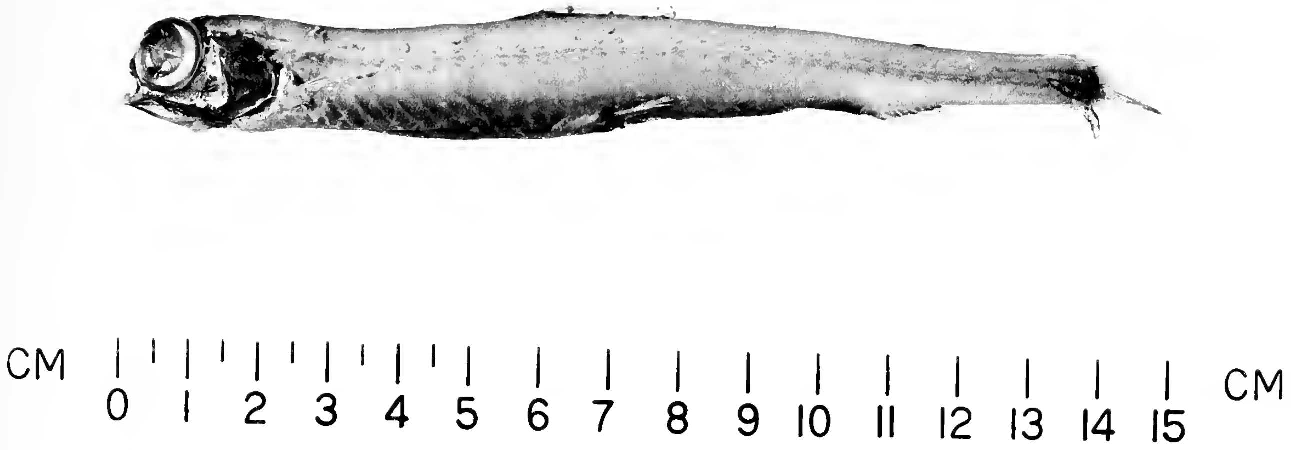

Figure 9. *Nansenia megalopa.* ISH 2013-71 (one of the two catalogued), 133.0 mm SL, holotype.

times lens placed anteriorly), its horizontal space usually three to four times as wide as the width of the iris at the anteriormost part, in specimens larger than 100 mm SL. This space is less well developed in smaller juveniles.

Upper end of pectoral fin base just below midpoint between the lateral line and ventral margin of body, its lower end separated from the ventral margin by a distance 1.8–3.0 times as long as its base. Origin of dorsal fin base in front of the center of the body. Ventral fin base just below the posterior end of the dorsal fin base. Adipose fin base above the posterior half of anal fin base.

Skin badly abraded in most specimens, light brown in alcohol. Dark colored scale pockets, which are extremely fragile, a few sometimes remaining along lateral line and the dorsal and ventral sides of body. Caudal and adipose fin bases usually slightly pigmented.

SIZE. The largest specimens studied, 207.5 mm, had mature ovaries with developing eggs.

DISTRIBUTION. This species occurs in the southern part of the subantarctic region between the antarctic and subtropical convergences of the Pacific (Fig. 21). Its distribution probably extends northward to the subtropical convergence in the Atlantic sector.

ETYMOLOGY. Named for its region of occurrence.

SPECIES WITH FOUR BRANCHIOSTEGAL RAYS

Nansenia megalopa new species

Figures 9, 21

Nansenia sp. 2 (?), Parin and Golovan, 1976:251–252, fig. 2, 04°10′N, off west Africa, 0–510 m.

HOLOTYPE. ISH 2013 a/71, 133.0 mm, FFS *Walther Herwig* sta. 463-III/71, 08°11′S, 14°12′W, 8 Apr. 1971, 0–640 m.

PARATYPES. ISH 1730/71 (1, 126.5), FFS *Walther Herwig* sta. 447–III/71, 18°36′S, 04°18′W, 4 Apr. 1971; ISH 2013b/71 (1, 108.5), FFS *Walther Herwig* sta. 463-III/71, 08°11′S, 14°12′W, 8 Apr. 1971, 0–640 m; ISH 2491/71 (1, 139.5), FFS *Walther Herwig* sta. 486-III/71, 07°32′N, 20°54′W, 14 Apr. 1971, 0–ca. 1300 m; UF 29912 (1, 126.0), R/V *Geronimo* cr. 2, sta. 82, 03°28′S, 00°14′W, Gulf of Guinea, 6 Aug. 1963, 0–710 m.

DIAGNOSIS. Differs from other *Nansenia* in having four branchiostegal rays, 44–45 vertebrae and 21–23 gill rakers on the first arch. This species is also separable from all other *Nansenia* by having a very large eye, eye diameter to snout length ratio >2.8 to 1.

DESCRIPTION. D 9–10; A 8–10; P 12–13; V 9–10; gill rakers 6–7 + 1 + 14–15, total 21–23 with 21(1), 22(2), and 23(2); branchiostegal rays four; vertebrae 44–45 with 44(3) and 45(2).

Pyloric caeca not counted; teeth on head of vomer, usually embedded in the tooth ridge and often indiscernible; 35–50 teeth on both dentaries.

Body slender and subcylindrical, body depth to width ratio 1.2–1.4 in specimens of 108.5–139.5 mm SL. Eye large, its diameter 2.1 to 2.4 in head length. A roughly crescent-shaped, silvery pigment patch on the posterior half of the iris; pupil elliptical with a large aphakic space in front of the lens. Upper end of pectoral fin base around midpoint between lateral line and ventral margin of body. Dorsal fin base originating in front of center of body. Ventral fin base below posterior end of dorsal fin base. Adipose fin origin above posterior third of anal fin base. Bases of ventral and adipose fins densely pigmented.

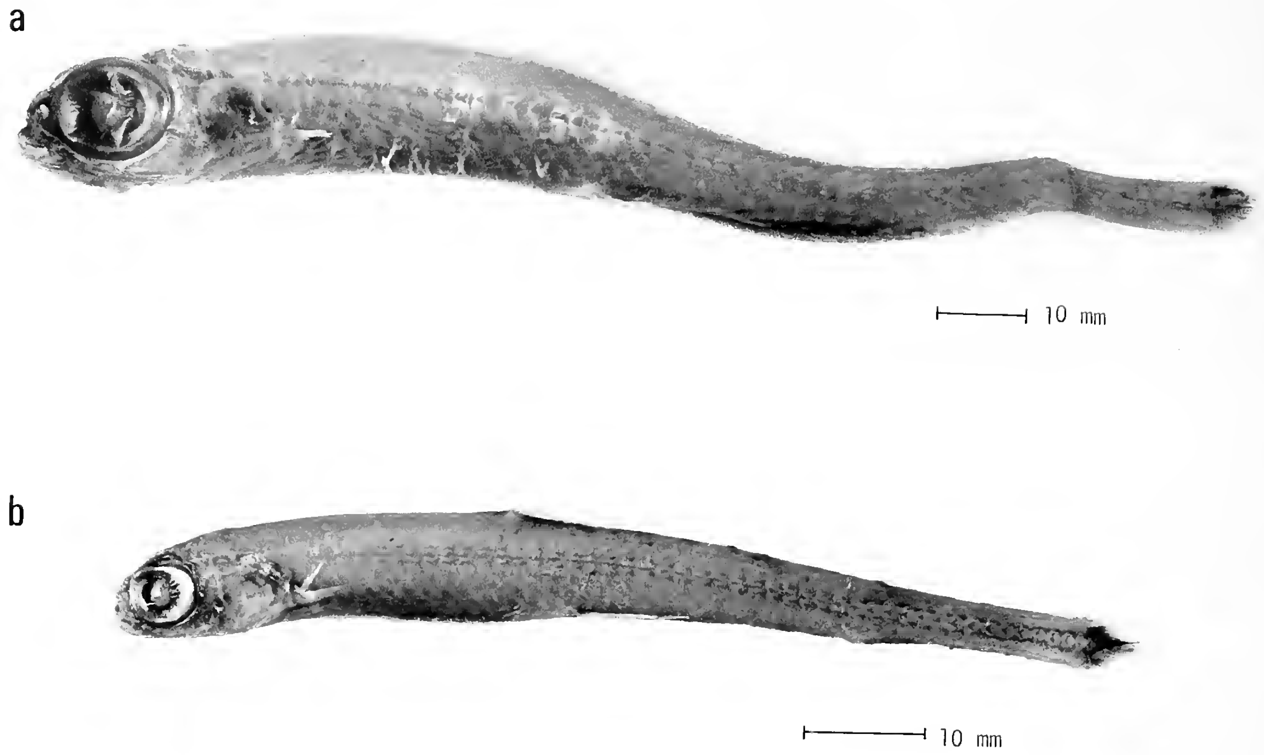

Figure 10. *Nansenia longicauda.* a. SIO 76-7-9, 133 mm SL, holotype; b. ISH 60-66, 78.0 mm SL, paratype.

SIZE. A specimen of 126.5 mm SL has ripe ovarian eggs.

DISTRIBUTION. All specimens were collected in the oceanic area of the tropical Atlantic between 10°N and 20°S.

ETYMOLOGY. *Nansenia megalopa* from Greek *megale,* great, and from *ops,* eye, referring to the extraordinarily large eye.

Nansenia longicauda new species

Figures 10, 11, 22

HOLOTYPE. SIO 76-9, 133.0 mm, 30°37.0′N, 147°24.0′W, 2027–2350, 10 Nov. 1971, IKMWT, 1800 mwo.

PARATYPES. Pacific: USNM 207530 (1, 104.6), Univ. of Hawaii, samp. no. 71-2-11, 21°20′N, 158°20′W, 28 Feb. 1971, 610–650 m; USNM 215703 (1, 97.2), R/V *Townsend Cromwell,* CR-52, sta. 16, 21°32.7′N, 158°21.8′W, 0355–1100, 12 Feb. 1971. Atlantic: ISH 60/66 (1, 78.0), FFS *Walther Herwig* sta. 177–66, 33°45′N, 16°00′W, 10 May 1966, MT1600, 0–600 m.

OTHER SPECIMENS EXAMINED. Pacific specimens: SIO 71-300 (1, 65.0), R/V *Thomas Washington* sta. Aries 9-H7, 27°24.5′N, 155°25.5′W, 0720–1100, 30 Sep. 1971, 10ft.—IKMT, 3000 mwo; USNM 207531 (1, 46.5), Univ. of Hawaii, samp. no. 71-6-10, 21°00′N, 158°20′W, 10 Jun. 1971, 560–600 m; USNM 215470 (1, 67.0), R/V *Townsend Cromwell,* samp. no. 73-8-29, 21°20′N, 158°20′W, 0745–

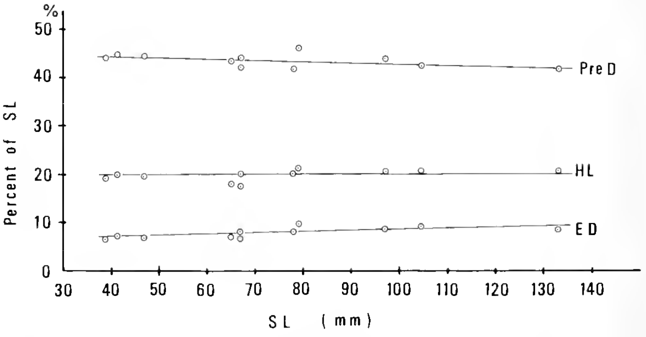

Figure 11. *Nansenia longicauda.* Predorsal, head lengths, and eye diameter in relation to standard length.

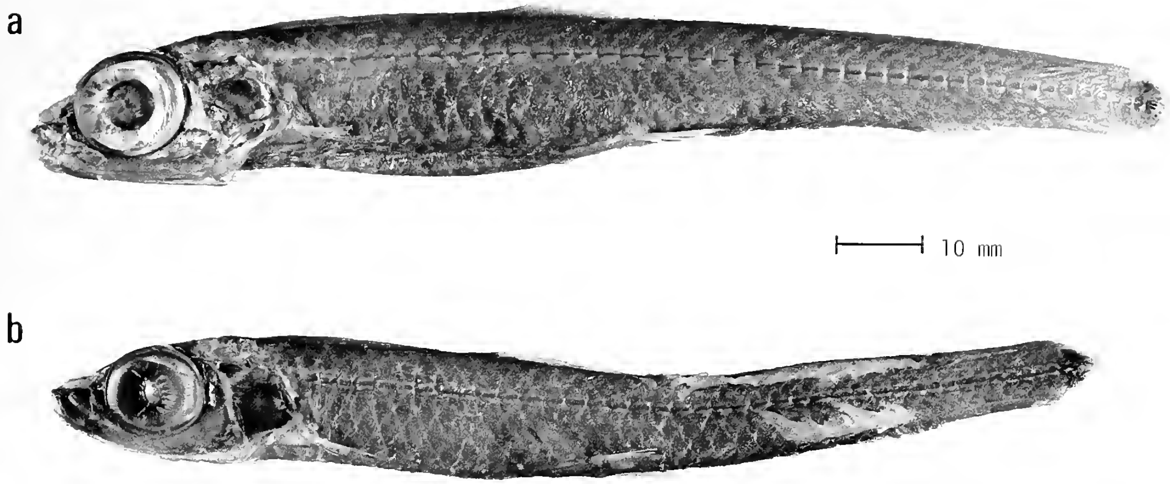

Figure 12. *Nansenia tenera.* a. ZMUC P19621-23 (one of the three cataloged), 129.0 mm SL, holotype; b. ISH 540-73, 117.0 mm SL, paratype.

1054, 29 Aug. 1973, 400–1100 m; SIO 71-302 (1, 67.0), R/V *Thomas Washington* Aries 9-H9, 27°24.5′N, 155°25.5′E, 30 Sep. 1971. Atlantic specimens: USNM 246799 (1, 41.5), Acre 6-22; USNM 246800 (1, 39.1), Acre 9-24. Both specimens were collected around 38°18′N and 64°12′W.

DIAGNOSIS. Differs from other *Nansenia* in having four branchiostegal rays, 23–27 gill rakers on the first arch, 47–50 vertebrae and a slender caudal peduncle, the least depth of which is 4.3–5.6 percent of SL. The body shape of this species resembles that of *N. megalopa.* Higher gill raker counts (23–27 vs. 21–23), higher vertebral counts (47–50 vs. 44–45) and longer snout (2.3–4.1 vs. 2.3–2.9 percent of SL) separate *N. longicauda* from *N. megalopa.*

DESCRIPTION. D 10 (rarely 11); A 10–11 (rarely 9); P 13–14 (rarely 11); V 10–11 (rarely 9); gill rakers 7–8 + 1 + 15–18, total 23–27 with 23(1), 24(4), 25(2), and 26(2); branchiostegal rays four; vertebrae 47–50 with 47(1), 48(1), 49(5), and 50(4). These counts are based mainly on 11 specimens, 39.1–133.0 mm SL. Pyloric caeca not counted. Irregularly sized and arranged conical teeth on head of vomer, which are embedded deeply in tooth ridge, about 24; compressed teeth closely set on dentaries, about 50 in a 104.6-mm specimen.

Body slender and subcylindrical with body depth to width ratio 1.3–1.6 in specimens larger than 45 mm SL. The ratio is larger in smaller specimens. Eye very large, indicating considerable allometric growth (Fig. 11); its diameter varying linearly from 6.4 percent of SL in a 39.1-mm specimen to 8.8 percent in a 133.0-mm specimen; eye diameter 2.2–2.6 times in head length in specimens larger than 50 mm, and 2.7–3.0 times in a specimen smaller than 50 mm.

Dorsal margin of eye protuding above dorsal margin of head in a specimen larger than 100 mm SL. Pupil oval, with aphakic space developed anteriorly. Base of uppermost pectoral fin at or slightly higher than midpoint between lateral line and ventral margin of the body. Origin of dorsal fin base well behind center of body. Predorsal length less than 47 percent of standard length with smaller values in larger specimen due to allometric growth (Fig. 11). Base of outermost ventral fin below or just behind posterior end of dorsal fin base. Adipose fin base just in front of vertical through center of anal fin base.

Tip of snout, upper jaw, anterior part of gular area, bases of ventral and caudal fins densely pigmented.

SIZE. The largest specimen is the 133.0-mm SL holotype.

DISTRIBUTION. *Nansenia longicauda* occurs in the subtropical and temperate waters of the Pacific and Atlantic oceans. Based on collection data, this species appears to be an oceanic mesopelagic species (Fig. 22).

ETYMOLOGY. The specific name is derived from Latin, *longus* meaning long and *cauda* meaning tail referring to the long and slender caudal peduncle.

Nansenia tenera new species

Figures 12, 21

HOLOTYPE. ZMC P19621-23 (1, 129.0), Dana sta. 3975-I, 35°42′S, 18°37′E, 31 Jan. 1930, 3000 mwo.

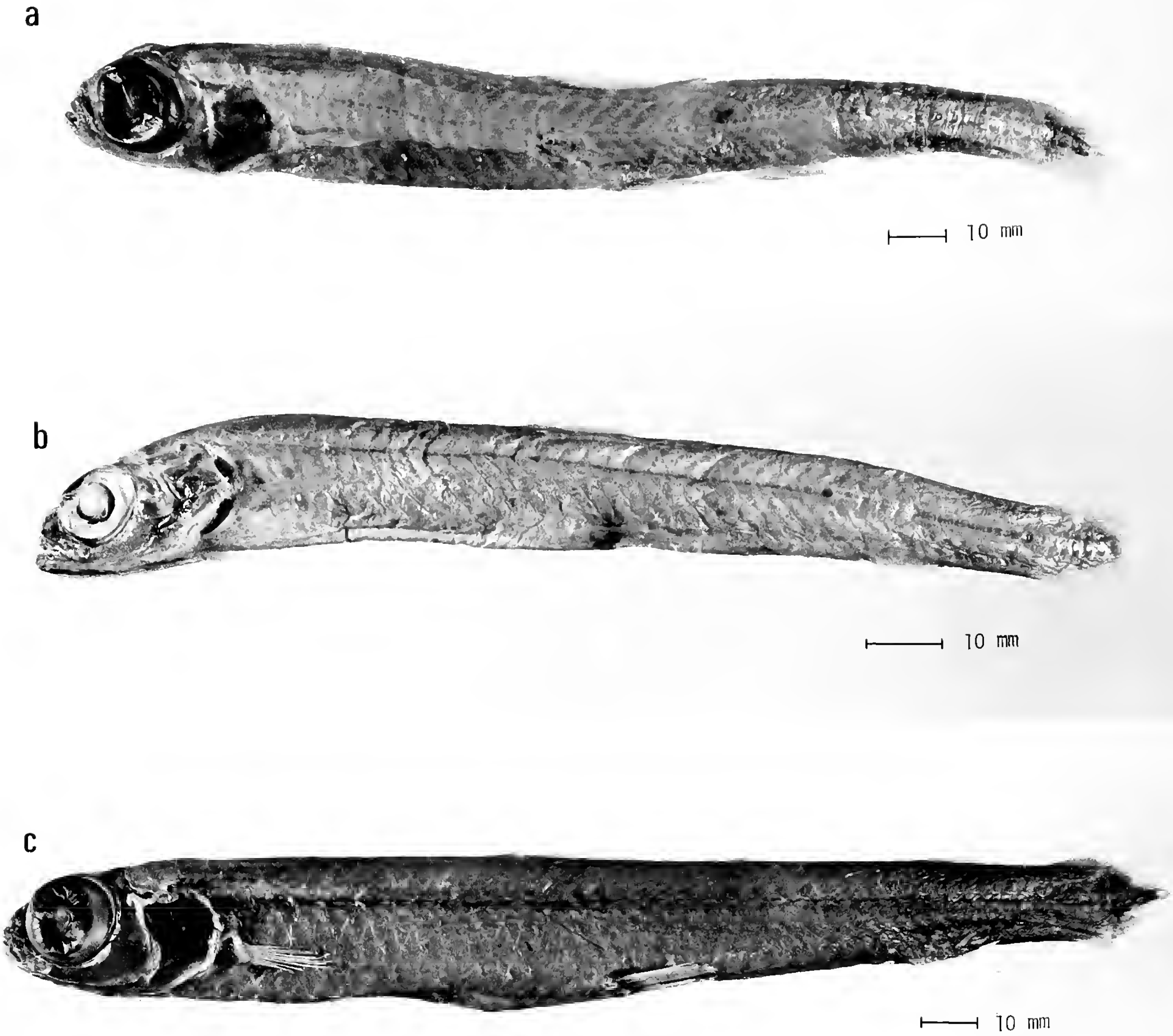

Figure 13. *Nansenia ardesiaca.* a. FMNH 57086, 164.5 mm SL, holotype from off Japan; b. USNM 93354, 136.0 mm SL, one of the seven paratypes of *N. schmitti* from off the Philippines; c. ZMUC P19624-25, 183.5 mm SL, from off the northeast coast of South Africa.

PARATYPES. ZMC P19621-23 (2, 112.0–117.4), collection data as for the holotype; ZMC not catalogued (1, 105.6), Dana sta. 3975-II, 35°42′S, 18°37′E, 31 Jan. 1930, 2500 mwo; ISH 1009/73 (1, 117.0), FFS *Walther Herwig* 696-73, 55°39′N, 25°42′W, 22 Sep. 1973, 400–410 m; ISH 829/71 (1, 101.0), FFS *Walther Herwig* 376/71, 39°55′S, 26°02′W, 11 Mar. 1971, 0–2000 m.

DIAGNOSIS. Differs from other species of *Nansenia* in having four branchiostegal rays, 42–43 vertebrae, and 43–46 gill rakers.

DESCRIPTION. D 11–12; A 8–9; P 11–12; V 11–12; gill rakers 13–15 + 1 + 28–32, total 43–46 with 43(1), 44(3), 45(1), and 46(1); branchiostegal rays four; vertebrae 42 in one North Atlantic specimen, 43 in the five South Atlantic specimens. Pyloric caeca 7–9 in three specimens; about 16 conical teeth irregularly arranged on head of vomer; about 60 compressed teeth on dentaries in a 112-mm specimen.

Eye large, its diameter 2.4–2.7 in head length; nearly one-third to one-quarter of eye protruding above the dorsal margin of head. A golden colored, crescent-shaped pigment on

Figure 14. *Nansenia tenuicauda.* ISH 1010-71, 69.0 mm SL, paratype.

posterior half of iris. Aphakic space developed; pupil acorn-shaped with tip anteriorly directed. This type of pupil was not observed in any other species.

Upper end of pectoral fin base below midpoint between lateral line and ventral margin of body; its lower end above ventral margin of body by a space greater than length of pectoral fin base. Dorsal fin originating in front of center of body. Ventral fin base above posterior half of anal fin base in the South Atlantic specimens, but above the midpoint in one specimen from the North Atlantic.

Body color of preserved specimens light brown. The entire body surface of three specimens, especially the ventral side, is sparsely covered with guanine, which resembles silver powder. Caudal fin base densely pigmented in the specimens from the South Atlantic, but the pigmentation extends forward becoming sparser anteriorly in the North Atlantic specimen.

SIZE. A specimen of 112.0 mm SL has maturing gonads.

DISTRIBUTION. Five specimens were collected in the South Atlantic between 35°S and 39°S, and one specimen from the subarctic region of the North Atlantie (55°39′N).

ETYMOLOGY. The specific name *tenera* is from Latin, soft, referring to the consistency of the body.

Nansenia ardesiaca Jordan and Thompson, 1914

Figures 13, 22

Nansenia groenlandica: Tanaka, 1911:15–16, pl. III, fig. 13 (non Reinhardt, 1840) (Sagami Bay, Japan).

Nansenia ardesiaca Jordan and Thompson, 1914:210–211, pl. XXIV, fig. 2 (orig. descr., off Japan).

Nansenia tanakai Schmidt, 1918:15 (orig. descr. Japan).

Bathymacrops microlepis Gilchrist, 1922:53–54, pl. IX, fig. 2 (orig. descr., east coast of South Africa).

Microstoma (Euproserpa) schmitti Fowler, 1934:256–257, fig. 18 (orig. descr. Philippines).

Nansenia macrolepis: Cohen, 1958:56 (east coast of South Africa).

Nansenia robusta Abe, 1976:27–31, figs. 1–6 (orig. descr. South China Sea).

MATERIALS. Off Japan: FMNH 57086, 164.5 mm SL, Okinose, Sagami Bay, central Japan (holotype of *N. ardesiaca*); KYO 4434 (2, 157.5, 144.0), southern Japan, KU 7013 (1, 120.0), Mimase fish market, Shikoku Is., Japan; KU 13012 (1, 141.5), Tosa Bay, Shikoku Is., 430–460 m; KU 13125–13130, 13243, 13244, 13279 (9, 124.0–155.0), 15 km east of Ashizuri Misaki Pt., Shikoku Is., bottom trawl 420–555 m.

Southeast Asian Seas: USNM 92327 (holotype of *N. schmitti*) (1, 194.5), R/V *Albatross,* sta. D5445, Atalaya Pt., Batag Is., off Samar, the Philippines, 3 Jun. 1909; USNM 93354 (1, 136.0), R/V *Albatross,* sta. 5589, 04°12.10′N, 118°38.08′E, Mabul Is., off the Philippines (one of seven paratypes of *N. schmitti*); KU 15792 (1, 88.5, damaged), R/V *Hakuho Maru,* Cr. KH72-1, sta. 20, 05°40.9′N, 119°46.3′E, bottom trawl 460–500 m; KU 16644 (1, 207.0), R/V *Hakuho Maru,* KH72-1, sta. 26, 09°27.0′S, 127°58.6′E, Timor Sea, bottom trawl 690–850 m.

Off South Africa: USNM 2034391-10 (10, 174.0–192.0), R/V *Anton Bruun,* 22°25′S, 35°54′E, shrimp trawl, 0–740 m; ZMC P19624-25 (2, 183.5, 185.0), *Galathea* exped. 1950–1952, sta. 203, 25°36′S, 35°21′E off Natal, 2015 m; USNM not catalogued, SOSC ref. no. 1701-2 (2, 150.0, 165.0), IIO Exped. R/V *Anton Bruun,* Cr. no. 8, sta. 397C, 26°07′S, 34°11′E, bottom trawl 600–665 m; CAS-SU-31501 (1, 127.5), off South Africa.

DIAGNOSIS. Differs in having four branchiostegal rays, predorsal length less than 49 percent of SL, length of caudal peduncle not more than 15 percent of SL, number of gill rakers on first arch 27–35.

DESCRIPTION. D 9–10; A 9–10; P 12–14 (rarely 11); V 11 (rarely 10, 12); gill rakers 9–11 + 1 + 19–23, total 29–35 with 29(1), 30(1), 31(1), 32(5), 34(2), and 35(2) in 12 specimens from off Japan; 9 + 1 + 18–21, total 27–31 with

Figure 15. *Nansenia pelagica*. ISH 649-74, 102.0 mm SL, holotype.

27(1), 30(1), and 31(1) in three specimens from off the Philippines; 8–10 + 1 + 19–21, total 28–31 with 28(1), 29(2), 30(7), and 31(4) in 14 specimens from off South Africa; branchiostegal rays four; vertebrae 46–48 with 46(6), 47(12), and 48(2).

Gill raker counts were rather variable and higher on the average in the specimens from off Japan. Ranges of these counts, however, overlap among specimens from the three different regions. No significant geographical variation was found in other counts and measurements.

Pyloric caeca 8, 8, and 9 in three specimens from off South Africa, and 7, 9, and 9 in two Japanese specimens; conical teeth on vomerine series 25–35 and teeth on dentaries 65–75.

Eye large, diameter 2.3–2.5 times in head length, dorsal margin protruding above the margin of head. A roughly crescent-shaped, yellowish pigment patch present in the posterior half of iris. Aphakic space well developed. Anterior horizontal space nearly equal to width of iris, about twice width of posterior space. Aphakic space probably less well developed in smaller specimens, as is the case in other species.

Upper end of pectoral fin base above midpoint between lateral line and ventral margin of body, its lower end well above ventral margin of body by a distance more than (usually 1.5 to twice) length of pectoral fin base. Dorsal fin origin in front of center of body. Ventral fin base below or just behind posterior end of dorsal fin base. Adipose fin base above posterior half of anal fin base. Tip of mouth, snout, adipose, caudal and ventral fin bases pigmented.

SIZE. This species reaches about 200 mm SL. A specimen of 196 mm SL is reported to have ripe eggs (Abe, 1976).

DISTRIBUTION. Based on previous records, *N. ardesiaca* occurs in slope waters of Southeast Asian Seas, as far north as off southern Japan. It also occurs in slope waters off the east coast of South Africa (Fig. 22).

Nansenia tenuicauda new species

Figures 14, 22

HOLOTYPE. ISH 658/71, 84.0 mm, FFS *Walther Herwig* sta. 363-II/71, 40°18′S, 39°12′W, 8 Mar. 1971, MT1600, 0–328 m.

PARATYPES. ISH 1010-71 (2, 70.5, 69.0), FFS *Walther Herwig* sta. 399-II/71, 40°34′S, 09°50′W, 18 Mar. 1971, MT1600, 0–310 m.

DIAGNOSIS. Differs in having four branchiostegal rays, predorsal length less than 49 percent of SL and 38–42 gill rakers on the first arch. Slender caudal peduncle the least depth of which is less than 5.5 percent of SL also distinguish this species from other species of *Nansenia*.

DESCRIPTION. D 10–11; A 8–10; P 11–13; V 11–12; gill rakers 11–15 + 1 + 25–26, total 38–42 with 38(1), 39(1), and 42(1); branchiostegal rays four; vertebrae 46. Counts are based on three specimens.

Pyloric caeca eight in one specimen. Conical teeth ca. eight, irregularly arranged on head of vomer and ca. 26 compressed teeth on dentaries. A pair of teeth on the symphysis longest of all. Other teeth of lower jaw, as usually observed in other species of *Nansenia*, are progressively smaller from the back of each dentary to the front.

Body subcylindrical, with a depth to width ratio of 1.3–1.4. Eye large, its diameter 2.8–3.0 times in head length; pupil ovoid in shape with aphakic space developed posteriorly.

Upper end of pectoral fin base just below the midpoint between lateral line and ventral margin of the body. Dorsal fin origin well in front of center of the body. Ventral fin base below the posterior end of dorsal fin base. Adipose fin base above base of the last two anal fin rays.

Base of caudal fin densely pigmented, but pigment becoming progressively sparser anteriorly. Body color of preserved specimens light brown.

SIZE. The specimens examined, 69.0–84.0 mm SL, are probably juveniles.

DISTRIBUTION. Restricted to the area near the subtropical convergence in the South Atlantic, around 40°S.

ETYMOLOGY. From Latin, *tenuis,* slender, and from *cauda,* tail, in reference to the slender caudal peduncle.

Nansenia pelagica new species

Figures 15, 16, 22

HOLOTYPE. ISH 649/74 (1, 102.0), sta. A.D. 61-11/74, 02°27'N, 34°52'W, 24 Jan. 1974, MT1600, 0–350 m.

PARATYPES. Atlantic: ISH 1865/66 (1, 75.5), FFS *Walther Herwig* sta. 182-66, 10°46'N, 23°54'W, 16 May 1966, 0–300 m; ISH 442/66 (1, 93.0), FFS *Walther Herwig* sta. 184-66, 06°25'N, 24°34'W, 17 May 1966, 0–320 m; ISH 571/66 (1, 101.0), FFS *Walther Herwig* sta. 186-66, 01°24'S, 25°58'W, 19 May 1966, 0–330 m; ISH 619/66 (1, 64.8), FFS *Walther Herwig* sta. 187-66, 05°34'S, 26°58'W, 20 May 1966, 0–320 m; ISH 2066/71 (2, 101.5, 107.5), FFS *Walther Herwig* sta. 467-71, 05°30'S, 16°28'W, 9 Apr. 1971, 0–1900 m. Pacific: USNM 207532 (1, 83.7), 21°20'N, 158°20'W (off Hawaii), 16 Sep. 1970, 0–725 m.

OTHER MATERIALS. Atlantic: ISH 928/68 (1, 58.5), FFS *Walther Herwig* sta. 17-68, 04°43'S, 26°39'W, MT1600, 0–ca. 2000 m. Pacific: USNM 201704 (1, 27.0), R/V *Swan,* 28°48'N, 141°59'W, 6 ft.—IKMT, 200–247 m; USNM 212102 (2, ca. 60.5, ca. 54, damaged), from the stomach of a *Thunnus albacares* collected off the New Hebrides Is., 20°00'S, 170°03'E.

DIAGNOSIS. Differs from other *Nansenia* in having four branchiostegal rays and 38–39 vertebrae. Although it is similar to *N. atlantica,* and their distributions overlap in the tropical Atlantic, *N. pelagica* differs from *N. atlantica* in having lower vertebral counts (38–39 vs. 41–42), a longer head (27–30 percent of SL vs. 20–26 percent), and a dark pigment spot on the gular area that becomes obscure with growth in specimens larger than 90 mm SL.

DESCRIPTION. D 9–10; A 8–9; P 9–10 (rarely 11); V 10–11; gill rakers 10–13 + 1 + 24–27, total 36–41 with 36(2), 37(1), 38(3), 39(2), and 41(1); branchiostegal rays four, vertebrae 38–39 with 38(6) and 39(4). Counts are based on 10 specimens, 58.5–107.5 mm. Gill raker count of the one Pacific specimen was higher than counts from the Atlantic (41 vs. 36–38). Other counts showed no remarkable difference between the Pacific and Atlantic specimens.

Pyloric caeca seven and eight in the two Atlantic specimens. About 35 conical teeth on vomerine series and about 60 teeth, resembling a closely spaced picket fence, on the lower jaw of the specimens of 68.4 mm SL.

Body slender and slightly compressed, with a body depth-width ratio of 1.3–1.6 in specimens larger than 58 mm SL. Eye large, diameter 2.7–2.8 in head length in specimens 58.5–93.0 mm SL, and 2.4 to 2.5 times in head length in specimens 99.5–107.5 mm SL. Yellowish pigment, in a roughly crescent-shaped patch, develops on posterior half of iris with growth. Aphakic space developed in front of lens. This space is inconspicuous in juveniles.

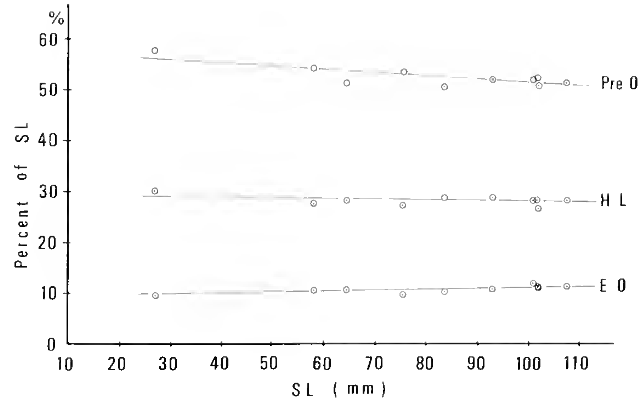

Figure 16. *Nansenia pelagica.* Predorsal, head lengths, and eye diameter in relationship to standard length.

Upper end of pectoral fin base just below midpoint between lateral line and ventral margin of body, its lower end above ventral margin of body by a distance about 1.5 times as long as length of pectoral fin base. Origin of dorsal fin base just behind center of body. Adipose fin base over anterior half of anal fin base.

Body skinned in most specimens, but lateral line pockets remaining in some. Bases of caudal, dorsal, ventral and adipose fins, and dorsal margin darker than lateral side of body. Inside of opercle lined with dark membrane. Dark pigment spot on gular area clearly recognizable, especially in juveniles less than 70 mm SL.

SIZE. The largest specimen examined, probably an adult, was 107.5 mm SL.

DISTRIBUTION. *Nansenia pelagica* occurs in the tropical Atlantic between 15°N and 10°S. In the Pacific it is known only from the subtropical eastern North Pacific between Hawaii and North America and the tropical western South Pacific off the New Hebrides Islands.

ETYMOLOGY. In reference to the pelagic life of this species.

Nansenia atlantica Blache and Rossignol, 1962

Figures 17, 21

Nansenia atlantica Blache and Rossignol, 1962:105–106, fig. 1 (orig. descr. 16 mm SL, 01°55'S, 8°30'E; 15 mm SL, 03°36'S, 09°10'E).

MATERIALS. ISH 335/66 (2, 88.5, one damaged), FFS *Walther Herwig* sta. 182-66, 10°46'N, 23°54'W, 0–300 m; ISH 457/68 (4, 90.5–112.8, one damaged), FFS *Walther Herwig* sta. 11-I-68, 16°14'N, 22°24'E, 0–160 m; ISH 686/68 (1, ca. 161, damaged), FFS *Walther Herwig* sta. 13-II-68, 08°21'N, 24°10'W, 0–520 m; ISH 13-II/68 (1, 167.5), FFS *Walther Herwig* sta. 11-III-68, 16°08'N, 22°22'W, 0–580 m.

Figure 17. *Nansenia atlantica.* ISH 475-68, 104.5 mm SL, showing proximal part of adipose fin densely pigmented.

DIAGNOSIS. Differs from other species of *Nansenia* in having four branchiostegal rays, origin of dorsal fin base in front of center of the body, 41–42 vertebrae and dark pigment spot at the base of adipose fin. This species is closely related to *N. oblita* as all counts overlap. The densely pigmented proximal part of the adipose fin base in *N. atlantica* distinguishes the two.

DESCRIPTION. D 9–10; A 8–9; P 12–13; V 10–11; gill raker on the first arch 9–13 + 1 + 19–23, total 30–36 with 30(1), 31(2), 33(2), 35(1), and 36(1); branchiostegal rays four; vertebrae 41–42 with 41(3) and 42(5). Counts are based on five to eight specimens.

Pyloric caeca seven in three specimens and nine in one specimen. Conical teeth on head of vomer 35, about 140 teeth on dentaries in one specimen.

Body slender and compressed laterally with body depth–width ratio, 1.4–1.6. Eye diameter 2.7–3.0 times in head length, viewed laterally its dorsal margin touching or protruding slightly higher than dorsal margin of head. Yellowish iridescent pigment pattern, roughly crescent-shaped, recog-

Figure 18. *Nansenia oblita.* USNM 92241, 39.1 mm SL, juvenile.

Figure 19. *Nansenia crassa.* LACM 9808-32, 165.2 mm SL.

nizable in the posterior half of iris. Pupil elliptical with aphakic space in front of lens.

Upper end of pectoral fin base well below midpoint between lateral line and ventral margin of body. Dorsal fin base originating just below center of body. Ventral fin base just in front of posterior end of dorsal fin base. Adipose fin base above center of anal fin base.

Body skin brown and easily rubbed off. The bases of adipose and caudal fins densely pigmented.

REMARKS. The original description of *N. atlantica* was based on two juvenile specimens of 16 and 15 mm SL. There is a considerable size gap between the type material and the smallest specimen available. Therefore, the present specimens are assigned to *N. atlantica* based on the coincidence of: (1) counts of branchiostegal and anal fin rays; (2) locality; (3) a wholly pigmented dark body surface. In the tropical Atlantic, two species of the Br-4 group occur, namely *N. atlantica* and *N. pelagica.* Juveniles of the latter differ from the former in the absence of complete pigmentation on the body.

SIZE. The largest specimens of 167.5 and 161 mm SL, collected in January, were mature males. An immature female of 112.0 mm SL was collected at the same time.

DISTRIBUTION. All specimens, including the types, were collected in the eastern tropical Atlantic between 20°N and 10°S (Fig. 21).

Nansenia oblita (Facciolà, 1887)

Figures 18, 21

Microstoma argenteum oblitum Facciolà, 1887:193 (orig. descr., Messina, Mediterranean).

Microstoma rissoanum Sarato, 1890 (orig. descr., Nice).

Microstoma oblitum: Belloti, 1888:224, figs. 3a, 3aA.

Nansenia oblita: Schmidt, 1918:19–22, figs. 13–14; Cohen, 1958:55.

Doubtful references:

Leuroglossus oblitus: Kuroda, 1947:25 (listed, no description, material unavailable); Kuroda, 1951:318.

Nansenia oblita: Matsubara, 1955:216 (cited from Kuroda, 1947).

MATERIALS. USNM 40075 (2, 40.5–48.5), from Messina, originally deposited in Royal Zool. Mus. Florence; USNM 92241 (3, 34.2–46.0), Mediterranean, originally deposited in Milano Mus.

DIAGNOSIS. Differs in having four branchiostegal rays, predorsal length longer than 50 percent of standard length, gill raker count 28–30 and proximal part of adipose fin unpigmented.

DESCRIPTION. D 10–11; A 9–10; P 10–11; V 10–11; gill rakers on the first arch 7–8 + 1 + 20–21, total 28–30 with 28(1) and 30(2); branchiostegal rays four on three spec-

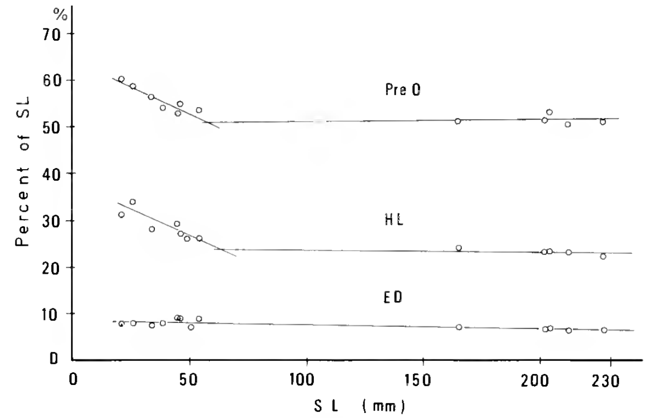

Figure 20. *Nansenia crassa.* Predorsal, head lengths, and eye diameter in relation to standard length.

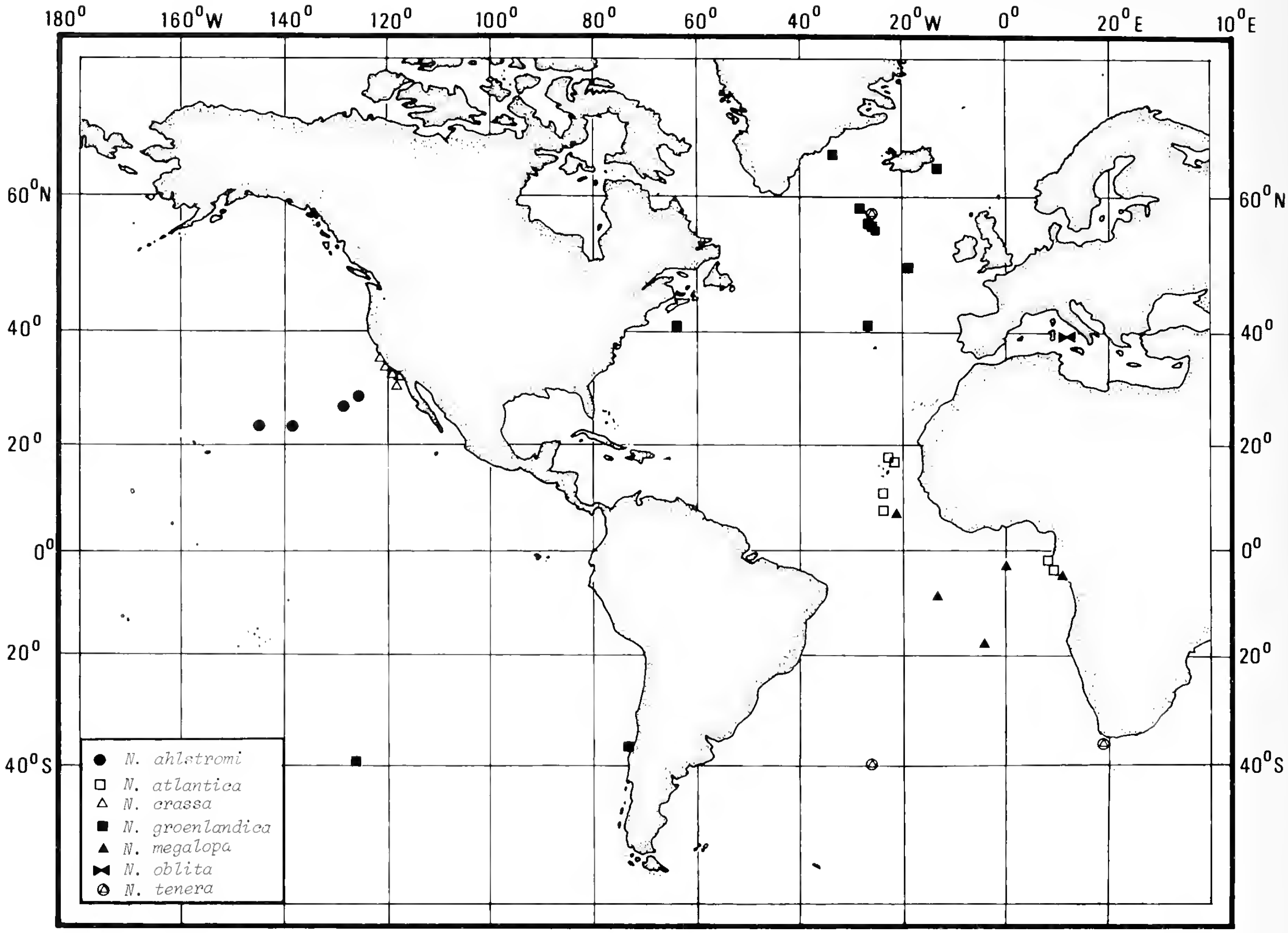

Figure 21. Distributions of specimens examined of seven species of *Nansenia.* A single symbol may indicate more than one record.

imens; vertebrae 42–45 with 42(1), 43(1), 44(2), and 45(1). Fin ray counts are based on four specimens.

Pyloric caeca eight in one specimen (seven reported by Schmidt, 1918); about 18 conical teeth irregularly arranged on head of vomer and about 30 compressed teeth on dentaries in a specimen of 48.5 mm SL. Measurements are based on four juveniles, 34.2–48.5 mm. The present counts and measurements are not very different from those presented for Mediterranean specimens by Schmidt (1918), except for the slightly lower pectoral and ventral fin ray counts in our material.

Body laterally compressed and stubby rather than slender with body depth–width ratio, 1.3–1.6. Eye diameter 3.0 to 3.4 in head length in juveniles (this ratio may be higher in adults due to negative allometry as observed in the closely related *N. crassa*); pupil nearly round in a specimen of 34.2 mm SL, horizontally elliptical in specimens larger than 39.1 mm.

Upper end of pectoral fin base above or on midpoint between lateral line and ventral margin of body, its lower end separated from ventral margin of body by a distance more than length of pectoral fin base. Dorsal fin origin behind center of body. Ventral fin base below posterior end of dorsal fin base. Adipose fin base above the middle of anal fin base or slightly in front of it.

Entire body covered with guanine; base of caudal and procurrent caudal fin rays pigmented.

SIZE. Largest specimen reported by Belloti (1888) about 18 cm. Therefore the present material is probably all juvenile.

DISTRIBUTION. Common in the western Mediterranean (Schmidt, 1918). Although Schmidt (1918) reported two juveniles, 21 and 31.5 mm, from the temperate eastern Atlantic south of the British Isles (48°43′N, 12°05′W), we have seen only Mediterranean specimens, in spite of considerable fishing effort by FFS *Walther Herwig* in the eastern North Atlantic.

Nansenia crassa Lavenberg, 1965

Figures 19, 20, 21

Nansenia crassa Lavenberg, 1965:282–285, fig. 1, table 1 (orig. descr.).

MATERIALS. LACM 4425, holotype, 212.0 mm, R/V *Velero,* sta. IV8296, 33°17′N, 118°40′W, 1336–1642, 9 Nov. 1962, 0–580 m; LACM 4426, paratype, 202 mm, R/V *Velero,* sta. IV7374, 33°28′N, 118°18′W, 0200–0550, 29 Jun., 1961, 0–865 m; LACM 4427, paratype, 266 mm (275 mm in original), R/V *Velero,* sta. IV8934, 33°14′N, 118°33′W, 1559–1858, 18 Sep. 1963, 0–485 m; LACM 9031-6 (1, 26.3), R/V *Velero* IV, 33°20.0′N, 118°38.22′W, 0704–1022, 10 ft.—IKMT, 0–504 m; LACM 9068-1 (1, 44.5), R/V *Velero* IV, 33°36′48″N, 118°26′26″W, 1241–1445, 10 ft.—IKMT, 0–ca. 500 m; LACM 9681 (2, 33.5, 39.0), R/V *Velero,* sta. 11616, Valero Basin, Mexico; LACM 9808-32 (1, 165.2), R/V *Velero,* San Clemente Basin, Calif.; LACM 9809-1 (2, 34.0, 35.0), R/V *Velero,* sta. 10682, 29°17′00″N, 118°10′30″W, 10 ft.—IKMT; LACM 9965-9 (4, 19.0–22.0), R/V *Velero,* sta. 9891, San Juan Seamount; LACM 35549 (1, 203.6), R/V *Velero,* San Clemente, Calif.; SIO H51-190 (1, 238.0), 32°49′N, 117°41′W, 0–548 m; SIO 57-87 (1, 93.0), 29°15′N, 126°07′W, off Baja Calif.

DIAGNOSIS. Differs from other species of the genus in the following charaters: (1) four branchiostegal rays; (2) predorsal length more than 49 percent of standard length; (3) 43–46 (usually 44–45) vertebrae; (4) length of caudal peduncle more than 13 percent of SL and depth of caudal peduncle less than 8.0 percent of SL (CPL/CPD ratio 1.7–2.2) in the specimens more than 30 mm SL. Gill raker count (35–37) also distinguishes this species from the closely related *N. oblita* (28–30).

DESCRIPTION. D 9–10; A 9 (rarely 8); P 11–13; V 10–11; gill rakers on the first arch 12–14 + 1 + 22–23, total 35–37 with 35(2), 36(2), and 37(2); branchiostegal rays four; vertebrae 43–46 with 43(1), 44(3), 45(5), and 46(2).

Pyloric caeca seven in two specimens; conical teeth in vomerine series 20–35, teeth on dentaries 150–180 in five specimens larger than 160 mm SL.

Morphometrics based on five juveniles and seven adults show remarkable allometric growth in head and predorsal lengths (Fig. 20).

Eye diameter 3.3 to 4.0 in head length with larger values in smaller specimens due to allometry; viewed laterally dorsal margin (supraorbital bone) protruding slightly above dorsal margin of head (less in juveniles); yellowish, crescent-shaped, pigment patch in posterior part of iris, sometimes obscure due to condition of preservation. Aphakic space well developed with its horizontal space about 1.5 times as large as width of anterior part of iris.

Upper end of pectoral fin base well below midpoint between lateral line and ventral margin of body; its lower end above ventral margin of body by a distance more than length of its base. Dorsal fin origin behind center of body. Ventral fin base below or slightly in advance of posterior end of dorsal fin base. Adipose fin base above center of anal fin base or slightly in front of it.

Skin around adipose fin base and caudal fin base pigmented. Ventral fin base slightly pigmented. Body color in preserved specimen brown.

SIZE. The largest specimen examined was 266 mm SL, with mature ovaries in September.

DISTRIBUTION. *Nansenia crassa* is found in the California Current region between 25°N and 35°N, where its distribution overlaps that of *N. candida* off mid- and southern California. It also occurs in the eastern tropical Pacific along the equator between 8°N and 7°S west to at least 126°W (Ahlstrom, 1971, 1972). The pattern of occurrence of adult specimens is associated with slope waters off California, suggesting that the adults there are benthopelagic life on the continental or insular slope. Larvae and juveniles are pelagic in the upper 200-m layer and are more broadly distributed than are adults. The larvae of *N. crassa* can be distinguished from those of *N. candida.* The geographical distributions of the larvae of the two species correspond largely to the distributions of the adults, although there is a larger area of overlap in the larvae. Specimens between 60 mm and 160 mm SL are completely lacking in our material. The size at which the specimens begin to disappear from our material corresponds to an abrupt change in allometric growth (Fig. 20). At this size, 50–60 mm SL, *N. crassa* may change its vertical distributional pattern from pelagic to benthopelagic life and become unavailable to either pelagic micronekton nets or bottom trawls with coarse mesh.

DISCUSSION

DISTRIBUTION PATTERN AND ZOOGEOGRAPHY

There are two types of distribution patterns, coastal and oceanic, among the species of *Nansenia.*

Nansenia ardesiaca is restricted to slope waters associated with insular or continental slopes, indicating a pseudo-oceanic distribution (Krefft, 1974). Sampling data suggest that this species is pelagic during larval and juvenile stages, but becomes benthopelagic as an adult. A distribution pattern similar to that of *N. ardesiaca* is not uncommon among slope water species of myctophids such as *Diaphus watasei, D. garmani, D. suborbitalis, Benthosema fibulatum,* and *B. pterotum* (Nafpaktitis, 1978; Gjøsaeter, 1981). These myctophids are distributed in Southeast Asian Seas and extend to off southern Japan and westward in the Indian Ocean to the Mozambique Channel, although few samples exist from the slope waters off India. Of the remaining 11 species, three (*N. crassa, N. oblita,* and *N. candida*) show an intermediate pattern of distribution between coastal and oceanic (Figs. 21, 22). Off southern California *N. crassa* has a coastal distribution, however the larvae are oceanic in the eastern tropical Pacific (Ahlstrom, 1971, 1972). The other nine species are all oceanic.

The 13 species may also be grouped into cold-water forms, four species; warm-water forms, seven species (*sensu* Johnson, 1982); and transitional forms, two species.

Of the four cold-water species, *N. candida* occurs only in the subarctic eastern Pacific. Kanayama and Amaoka (1983) described *Nansenia sanrikuensis,* the validity of which requires further confirmation, from the subarctic waters of the western Pacific off Japan. Species assemblages have been recognized in the myctophids of both the eastern and western

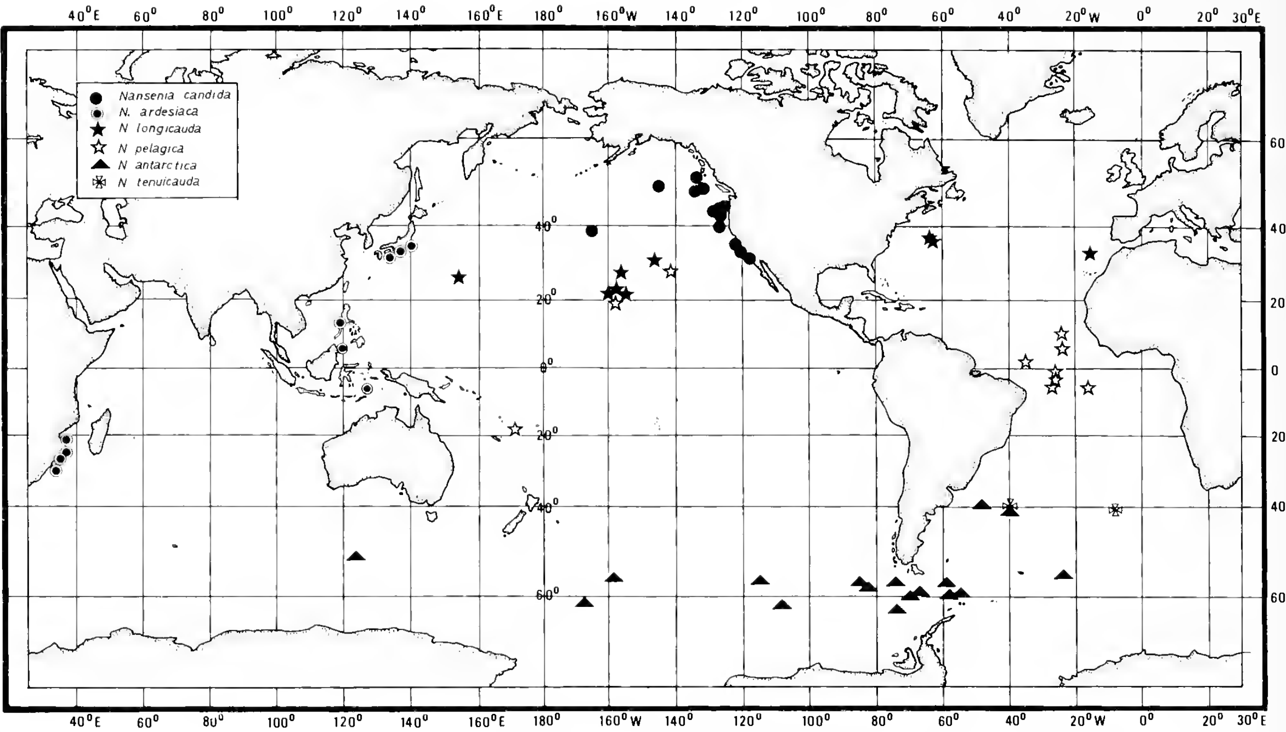

Figure 22. Distributions of specimens examined of six species of *Nansenia.* A single symbol may indicate more than one record.

parts of the subarctic Pacific, which includes *Diaphus theta, Lampanyctus ritteri, L. jordani, Stenobrachius leucopsarus, S. nannochir, Symbolophorus californiensis,* and *Tarletonbeania crenularis* (Wisner, 1974). Clinal variation occurs in the eye diameter of *D. theta* (Nafpaktitis, 1978; Kawaguchi and Shimizu, 1978) and in the shape of the caudal luminous scales of *S. californiensis* (Wisner, 1974 and pers. commun.) A similar species-subspecies problem exists in *Tarletonbeania* (Wisner, 1959; Becker, 1966). Definitive comparative examination of these species assemblages based on materials not only from both sides of the subarctic Pacific, but from the central area is needed. At present, it is not possible to establish either a clear break in the distribution of the eastern and western populations (or species) or clinal variations in characters.

Other cold-water species, *N. tenera* and *N. groenlandica,* belong to a subpolar-temperate group based on the system of distribution patterns recognized for Atlantic midwater fishes by Backus et al. (1977). These two species occur in both hemispheres, although *N. groenlandica* in the southern hemisphere is restricted to the subpolar-temperate region of the eastern South Pacific. However, some bipolar species of the subpolar-temperate group in the Atlantic such as *Lampanyctus macdonaldi* (Wisner, 1974; Backus et al., 1977) and *Gonostoma bathyphilum* (Mukhacheva, 1972) are found westward to the eastern South Pacific and occur north to Chile. Therefore additional sampling might establish the presence of *N. groenlandica* in the subantarctic Atlantic. Of the remaining cold-water species, *N. antarctica* is probably circumpolar along the Antarctic convergence, although collections are needed in the Indian Ocean sector.

Two of the seven warm-water species, *N. atlantica* and *N. megalopa,* occur only in the eastern tropical Atlantic. According to the Atlantic faunal regions recognized by Backus et al. (1977), both species inhabit the Guinean Province of Atlantic Tropical Region (Fig. 21). The distribution of *N. atlantica* appears to be restricted to the more productive area near the Mauritanian upwelling and to just off the Guinean coast. The other two warm-water species, *N. longicauda* and *N. pelagica,* are widely distributed in the Atlantic and Pacific oceans with the former restricted to the subtropical region between 20°N and 40°N and the latter to the tropical region between 20°N and 20°S in the Atlantic and between 30°N and 20°S in the Pacific. *Nansenia ahlstromi* is restricted to the central Eastern North Pacific. There is nothing to add to the previous discussion of the distribution of the remaining two warm-water species, *N. oblita* and *N. ardesiaca.*

BODY COLOR

There have been many descriptions of the body color of *Nansenia,* which suggest two patterns, silvery and colored. During the course of this study, however, it has been observed that the silvery color pattern is variable, depending upon preservative; it is easily lost in formalin. For example, the type of *N. ardesiaca* (Fig. 13a), which is now dark colored, was originally described as "color brilliant silvery . . . scales of a bright, silvery appearance" (Jordan and Evermann, 1896).

Some specimens examined (Fig. 13b) still bear complete guanine after more than 50 years of preservation in ethanol in a dark place. But these specimens are usually so soft that careful handling is necessary, indicating that they were not fixed well in formalin.

INTERRELATIONSHIPS

Various character states studied here are shared independently among 13 species and it is difficult to discuss the relationships within the species of *Nansenia*. Although the key separates species on the number of branchiostegal rays, loss of a branchiostegal ray could have occurred more than once. It is also possible to separate the species of this genus into three groups based on morphology, mainly of the caudal peduncle. With the exception of *N. antarctica*, the species of *Nansenia* are separable into the following three distinctive groups based on the ratio of caudal peduncle length to caudal peduncle depth (CPL/CPD, Tables 1 and 2):

Stubby-tailed group CPL/CPD = 1.0–1.5
Intermediate group CPL/CPD = 1.7–2.3
Slender-tailed group CPL/CPD = 2.7–4.1

The ratios are not overlapping. The stubby-tailed group includes four species: *N. ahlstromi* (Br 3), *N. oblita* (Br 4), *N. atlantica* (Br 4), and *N. pelagica* (Br 4). The slender-tailed group includes: *N. groenlandica* (Br 3), *N. tenuicauda* (Br 4), *N. megalopa* (Br 4), and *N. longicauda* (Br 4). Of the remaining five, four species, *N. candida* (Br 3), *N. crassa* (Br 4), *N. ardesiaca* (Br 4), and *N. tenera* (Br 4), are included in the intermediate group. *Nansenia antarctica* (Br 3) shows remarkable allometric growth in the caudal peduncle; the range of the CPL/CPD ratio for specimens less than 110 mm SL was 2.5–3.0; but the ratio for specimens larger than 110 mm SL was 2.0–2.5. This overlaps the range between intermediate and slender-tailed groups.

No correspondence is recognized between groupings based on the number of branchiostegal rays or morphology. This suggests that natural groups cannot be defined by branchiostegal ray counts alone.

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LITERATURE CITED

Abe, T. 1976. Notes on some fishes collected by the fisheries research vessel "Kaiyo-maru" in the South China Sea. IV. Bulletin of the Biogeographical Society of Japan 31(4): 27–31.

Ahlstrom, E.H. 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fishery Bulletin (U.S.) 69:3–77.

———. 1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fishery Bulletin (U.S.) 70:1153–1242.

Ahlstrom, E.H., H.G. Moser, and D.M. Cohen. 1984. Ontogeny and systematics of fishes Suborder Argeninoidei. *In* Moser, H.G., W.J. Richards, et al., Ontogeny and systematics of fishes. Spec. Publ. No. 1, Amer. Soc. Ichthyol. Herpetol. (in press).

Backus, R.H., J.E. Craddock, R.L. Haedrich, and R.H. Robison. 1977. Atlantic mesopelagic zoogeography. Memoir Sears Foundation for Marine Research, I (part 7): 266–287.

Becker, V.E. 1966. Slender tailed myctophids (genera *Loweina, Tarletonbeania, Gonichthys,* and *Centrobranchus*) of the Pacific and Indian oceans, systematics and distribution. Pages 10–78 *in* Rass, T.S., ed. (L. Penney, E. Roden, and E. Roifer, trans.), Fishes of the Pacific and Indian oceans, biology and distribution. Israel Program for Scientific Translation, Jerusalem.

Belloti, C. 1888. Note ittiologiche. Osservazione fatte sulla collezione ittiologica. Atti della Societe Italiana Scienza Naturali 31:213–229.

Blache, J., and M. Rossignol. 1962. III. *Nansenia atlantica* nov. sp. (Teleostei, Clupeiformes, Opisthoproctoidei, Microstomidae), Poisson bathypélagique nouveau du Golfe de Guinée. Cahiers O.R.S.T.O.M. Série Océanographie (2):103–106.

Chapman, W.M. 1942. The osteology and relationships of the Argentinidae, a family of oceanic fishes. Journal of the Washington Academy of Sciences 32:104–117.

———. 1943. The osteology and relationships of the bathypelagic fishes of the genus *Bathylagus* Gunther, with notes on the systematic position of *Leuroglossus stilbius* Gilbert and *Therobromus callorhini* Lucas. Journal of the Washington Academy of Sciences 33(5):147–160.

———. 1948. The osteology and relationships of the Microstomidae, a family of oceanic fishes. Proceedings of the California Academy of Sciences, Ser. 4, 26(1):1–22.

Cohen, D.M. 1958. *Nansenia candida,* a new species of argentinid fish from the north Pacific, with notes on the other species of *Nansenia.* Stanford Ichthyological Bulletin 7:52–57.

———. 1964. Suborder Argentinoidea. Memoir Sears Foundation for Marine Research, New Haven 1(4):1–70.

Facciolà, L. 1887. Sull esistenza di due forme diverse di *Microstoma* nel mar di Messina. Naturalista Siciliano, Palermo 6:193–197.

Follet, M.I., and D.M. Cohen. 1958. Request for a ruling as to the species to be accepted as the type species of the nominal genus "*Bathylagus*" Gunther (A.C.L.G.), 1878 (class Pisces). Bulletin of Zoological Nomenclature 16(2): 73–78.

Fowler, H.W. 1934. Descriptions of new fishes obtained 1907 to 1910 chiefly in the Philippine Islands and adjacent seas. Proceedings of the Academy of Natural Sciences, Philadelphia 85:233–367.

Gilchrist, J.D.J. 1922. Deep-sea fishes procured by the SS 'Pickle' (Part I). Report of the Fisheries Marine Biological Survey, Republic of South Africa, 2 (Special Report 3):41–79, pls. VII–XIII.

Gjøsaeter, J. 1981. Growth, production and reproduction of the myctophid fish, *Benthosema glaciale,* from western Norway and adjacent seas. Fiskerdirektorates Skrifter. Serie Havundersokelser 17:79–108.

Hubbs, C.L., and K.F. Lagler. 1964. The fishes of the Great Lakes region. University of Michigan Press, Ann Arbor. 213 pp.

Johnson, R.K. 1982. Fishes of the families Euermannellidae and Scopelarchidae: Systematics, morphology, interrelationships, and zoogeography. Fieldiana 12:1–252.

Jordan, D.S., and B.W. Evermann. 1896. The fishes of North and Middle America, descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. United States National Museum, Bulletin (47), Part 1, lx + 1240 pp.

Jordan, D.S., and W.F. Thompson. 1914. Record of the fishes obtained in Japan in 1911. Memoirs of the Carnegie Museum 6:205–313.

Kanayama, T., and K. Amaoka. 1983. *Nansenia sanrikuensis* (Kurosake-iwashi). Pages 77–79 *in* Amaoka et al. (eds.), Fishes from the northeastern sea of Japan. Japan Fisheries Resource Conservation Association.

Kawaguchi, K., and H. Shimizu. 1978. Taxonomy and distribution of the lanternfishes, genus *Diaphus* (Pisces, Myctophidae) in the western Pacific, eastern Indian Oceans and the Southeast Asian Seas. Bulletin of the Ocean Research Institute, University of Tokyo, No. 10, 145 pp.

Krefft, G. 1974. Investigations on midwater fish in the Atlantic Ocean. Berichte der Deutschen Wissenshaftlichen Kommission für Meeresforschung 23:226–254.

Kuroda, N. 1947. Additional list of fishes in Suruga Bay off Sizu-ura (No. 8) Seibutsu (Life) (1):25–31.

———. 1951. A nominal list with distribution of the fishes of Suraga Bay, inclusive of the fresh water species found near the coast. Japanese Journal of Ichthyology 1(5): 314–338, 376–394.

Lavenberg, R.K. 1965. A new species of microstomatid fish (*Nansenia*) from California waters. Copeia 1965(3): 281–385.

Matsubara, K. 1955. Fish morphology and hierarchy, Parts I–III. Ishi-zaki Shoten, Tokyo. 1605 pp.

Mukhacheva, V.A. 1972. On systematics, distribution and biology of the *Gonostoma* species (Pisces, Gonostomatidae). Trudy Instituta Okeanologii Akademiya Nauk, SSSR 93:205–249.

Nafpaktitis, B.G. 1978. Systematics and distribution of lanternfishes of the genera *Lobianchia* and *Diaphus* (Myctophidae) in the Indian Ocean. Natural History Museum of Los Angeles County, Bulletin No. 30, 92 pp.

Parin, N.V., and G.A. Golovan. 1976. Pelagic deep-sea fishes of the families characteristic of the open ocean collected over the continental slope off west Africa. Trudy Instituta Okeanologii, Akademiya Nauk, SSSR 104: 250–276.

Reinhardt, J.C.H. 1840. [Gronlands Fiske]:8–10. *In* Orsted, H.C., Oversikt Konelige Danske Videnskabernes Selskabs Forhandlinger (1839):1–44.

Sarato, C. 1890. Notes sur les poissons de Nice. (Reprint: 1–3.) Nice.

Schmidt, E.J. 1918. Argentinidae, Microstomidae, Opisthoproctidae, Mediterranean Odontostomidae. Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and adjacent seas, 2. Biology (A5): 1–40.

Tanaka, S. 1911. Figures and descriptions of the fishes of Japan. Vol. 1. Dai-ichi shoin, Tokyo. 18 pp.

Wisner, R.L. 1959. Distribution and differentiation of the North Pacific myctophid fish, *Tarletonbeania taylori.* Copeia 1959(1):1–7.

———. 1974. The taxonomy and distribution of lanternfishes (Family Myctophidae) of the eastern Pacific Ocean. NORDA Report 3, Department of the Navy (U.S.). 229 pp.

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CONTRIBUTIONS IN SCIENCE

KENTRIODON OBSCURUS (KELLOGG, 1931), A FOSSIL DOLPHIN (MAMMALIA: KENTRIODONTIDAE) FROM THE MIOCENE SHARKTOOTH HILL BONEBED IN CALIFORNIA

Lawrence G. Barnes and Edward Mitchell

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KENTRIODON OBSCURUS (KELLOGG, 1931), A FOSSIL DOLPHIN (MAMMALIA: KENTRIODONTIDAE) FROM THE MIOCENE SHARKTOOTH HILL BONEBED IN CALIFORNIA

Lawrence G. Barnes[1] and Edward Mitchell[2]

ABSTRACT. The fossil odontocete genus *Kentriodon* Kellogg, 1927, is the type genus of the delphinoid family Kentriodontidae, a family which has no living representatives. The genus *Kentriodon* has previously included only one named species, a small dolphin called *Kentriodon pernix* Kellogg, 1927, from the Middle Miocene Calvert Formation in Maryland and Virginia on the east coast of North America. Some bones from Japan and California have previously been tentatively referred to the genus. We have concluded that the species *Grypolithax obscura* Kellogg, 1931, heretofore known only by isolated periotics from the Middle Miocene Sharktooth Hill Bonebed in California, belongs in *Kentriodon.* The genus *Grypolithax* Kellogg, 1931, is therefore a junior synonym of *Kentriodon* Kellogg, 1927. A second species named on isolated periotics from the Sharktooth Hill Bonebed, *Grypolithax pavida* Kellogg, 1931, is a synonym of *G. obscura.* The appropriate binomen for the species is *Kentriodon obscurus* (Kellogg, 1931). We assign to this species a partial skull and additional isolated periotics from the same bonebed.

Other isolated periotics from rocks stratigraphically below the Sharktooth Hill Bonebed in California resemble those of *Kentriodon* spp. and a closely related kentriodontid, *Delphinodon dividum* True, 1912, which was also originally described from the Calvert Formation. Some of these have been referred to in previous literature, but are illustrated and described here for the first time.

These newly reported specimens from California reinforce some previous correlations between the upper part of the Round Mountain Silt in California and the Calvert Formation in Maryland and Virginia. They also provide additional indications of a general pattern of generic cosmopolitanism and specific endemism among the Miocene odontocetes of the North Atlantic and North Pacific Oceans.

INTRODUCTION

Fossil odontocetes of the genus *Kentriodon* Kellogg, 1927, are small Miocene dolphins in the extinct family Kentriodontidae. Kellogg (1928:33, 68) assigned the genus to the family Delphinidae. Slijper later (1936:556) named a new subfamily Kentriodontinae, which he placed within the Delphinidae, to include *Kentriodon* as well as *Delphinodon dividum* True, 1912, another Miocene dolphin. Barnes (1978) altered the context and rank of Slijper's family group name by recognizing the family Kentriodontidae within the superfamily Delphinoidea. He recognized three subfamilies (Kampholophinae, Kentriodontinae, and Lophocetinae) within the Kentriodontidae, and the species included in this family are now known by described fossils from Europe, Japan, New Zealand, and both the east and west coasts of North America. The importance of this family and its relationships to some other odontocete families was commented on by Barnes. He stated that kentriodontids might comprise the group from which other living families of delphinoids, including modern dolphins in the Delphinidae, have evolved, and they might also be expected to occur widely in rocks of appropriate age around the world. Our interests in delphinoid evolution and in the Middle Miocene cetaceans in the Sharktooth Hill Local Fauna in California have led us to the present study.

The type species of *Kentriodon, K. pernix* Kellogg, 1927, was named on the basis of two skulls, one of which was collected with earbones and an articulated partial postcranial skeleton (the holotype), of Middle Miocene age from the Calvert Formation in Maryland. Until the present study, this genus has had assigned to it only this one named species, however, some references in the paleontologic literature have suggested the former presence of the genus in the North Pacific Ocean. The genus *Kentriodon* was questionably identified from Miocene rocks in Japan by Shikama, Hasegawa, and Otsuka (1973; also cited in Okazaki, 1976:25), but specimens documenting this identification have not been described. Barnes (1976:326) identified as cf. *Kentriodon* and as a related kentriodontid, cf. *Delphinodon dividum* True, 1912, some isolated periotics of early Middle Miocene age from the lower part of the Round Mountain Silt in Kern County, California. The source of these is stratigraphically lower than the Middle Miocene Sharktooth Hill Bonebed. Other kentriodontid genera have been recognized based on skulls from Miocene rocks in Europe and California (Kellogg, 1925:4–6; Barnes, 1976, 1978), and from late Oligocene rocks in New Zealand (Fordyce, 1980:328).

Kellogg (1931) prepared a preliminary description of the mammals from the Sharktooth Hill Bonebed that comprise a part of what we now call the Sharktooth Hill Local Fauna (Mitchell, 1965:33; Mitchell and Tedford, 1973: fig. 3; Barnes, 1976:326–327). In this study, Kellogg named ten new species of small odontocetes based solely on isolated periotics from the bonebed. For many years the true identities and relationships of these species have remained unknown. The problem of disparate skeletal parts has in some instances precluded objective morphologic and taxonomic comparisons between the odontocetes from the Sharktooth Hill Bonebed and other taxa (even some studied by Kellogg himself) known by skulls and skeletons from elsewhere in the world. For example, Barnes (1978) showed that *Liolithax kernensis* Kellogg, 1931, from the Sharktooth Hill Bonebed is congeneric with *Lophocetus pappus* Kellogg, 1955, from the Calvert Formation in Maryland.

In the present study, we show that *Grypolithax obscura* Kellogg, 1931, from the Sharktooth Hill Bonebed is conge-

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[1] Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

[2] Arctic Biological Station, Fisheries and Oceans, Ste. Anne de Bellevue, Quebec, Canada H9X 3R4; and Research Associate, Natural History Museum of Los Angeles County.

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neric with *Kentriodon pernix.* Another species Kellogg named from the bonebed, *G. pavida* Kellogg, 1931, is synonymous with *G. obscura* and the properly emended binomen for the species from California is *Kentriodon obscurus* (Kellogg, 1931). We refer a partial skull and several more isolated periotics from the Sharktooth Hill Bonebed to *K. obscurus,* and with these we have been able to more fully characterize the species and compare it with *K. pernix.* We also describe and illustrate the specimens of kentriodontids that Barnes (1976) mentioned from stratigraphically lower levels of the Round Mountain Silt in California.

MATERIALS AND METHODS

INSTITUTIONAL ACRONYMS

The specimens examined in the course of this study are in the collections of the following scientific institutions: California Academy of Sciences, San Francisco, California (CAS); Natural History Museum of Los Angeles County, Los Angeles, California (LACM); University of California Museum of Paleontology, Berkeley, California (UCMP); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Institutional locality numbers are given for specimens where appropriate. Qualified investigators may obtain precise locality information by contacting the appropriate institutions.

COMPARATIVE MATERIAL

We have made extensive reference to and comparisons with the type species of *Kentriodon, K. pernix* from the Middle Miocene Calvert Formation in Maryland. We believe that the holotype (USNM 8060) of *K. pernix,* which was collected from Zone 5 relatively low in the Calvert Formation, and Kellogg's original (1927a) published referred skull (USNM 10670) from Zone 3 slightly lower in the formation, represent the same species. These are the only skulls of *K. pernix* that have been described in the literature.

We have identified one other small skull (USNM 21027) as *K. pernix.* It was found at Plum Point, Maryland, where Zone 6 of the Calvert Formation (also relatively low in the rock unit) is exposed at sea level (see Clark, Shattuck, and Dall, 1904: pl. 5). These three specimens, therefore, comprise our current concept of the species, but provide only limited information on individual and ontogenetic variation within the species.

There are several additional fossils of *Kentriodon* from the Calvert Formation in Virginia and Maryland in the USNM collections that are undescribed in the scientific literature. Some of these are significantly different from both the holotype and referred specimens of *K. pernix.* Most are from zones higher in the Calvert Formation, and are therefore geologically younger than the holotype and referred specimens of *K. pernix.* We conclude that one or more species in addition to *K. pernix* are represented by these additional specimens, but a detailed variability and taxonomic study of *Kentriodon* from the Calvert Formation is beyond the scope of the present study. In the absence of such a study of these other *Kentriodon* specimens, we made some observations on them that have influenced our diagnoses and comparisons. Additionally, we have illustrated some of the periotics (Figs. 8–9) to demonstrate variable characters within the genus.

TERMINOLOGY

The morphology of a kentriodontid periotic is shown in Fig. 1. The terminology used is derived or adapted from Denker (1902), Boenninghaus (1904), and Kellogg (1928). Cranial terminology is derived from Kellogg (1927a) and Fraser and Purves (1960). Where we employ family group names with different rank than originally proposed, we cite the author of the emended rank following the original author.

Statistical analysis follows Simpson, Roe, and Lewontin (1960).

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Delphinoidea (Gray, 1821) Flower, 1864

Family Kentriodontidae (Slijper, 1936) Barnes, 1978

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.

Kentriodontidae. Slijper, 1958: label in fig. 36, emended rank without explanation in text.

Kentriodontidae. Barnes, 1978:3; emended rank, as a family of the superfamily Delphinoidea.

DISCUSSION. Barnes (1978) stated that a lack of fossae in bones of the basicranium, reflecting a presumed lack of extensive development of air sinuses of the middle ear air sinus system, was a characteristic feature of the family Kentriodontidae. Aside from the usual, primitive odontocete combination of peribullary and pterygoid air sinuses, we find in *Kentriodon* spp. osteological evidence only for a middle sinus adjacent to the glenoid fossa and for a postorbital lobe of the pterygoid sinus. We find no fossae that would provide evidence for a posterior sinus in the exoccipital, for any sinuses in the basioccipital or above the optic nerve (as in phocoenids), for a large orbital lobe, or for an anterior sinus extending onto the posterior part of the palate. These are all locations where various modern odontocetes have been shown to have air sinuses in their skulls (Fraser and Purves, 1960). The fossa for the lobe of the pterygoid sinus within the pterygoid hamulus is characteristically small in Kentriodontidae compared with Delphinidae, Phocoenidae, Ziphiidae or Physeteridae. No fossil kentriodontid skull has yet been described with an ossified pterygoid hamulus flooring the ventral surface of this sinus as in modern delphinids, phocoenids, and monodontids, and it cannot be determined from the specimens presently available whether or not these animals had an incomplete or non-ossified hamulus as in modern platanistoid dolphins (see Fraser and Purves, 1960).

Subfamily Kentriodontinae Slijper, 1936

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.

Kentriodontinae. Barnes, 1978:24; emended context, as a subfamily of the family Kentriodontidae.

Kentriodon Kellogg, 1927

Kentriodon Kellogg, 1927a:4.

Grypolithax Kellogg, 1931:393.

EMENDED DIAGNOSIS OF GENUS. A genus of the subfamily Kentriodontinae differing from *Delphinodon dividum* by having a skull with a longer rostrum, the mesorostral gutter not roofed over by the premaxillae at the anterior end, a more concave lateral margin of the supraorbital process, palatal surfaces of maxillae more transversely convex, and a fossa for the postorbital lobe of the pterygoid air sinus on the ventral surface of the frontal; differing from *Leptodelphis, Microphocaena, Pithanodelphis,* and *Sarmatodelphis* by having a more convex lateral margin of the supraorbital process, flat rather than bulbous or convex nasal bones, and more widely separated posterior ends of the maxillae at the cranial vertex with a concomitantly wider exposure of the frontals, differing from *Leptodelphis* and *Pithanodelphis* by having a less elevated cranial vertex; and differing from *Liolithax, Delphinodon, Lophocetus,* and perhaps other described genera of Kentriodontidae by having the anterior-most premaxillary tooth on each side elongated into a small tusk and pointing anteriorly from the tip of the rostrum.

TYPE SPECIES. *Kentriodon pernix* Kellogg, 1927; type by original monotypy.

INCLUDED SPECIES. *Kentriodon pernix* Kellogg, 1927; and *Kentriodon obscurus* (Kellogg, 1931), new combination.

***Kentriodon obscurus* (Kellogg, 1931), new combination**

Figures 2–7, 8d–t, 9d–t, 13b, 14b

Grypolithax obscura Kellogg, 1931:394.

Grypolithax pavida Kellogg, 1931:396.

EMENDED DIAGNOSIS OF SPECIES. A species of *Kentriodon* characterized by and differing from *K. pernix* by having skull with vertically short postorbital process of frontal, posterior part of alveolar row curved medially on palatal surface instead of extending along lateral margin of rostrum, posterior maxillary alveoli directed more laterally than ventrally, lateral margin of maxilla adjacent to posterior part of alveolar row thickened and squared off instead of being thin and rounded, alveoli for maxillary teeth averaging 1.5 mm in diameter instead of 3 mm, antorbital notch narrow and directed anteriorly instead of wide and directed anterolaterally, supraorbital process of frontal thicker and more arched, medial margins of dorsal premaxillary surfaces on proximal part of rostrum between antorbital notches flat instead of inclined medially toward mesorostral gutter, palatine bone and pterygoid sinus fossa extended farther anteriorly onto palate instead of ending at level of antorbital processes, postorbital lobe of pterygoid sinus of middle ear air sinus system occupying large fossa on ventral surface of supraorbital process of frontal, internal acoustic meatus of periotic more elliptical and less circular in shape.

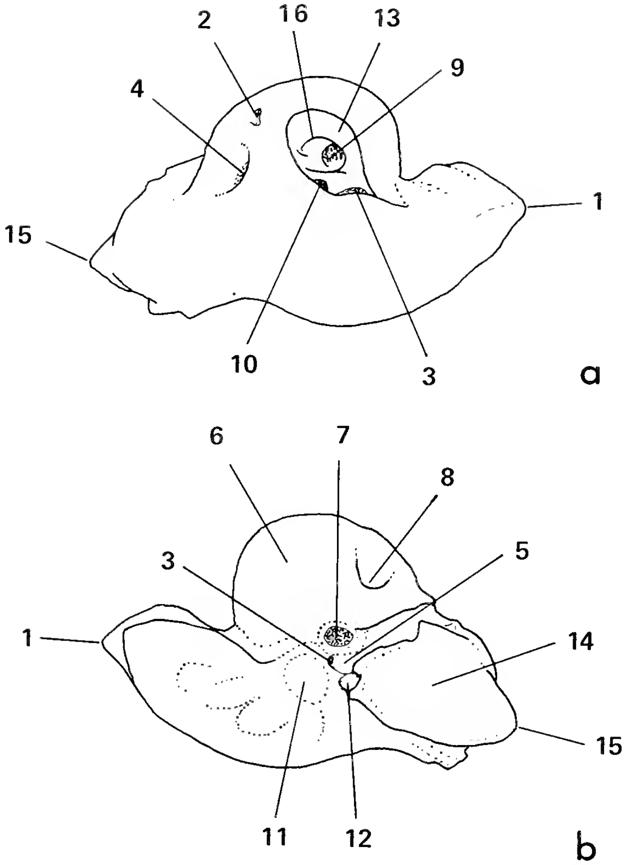


Figure 1. Right periotic of a kentriodontid, cf. *Kentriodon* sp., UCMP 83605, with anatomical structures labeled; **a,** cerebral or dorsal view; **b,** tympanic or ventral view, natural size. 1—anterior process, 2—*aquaeductus cochleae,* 3—*aquaeductus Fallopii,* 4—*aquaeductus vestibuli,* 5—canal for facial nerve, 6—cochlear portion, 7—*fenestra ovalis,* 8—*fenestra rotunda,* 9—*foramen centrale,* 10—*foramen singulare,* 11—fossa for head of the malleus, 12—*fossa incudis,* 13—internal acoustic meatus, 14—posterior articular facet for tympanic bulla, 15—posterior process, 16—*tractus spiralis foraminosus.*

HOLOTYPE. CAS 4349, right periotic, collected by Charles Morrice in 1924.

TYPE LOCALITY. CAS locality 905, Sharktooth Hill Bonebed, Kern County, California.

PARATYPE. CAS 4347, left periotic collected by Charles Morrice in 1924 from CAS locality 905.

REFERRED SPECIMENS FROM THE SHARKTOOTH HILL BONEBED. LACM 21256, an incomplete skull lacking the extremity of the rostrum, the occipital shield, and the basicranium, from LACM locality 1625, and 31 isolated periotics as follows: CAS 4348, left (holotype of *Grypolithax pavida*), CAS 4350, left (paratype of *G. pavida*), both from CAS locality 905; LACM 21134, right, LACM 44916, left, LACM 63800, left, all from LACM locality 1625; LACM 21238, right, and LACM 48925, left, both from LACM locality 1557; LACM 39696, left, from LACM locality 3232; LACM 41473, left, from LACM locality 1655; LACM 58893, left, from LACM locality 6688; LACM 75371, left, from LACM locality 3208; LACM 96150, right, LACM 121998, LACM 121999, LACM 123477–123481, eight right, LACM 123482 and 123483 left, all from LACM locality 3162; LACM 98712, left, from LACM locality 3160; LACM 104094, left, from LACM locality 1622; LACM 123471–123473, three right, from LACM locality 4672; LACM 123474, left, from LACM locality 4874; LACM 123475, right, and LACM 123476, left, from LACM locality 4956.

FORMATION AND AGE. The holotype, paratype, and all specimens here referred to *Kentriodon obscurus* were collected from several localities scattered over several square kilometers in the Sharktooth Hill Bonebed in the upper part of the Round Mountain Silt. This bonebed is a single thin stratum and is the source of the Sharktooth Hill Local Fauna (Wood et al., 1941; Mitchell, 1966:28–29; Mitchell and Tedford, 1973; Barnes, 1976). It is correlated with the Barstovian North American land mammal age, the "Temblor" provisional provincial molluscan stage, the Relizian or Luisian foraminiferal stage, and is approximately between 13 and 15 million years old (Wood et al., 1941:31, pl. 1; Weaver et al., 1944:582, pl. 1; Evernden et al., 1964; Addicott, 1972; Savage and Barnes, 1972:133, 140; Berggren and Van Couvering, 1974: fig. 11; Barnes, 1976:326–327; 1978:5–6; Repenning and Tedford, 1977: table 1). Based on these correlations, the upper part of the Round Mountain Silt, including the bonebed, is approximately contemporaneous with the Calvert Formation in Virginia and Maryland (Gazin and Collins, 1950:3; Kellogg and Whitmore, 1957:1022; Ray, 1976: fig. 1).

DESCRIPTION AND COMPARISONS. Skull. The referred skull (LACM 21256, Figs. 2–7) of *Kentriodon obscurus* from the Sharktooth Hill Bonebed is incomplete and has suffered pre-depositional breakage and abrasion. The basicranium, occipital area, rostral extremity, vomer and pterygoid sinus fossae have been broken off. The sutures between the remaining bones were unfused, and the two halves were separated along the midline when the skull was found in the field. We have re-assembled it in its presumed original configuration based on comparisons with specimens of *Kentriodon pernix* from the Calvert Formation. Due to some distortion, however, the left supraorbital process fits incorrectly and attaches too low on the skull (Fig. 4a). On the right side (Fig. 4b) the supraorbital process is in the correct position. The measurements of the skull are as follows: total length as preserved, 193.5 mm; breadth of rostrum at antorbital notches, 67.7 mm; breadth of cranium at antorbital processes, 122.3 mm; interorbital width, 115.2 mm.

The skull is nearly the same size as both the holotype and Kellogg's (1927a) referred skull of *K. pernix*. All three appear to represent young adult animals because none has the advanced suture fusion and/or extreme development of rugosities and processes seen on skulls of extremely old individuals of living delphinoids. Additionally, in the holotype skeleton of *K. pernix* most of the vertebral epiphyses, including those on cervicals and caudals, are tightly appressed to the vertebral centra but not fused, indicating that the individual had not yet achieved physical maturity. Overall skull shape and proportions are similar in the two species, as far as is known. It is in cranial details that the two species differ.

The open mesorostral gutter on the distal part of the rostrum is apparently characteristic of *Kentriodon pernix* (Kellogg, 1927a: pls. 2, 6), but is uncharacteristic of species in the family Kentriodontidae as a whole (Barnes, 1978: figs. 14–17). The premaxillae on the referred skull of *K. obscurus* are partly broken away distally, but in addition to having the usual wide open mesorostral gutter at the proximal end, they begin to diverge anteriorly as though they would have also left the gutter exposed distally as in *K. pernix*. There is no indication that the medial margins of the premaxillae were elevated adjacent to the posterior part of the mesorostral gutter as they are in *K. pernix*. The anterior (= rostral) parts of the premaxillae are comprised of bone which is denser and of smoother surface than the adjacent maxillae.

On the skull of *K. obscurus*, the premaxillary foramina are located on a transverse line between the antorbital notches (Figs. 2–3). These foramina are located more posteriorly on both the holotype and the referred skull of *K. pernix*. The premaxillary sulci associated with these foramina are somewhat damaged from breakage and abrasion, but between the right and left sides, the typical odontocete condition of three sulci (anteromedial, posteromedial, and posterolateral, see Barnes, 1978:13; Fordyce, 1981:1034, text-fig. 2) can be seen. Medial to the anteromedial sulcus and the premaxillary foramen, the premaxillary surface is rough and indicates the area where the nasal plug muscle was attached (Lawrence and Schevill, 1956: fig. 23; Mead, 1975). The part of the premaxilla that in life underlay the premaxillary sac (the premaxillary sac fossa of Fordyce, 1981:1035, text-fig. 2; Mead, 1975) lies posterior to the posteromedial and posterolateral sulci and lateral to the nares. This area is also roughened, but this is the result of postmortem abrasion because one small remnant of surficial bone on the left premaxilla indicates the previous existence of a thin, smooth bone surface on the premaxillary sac fossa as is typical of delphinoids. The more anterior location in *K. obscurus*, compared with *K. pernix*, of the premaxillary foramina, the three associated sulci, and concomitantly the anterior margin of the premaxillary sac fossae, is primitive, because these structures have moved progressively posteriorly during the odontocete cranial telescoping process (Miller, 1923). The area that was occupied by the premaxillary sacs is more elongate anteroposteriorly in *K. obscurus*, and we consider this to be primitive as well. These sacs in *Kentriodon* might have been symmetrical because the premaxillary sac fossae are not asymmetrical as they are in modern delphinids (cf. Mead, 1975).

Both species of *Kentriodon* have relatively small bony nares that are narrowly pointed anteriorly. This is also typical of many other species of Kentriodontidae (see Barnes, 1978: figs. 14–17), and contrasts with the large, round nares of species of Delphinidae.

The lateral margin of the maxilla dorsal to the posterior end of the tooth row and medial to the antorbital notch typically is formed into a relatively thick, horizontally projecting shelf in most kentriodontids. In *K. obscurus,* this part of the maxilla is proportionally wider and has a more squared off and vertical lateral margin than in *K. pernix,* in which the maxilla has a thinner, more rounded margin. The antorbital notches of *K. obscurus* are relatively narrower than those of *K. pernix,* because in *K. obscurus,* both the lacrimal and the maxilla project in a more anteromedial direction, thereby giving the antorbital process a different shape (Fig. 13).

On the supraorbital process, both the frontal and maxilla are significantly thicker and thus more convex or domed in *K. obscurus* than in *K. pernix.* The lateral margins of the maxillae have been both chipped and abraded over the orbit on the skull of *K. obscurus.* The frontal is therefore probably exposed more in dorsal view than it was in life.

The postorbital process of the frontal of *K. obscurus* is narrower, shorter, and more tapered distally than in *K. pernix.* These differences do not appear to be related to ontogeny because the juvenile skull that we refer to *K. pernix* (USNM 21027) from the Calvert Formation is smaller than the skull of *K. obscurus,* has characters indicating physical immaturity, but has substantially longer postorbital processes. Additionally, the postorbital processes on the three skulls of *Kentriodon pernix* from the Calvert Formation have a hook-like shape, in contrast to the straight process of *K. obscurus.*

Among modern Delphinidae, there is a fossa located at the posterolateral corner of the palate lateral to the pterygoid sinus fossa and which marks the position of an air sinus called the anterior sinus (see Fraser and Purves, 1960). This area of the palate of *K. obscurus* is convex and shows no development of such a fossa. On skulls of *K. pernix,* this area of the palate is distinctly less convex so that a transverse section through the proximal part of the rostrum is nearly V-shaped. Neither species has the type of fossa or concave area that in some living odontocetes marks the location of an anterior sinus, and there probably was no such sinus present in either species of *Kentriodon.*

The fossa for the lobe of the pterygoid air sinus that filled the pterygoid hamulus is larger and extends farther anteriorly in *K. obscurus* than in *K. pernix.* The roof of this pterygoid sinus fossa is marked by a tapered cavity on the ventral surface of the left palatine bone. The palatines concomitantly extend farther anteriorly and are more pointed in *K. obscurus.* The anterior-most extent of the palatines in *K. obscurus* is 35 mm anterior to the antorbital notch, whereas the same parameter on the holotype of *K. pernix* is only 10 mm and on Kellogg's referred skull (USNM 10670) it is 14.4 mm.

As on the referred skull (USNM 10670) of *K. pernix,* the ventral surface of the vomer was only exposed in a very narrow opening between the maxillae at about the middle of the rostrum of *K. obscurus* (Figs. 14a, b). In both species, posterior palatine foramina flank this area, and slightly farther anteriorly a single anterior palatine foramen occurs in each maxilla adjacent to the posterior-most palatal exposure of the premaxillae.

The teeth of *K. obscurus* were significantly smaller in diameter than those of *K. pernix* (Figs. 14a, b). In *K. pernix,* throughout the tooth row, the alveoli have uniform diameter (3 mm) and nearly equal spacing. In *K. obscurus,* however, the alveoli that are still intact on the right side located just posterior to the mid-length of the rostrum are only 1.5 mm in diameter; one-half the size of those in *K. pernix.* The alveolar rows on both sides of the specimen of *K. obscurus* are incomplete because of breakage and abrasion. A row of eight consecutive alveoli in a distance of 32 mm in the right maxilla indicates that the species had more teeth than *K. pernix,* which Kellogg (1927a:32) estimated at about 40 on each side of each upper jaw. The alveoli of *K. obscurus* are oriented in the maxilla so that they face more laterally than in *K. pernix.* The alveolar rows do not extend as far posteriorly on the palate, and the posterior end of each tooth row curves medially toward the midline.

Posterior to the orbit, *K. obscurus* has a large, oval fossa in the ventral side of the supraorbital process of the frontal that measures approximately 15 by 20 mm. In modern delphinoids, a fossa in this location holds the postorbital lobe of the pterygoid air sinus (Fraser and Purves, 1960). We conclude that *K. obscurus* had a relatively large sinus here. On both the holotype and Kellogg's referred skull (USNM 10670) of *K. pernix,* there is only a slight depression at this place. This apparent difference in air sinus size is not clearly diagnostic because the juvenile referred skull, USNM 21027 of *K. pernix,* has a deep recess for the sinus at this place. Without a larger sample of specimens we cannot determine whether the size or the extent of invasion of bone by the sinus is variable in *K. pernix,* whether it is larger in geologically more recent individuals of *K. pernix* that occur higher in the Calvert Formation, or whether it is a significant taxonomic character that separates species.

Periotic. When Kellogg (1931) described *Grypolithax obscura* and *G. pavida* from the Sharktooth Hill Bonebed, he noted only a few differences between their holotypes. He noted that the periotics of *G. pavida* had a flatter cerebral surface. We now benefit from having a larger sample to study and find that, within the anticipated range of morphology of what we interpret as one species, the presence of a flat cerebral surface is variable.

Among the 31 isolated periotics from the Sharktooth Hill Bonebed that we refer to *Kentriodon obscurus,* there are at least six (LACM 63800, 48925, 21238, 41473, 75371, 123476) that are nearly identical in morphology to the periotic of the holotype of *K. pernix* (USNM 8060). Each of the others has some minor degree of difference. There was no periotic found with the skull we have referred to *K. obscurus,* and except for the holotype of *K. pernix,* there has been found only one other skull of *Kentriodon* sp. in the Calvert Formation that has an associated periotic. This specimen, USNM 187313, which we believe is a different and probably undescribed

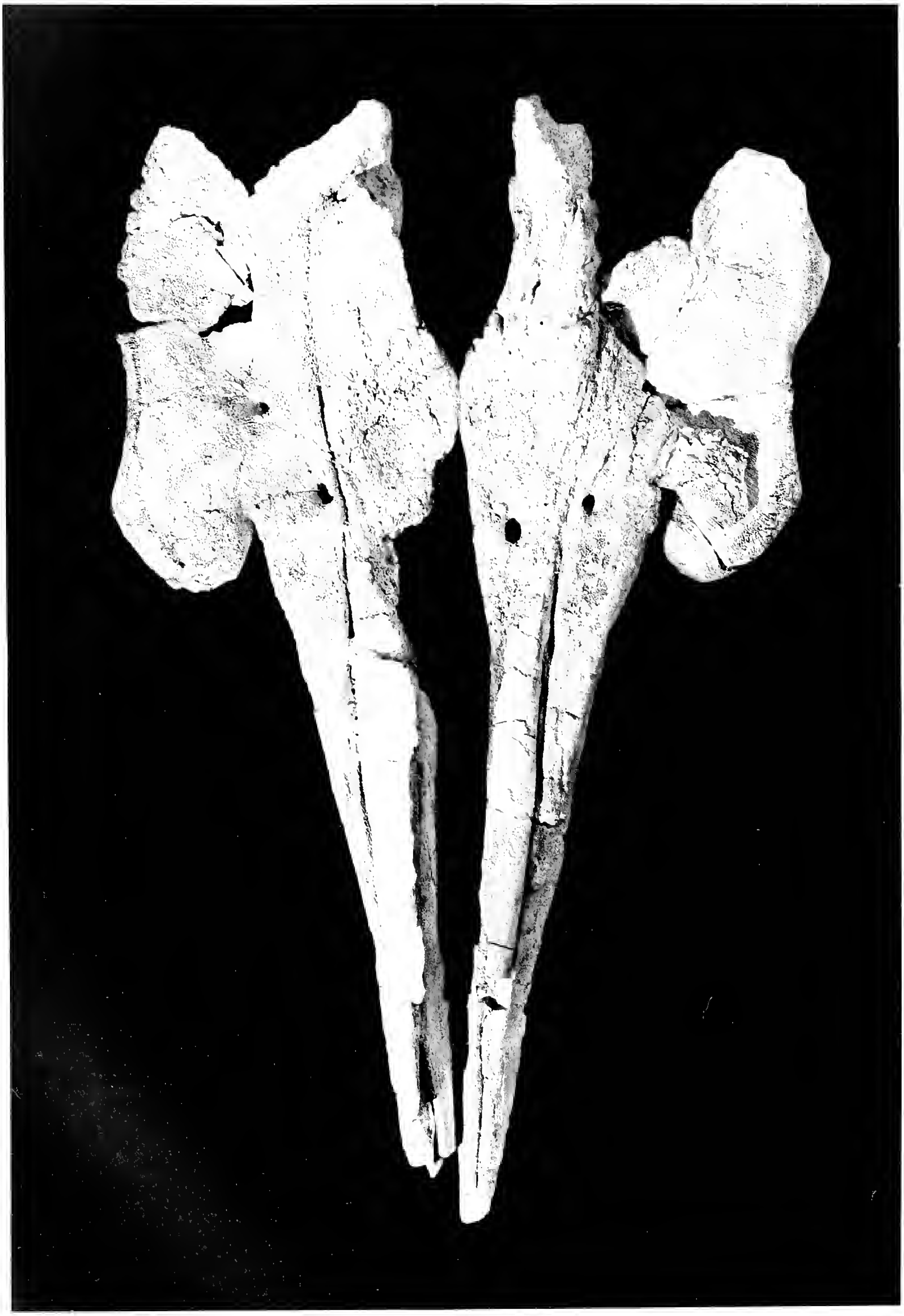


Figure 2. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, dorsal view, natural size.

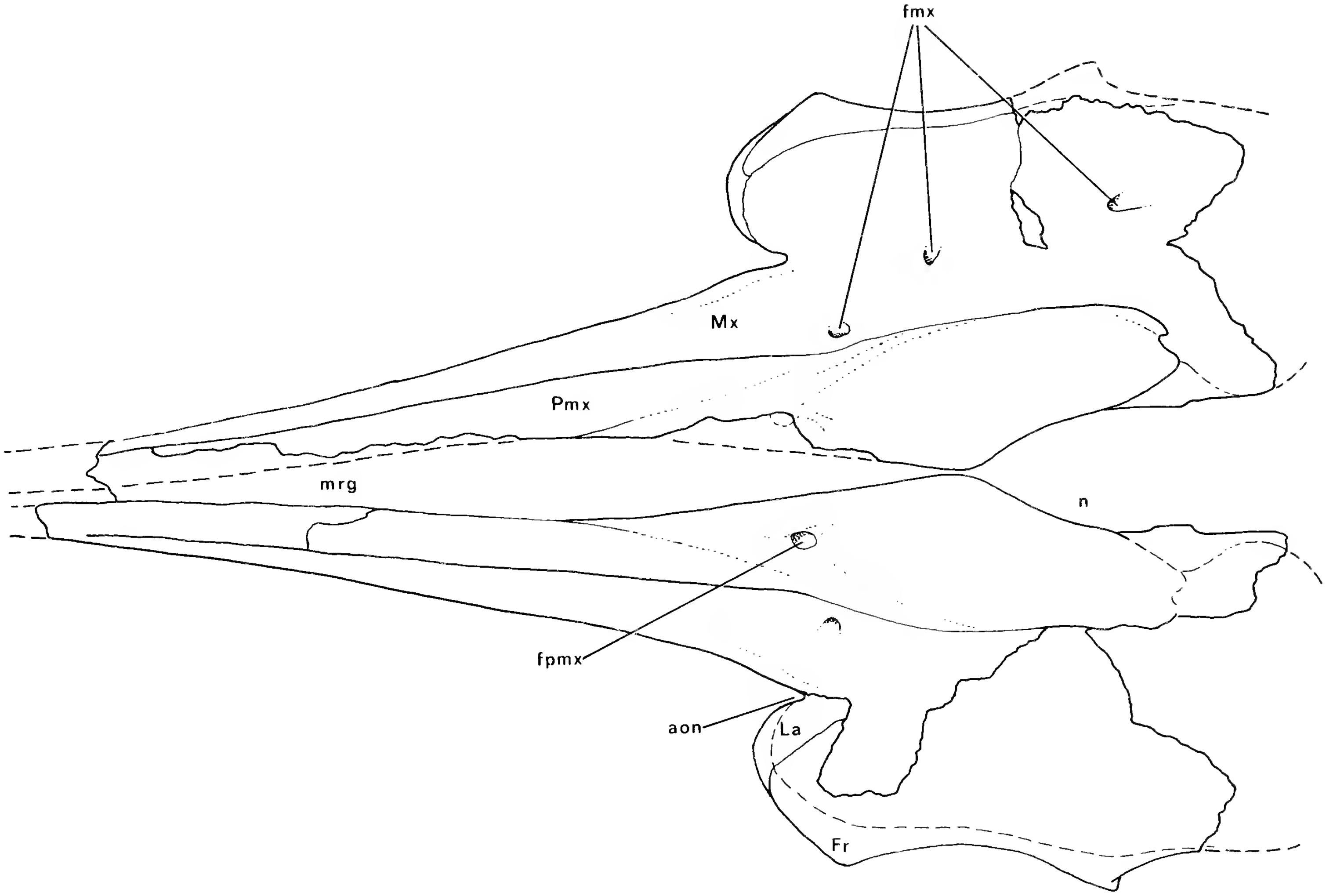


Figure 3. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, dorsal view, natural size. Abbreviations: aon—antorbital notch, fmx—maxillary foramen, fpmx—premaxillary foramen, Fr—frontal, La—lacrimal, mrg—mesorostral gutter, Mx—maxilla, n—narial opening, Pmx—premaxilla.

Figure 4. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, **a,** left lateral view; **b,** right lateral view, natural size.

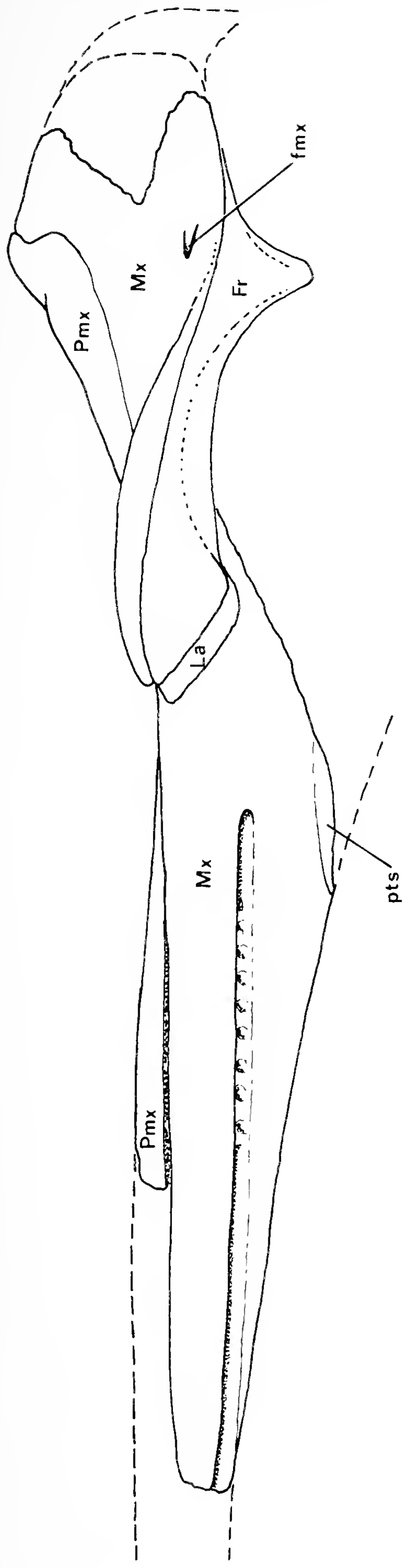


Figure 5. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, composite left lateral view based on both sides of skull, natural size. Abbreviations: fmx—maxillary foramen, Fr—frontal, La—lacrimal, Mx—maxilla, Pmx—premaxilla, pts—fossa for pterygoid sinus of the middle ear air sinus system.

Table 1. Some characters differentiating *Kentriodon pernix* and *K. obscurus*. An asterisk denotes the more derived character states, as deduced from the morphology of *Agorophius* and species of Squalodontidae.

Kentriodon obscurus	*Kentriodon pernix*
1. Premaxillary foramina between level of antorbital notches.	1. Foramina posterior to level of notches.*
2. Lateral maxillary margin anterior to antorbital notches thick and squared off.*	2. Lateral margin thin and rounded.
3. Antorbital notch narrow.	3. Antorbital notch wider.*
4. Premaxillae flat in area of attachment of nasal plug muscles.*	4. Premaxillae elevated medially.
5. Postorbital process of frontal short and thick.*	5. Process long and curved.
6. Alveoli for teeth small (circa 1.5 mm in diameter).	6. Alveoli larger (circa 3 mm in diameter).*
7. Posterior end of alveolar row bends medially on palate.	7. Posterior end of alveolar row follows lateral margin of palate.*
8. Teeth implanted in middle and posterior part of alveolar row so as to face ventrolaterally.*	8. Teeth face more ventrally.
9. Palatines and pterygoid air sinus fossae on palate extend farther anteriorly beyond location of antorbital processes.*	9. Palatines and fossae do not extend beyond level of antorbital processes.
10. Posterior part of palate lateral to fossae for pterygoid air sinus convex.	10. Palatal surface less convex.*
11. Large fossa in ventral surface of frontal for postorbital lobe of pterygoid air sinus.*	11. Fossa small or absent.
12. Internal acoustic meatus of periotic elliptical in shape.	12. Meatus circular in shape.*

species of *Kentriodon* was collected from Zone 14, near the top of the Calvert Formation, and the skull, periotic, and postcranial skeleton show several significant differences from the holotype and referred specimen of *K. pernix*. The periotic of this specimen, USNM 187313 (Figs. 8a, 9a), has a prominent, elevated, flat area on its cerebral surface that is more pronounced than on any of the other periotics referred to

Figure 6. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM 1625, ventral view, natural size.

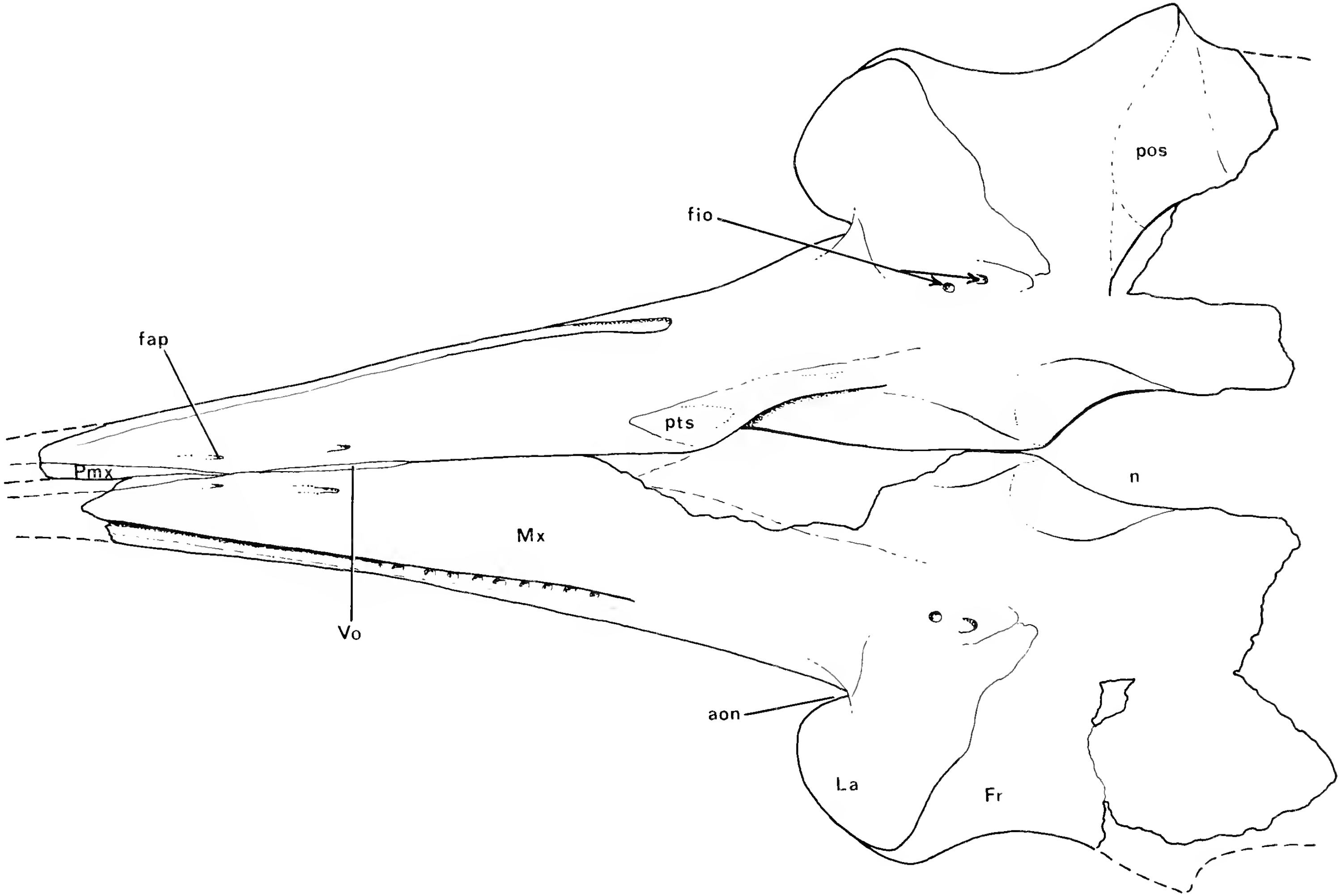


Figure 7. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, ventral view, natural size. Abbreviations: aon-antorbital notch, fap—anterior palatine foramen, fio—orbital apertures of the infraorbital foramen, Fr—frontal, La—lacrimal, Mx—maxilla, n—narial opening, pos—fossa for postorbital lobe of the pterygoid sinus of the middle ear air sinus system, Pmx—premaxilla, pts—fossa for pterygoid sinus of the middle ear air sinus system, Vo—cleft that originally contained the palatal exposure of the vomer.

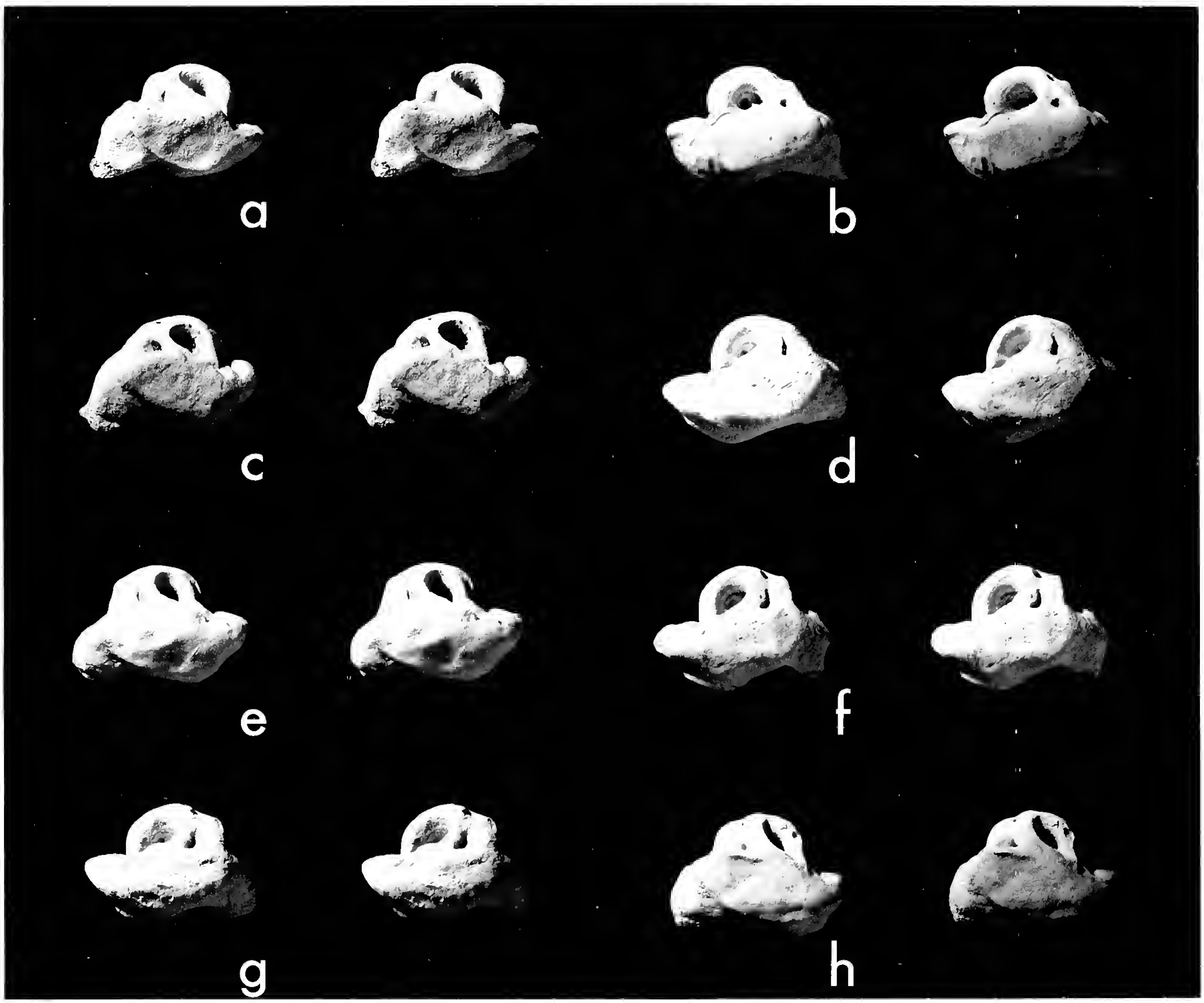
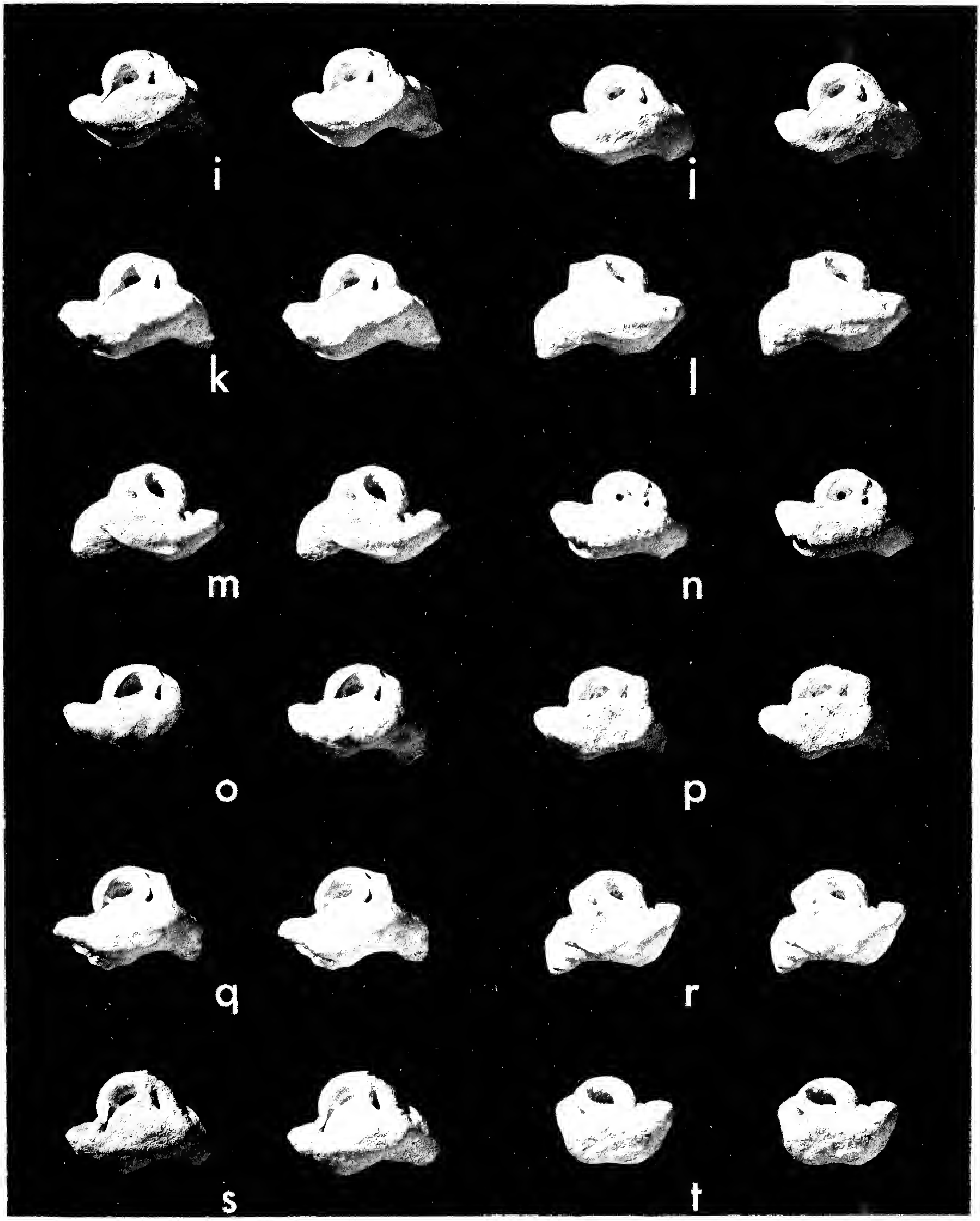


Figure 8. Periotics of *Kentriodon* Kellogg, 1927: **a,** *Kentriodon* sp., Calvert Fm., Virginia, USNM 187313, right; **b,** *Kentriodon pernix* Kellogg, 1927, holotype, USNM 8060, left; **c,** *Kentriodon* sp., Calvert Fm., Virginia, USNM 214754, right; *Kentriodon obscurus* (Kellogg, 1931) from the Sharktooth Hill Bonebed; **d,** LACM 41473, left; **e,** CAS 4349, holotype, right; **f,** CAS 4348, left (holotype of *Grypolithax pavida* Kellogg, 1931); **g,** CAS 4350, left (paratype of *Grypolithax pavida*); **h,** LACM 75371, right; **i,** LACM 63800, left; **j,** LACM 48925, left; **k,** CAS 4347, paratype, left; **l,** LACM 21238, right; **m,** LACM 121998, right; **n,** LACM 58893, left; **o,** LACM 104094, left; **p,** LACM 44916, left; **q,** LACM 98712, left; **r,** LACM 21134, right; **s,** LACM 39696, left; **t,** LACM 96150, right; all figures are stereophotographs of the cerebral (or dorsal) surface, natural size.

Kentriodon. Such a flat surface is present, however, in varying lesser degrees on eight of the periotics from the Sharktooth Hill Bonebed referred to *K. obscurus* (including the holotype of *Grypolithax pavida*), as well as on the holotype periotic of *K. pernix.* Another isolated periotic (USNM 214754, Figs. 8c, 9c) from the Calvert Formation in Virginia closely matches the holotype periotic of *K. pernix,* and although it has a more rounded cerebral surface, we refer it to that species.

All of the periotics from the Sharktooth Hill Bonebed that we refer to *Kentriodon obscurus* resemble the holotype periotic of *K. pernix* by having the following characters: (1) similar size; (2) relatively small anterior and posterior processes; (3) an overall sinuosity in either cerebral or ventral view owing to the fact that the anterior process is bent medially and the posterior process is bent laterally; (4) cochlear portion relatively small and broadly joined to the body of the periotic, not narrowly joined to the body and extended medially as in many primitive odontocetes; (5) posterior process bent ventrally at a sharp angle from the body of the periotic thereby forming a sharp peak or angle on the posterior part of the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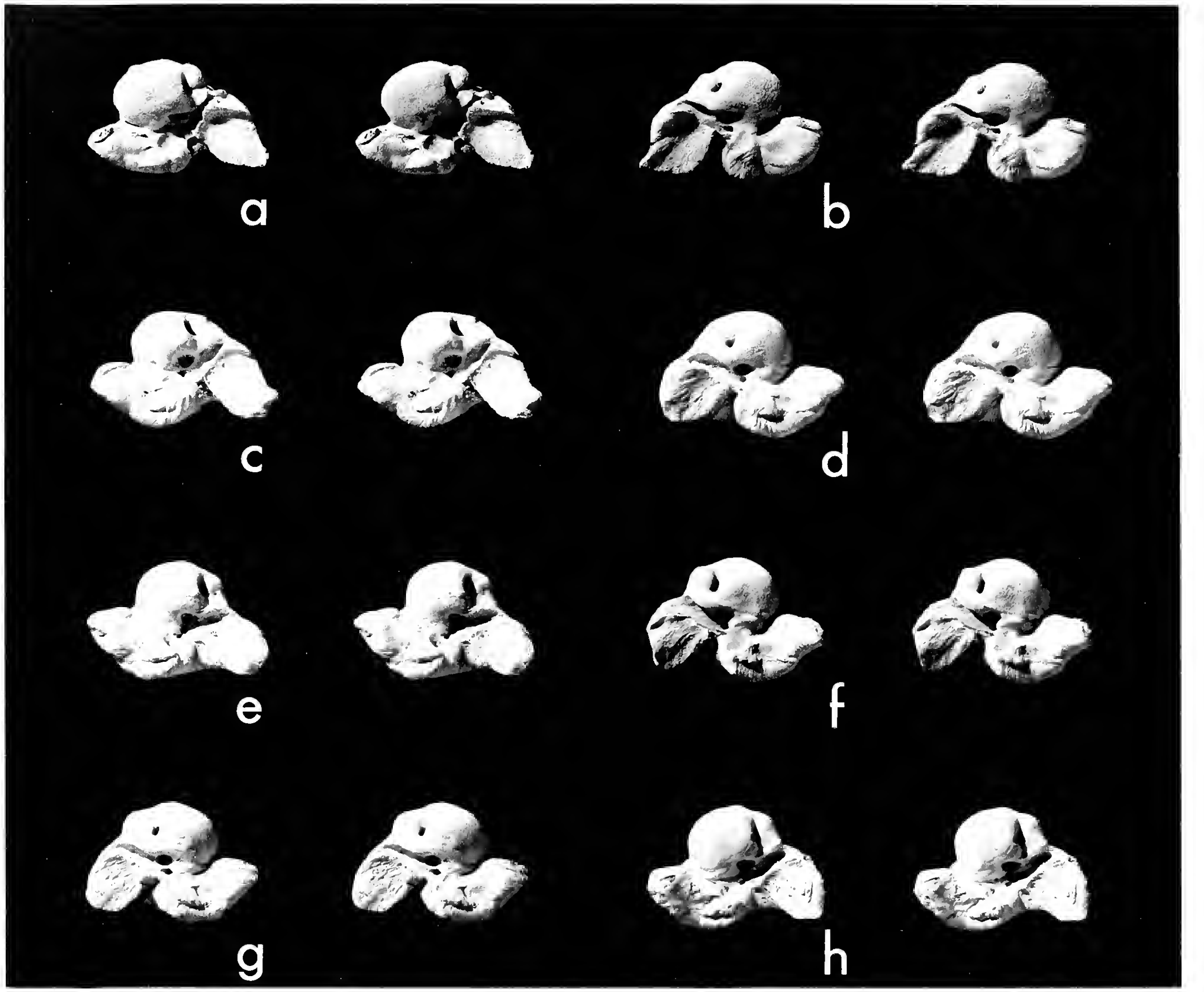

Figure 9. Periotics of *Kentriodon* Kellogg, 1927: **a,** *Kentriodon* sp., Calvert Fm., Virginia, USNM 187313, right; **b,** *Kentriodon pernix* Kellogg, 1927, holotype, USNM 8060, left; **c,** *Kentriodon* sp., Calvert Fm., Virginia, USNM 214754, right; *Kentriodon obscurus* (Kellogg, 1931) from the Sharktooth Hill Bonebed; **d,** LACM 41473, left; **e,** CAS 4349, holotype, right; **f,** CAS 4348, left (holotype of *Grypolithax pavida* Kellogg, 1931); **g,** CAS 4350, left (paratype of *Grypolithax pavida*); **h,** LACM 75371, right; **i,** LACM 63800, left; **j,** LACM 48925, left; **k,** CAS 4347, paratype, left; **l,** LACM 21238, right; **m,** LACM 121998, right; **n,** LACM 58893, left; **o,** LACM 104094, left; **p,** LACM 44916, left; **q,** LACM 98712, left; **r,** LACM 21134, right; **s,** LACM 39696, left; **t,** LACM 96150, right; all figures are stereophotographs of the tympanic (or ventral) surface, natural size.

cerebral surface; (6) anterior process bent anteroventrally and having a groove or pit on its medial side; (7) the cleft between the anterior process and the cochlear portion bearing a small crease between the groove for the tensor tympani muscle and the cochlear portion; (8) articular facet for the auditory bulla on the posterior process large, concave and striated; and (9) a raised rugosity lateral to the fossa for the head of the malleus.

Statistical analysis of the Sharktooth Hill Bonebed sample of *K. obscurus* periotics (Table 2) proved useful. The parameters chosen were width and length measurements. The measurement of the cochlear portion is probably less variable individually or allometrically than the other two, because the sizes of the anterior and posterior processes apparently change during ontogeny. Measurements of the holotype of *K. obscurus* fall within the range of measurements for the sample, and they differ from the mean less than the standard deviation in all three parameters. The same situation exists when

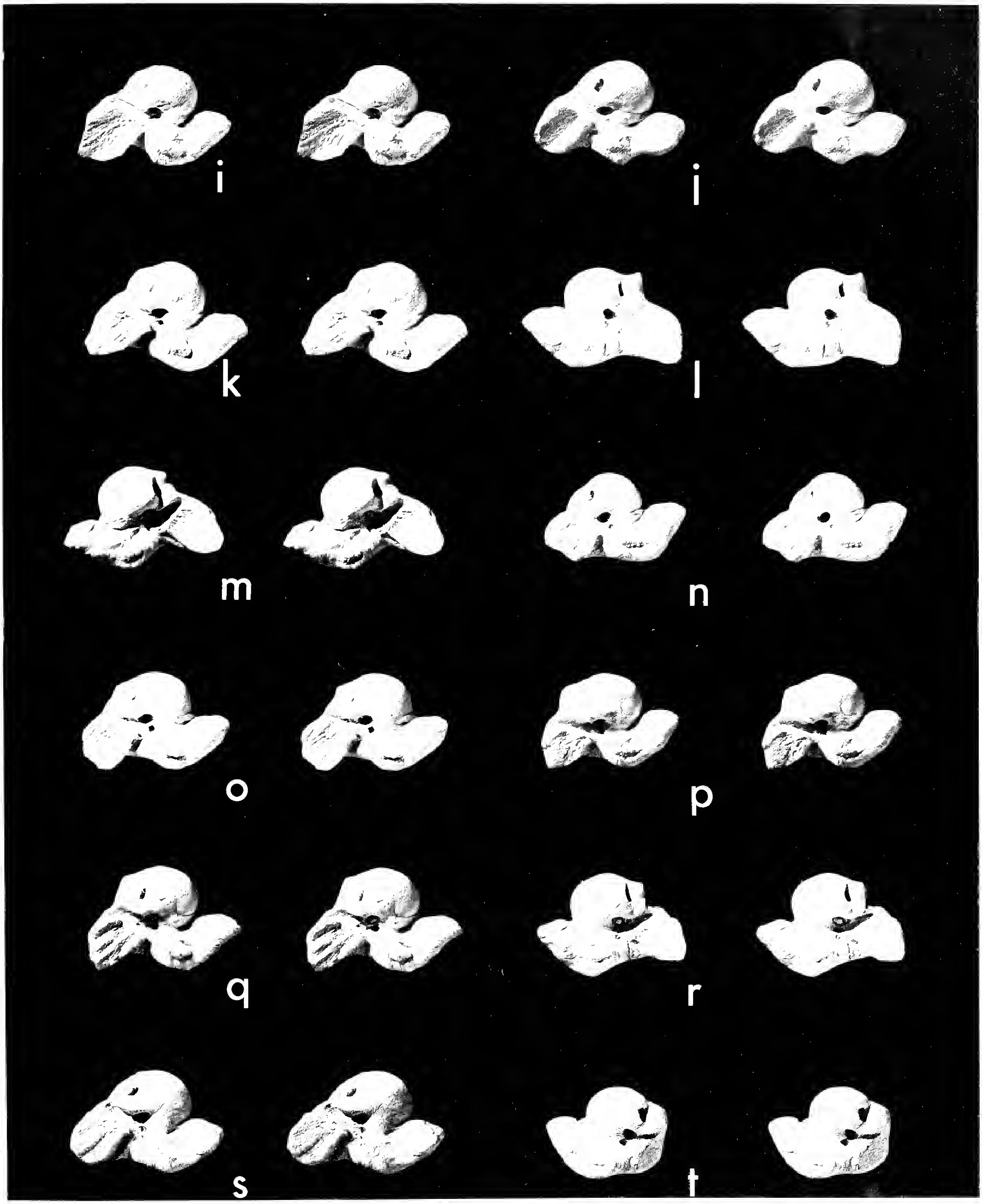
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Table 2. Statistical comparisons of the holotype periotic of *Kentriodon pernix* and the holotype and referred periotics of *K. obscurus* from the Sharktooth Hill Bonebed.

	Bonebed sample of *K. obscurus**					*K. obscurus* holotype		*K. pernix* holotype	
Measurement	Number	Observed range	Mean	Standard deviation	Coefficient of variation	Measurement	Difference from mean	Measurement	Difference from mean
Total length	27	25.2–29.4	27.2	1.2	4.41	26.9	−0.3	28.3	1.1
Width at pars cochlearis	29	16.5–19.5	18.0	0.8	4.44	18.2	0.2	17.4	−0.6
Antero-posterior dimension of pars cochlearis	28	13.2–15.9	14.7	0.7	4.76	14.1	−0.6	14.2	−0.5

* Sample includes paratype of *K. obscurus* and holotype and paratype of *Grypolithax pavida.*

the holotype of *K. pernix* is compared to the sample of *K. obscurus,* except that it differs somewhat more from the mean than does the holotype of *K. obscurus,* but is still within the standard deviation.

The similarities among these periotics from the Atlantic and Pacific coasts are not surprising. Kasuya (1973:72) and Barnes (1976:321–322, 327) have pointed out that periotics of congeneric species of cetaceans are very similar and that in some instances closely related modern or fossil species simply may not be differentiated based on periotics alone.

Among the periotics of *K. obscurus,* some characters are variable. These are: (1) shape and relative size of the posterior articular facet for the bulla; (2) degree of rugosity of this articular facet; (3) position of the groove or pit on the medial side of the anterior process; (4) presence or absence of a tuberosity on the posterior side of the cochlear portion between the *fenestra rotunda* and the orifice of the *aquaeductus cochleae;* (5) extent of development of an attenuated groove in the anterior margin of the internal acoustic meatus at the cerebral orifice of *aquaeductus Fallopii;* and (6) extent of development of a flat area on the cerebral surface of the body of the periotic in contrast with a rounded, convex surface. The only character that we recognize whereby the holotype periotic of *Kentriodon pernix* may be separated from this sample of periotics of *K. obscurus* is its more circular internal acoustic meatus. Every other character exists in at least one of the periotics from the Sharktooth Hill Bonebed that we refer to *K. obscurus.*

The only other significantly large, documented sample of periotics of a species of Kentriodontidae is the series of *Liolithax kernensis* from the Sharktooth Hill Bonebed that was described and analyzed by Barnes (1978). The periotics from the bonebed that we now refer to *Kentriodon obscurus* are as variable as the sample Barnes referred to *L. kernensis.* These periotics are not referable to any of the other odontocetes that Kellogg (1931) named based upon periotics from the Sharktooth Hill Bonebed.

Among these other species, the problematic odontocete *Platylithax robusta* Kellogg, 1931, the primitive sperm whale *Aulophyseter morricei* Kellogg, 1927, the platanistoid dolphin "*Squalodon*" *errabundus* Kellogg, 1931, and the kentriodontid dolphin *Liolithax kernensis* all have periotics that are substantially different from those belonging to *Kentriodon.* Periotics of another dolphin, *Loxolithax sinuosa* Kellogg, 1931, differ subtly by being flatter dorsoventrally, having a larger cochlear portion, a differently shaped posterior process, a larger fossa for the head of the malleus, a groove on the lateral surface of the anterior process, and by lacking any notable flattening of the cerebral surface. Periotics of the two species of *Lamprolithax* Kellogg, 1931, differ from those of *Kentriodon* in many of the same ways as do those of *Loxolithax sinuosa. Nannolithax gracilis* Kellogg, 1931, has a smaller periotic with a large anterior process. *Oedolithax mira* Kellogg, 1931, has a larger periotic with a deeper cleft separating the anterior process from the cochlear portion.

cf. *Kentriodon* sp.

Figures 10–11

cf. *Kentriodon* Kellogg, 1927. Barnes, 1976:326.

REFERRED SPECIMENS. LACM 29549, left periotic, collected by Richard W. Huddleston in 1969 from LACM locality 3066, Kern River, Kern County, California; and UCMP 83605, right periotic, collected by Richard C. Bishop from UCMP locality V-6953, Kern County, California.

FORMATION AND AGE. Both of these specimens are from localities stratigraphically below the Sharktooth Hill Bonebed in the lower part of the Round Mountain Silt. This part of the formation is early Middle Miocene in age, about 15 to 19 million years old (see Barnes, 1976:326). Savage and Barnes (1972:133) have reported Hemingfordian land mammals from these same strata. Addicott (1972) characterized the age of these beds further as representing part of the "Temblor" provisional provincial molluscan stage and the upper part of the Saucesian or the Relizian foraminiferal stage.

DESCRIPTION AND COMPARISONS. These two periotics differ from each other in both size and morphology and may actually represent two different species. Each shares characters in common with both *Kentriodon obscurus* and *K. pernix,* such as the strong apex on the cerebral surface

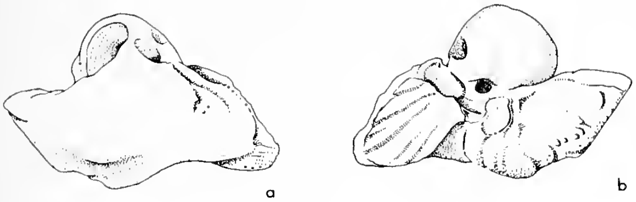

Figure 10. cf. *Kentriodon* sp., left periotic, LACM 29549 from LACM locality 3066; **a,** cerebral or dorsal view; **b,** tympanic or ventral view; both natural size.

posterolateral to the orifice of *aquaeductus vestibuli,* small internal acoustic meatus, and anteromedially projecting anterior process—all characters that could be regarded as primitive. The smaller of the two periotics, UCMP 83605, has an anteroposteriorly elongate cochlear portion as in other specimens of *Kentriodon.* The larger periotic, LACM 29549, has a relatively smaller and more globose cochlear portion, and in this respect it resembles the holotype periotic of the primitive kentriodontid *Kampholophos serrulus* Rensberger, 1969 (see Rensberger, 1969: pl. 4, figs. f–h).

aff. *Delphinodon dividum* True, 1912

Figure 12

cf. *Delphinodon dividum* True, 1912. Barnes, 1976:326.

REFERRED SPECIMEN. LACM 41041, left periotic with stapes, lacking extremity of posterior process, collected by the late John E. Fitch, about 1970 from LACM locality 6602, "Barker's Ranch Faunal Site," Kern County, California.

FORMATION AND AGE. This specimen is from a locality in the lower part of the Round Mountain Silt, below the Sharktooth Hill Bonebed, in roughly the same strata as the two previously described periotics. Its age is likewise early Middle Miocene and between approximately 15 and 19 million years old.

DESCRIPTION AND COMPARISONS. The comparisons that we have made are specifically only with *Delphinodon dividum,* because that is the only species of the genus for which a periotic is known. The holotype is a specimen collected from the Calvert Formation and includes a skull, mandible, and part of the postcranial skeleton. The type species of the genus, *D. mento* Cope, 1868, as fixed by Hay (1902), is known only by teeth.

As noted by Barnes (1976:326) this periotic closely resembles that of *Delphinodon dividum. Kentriodon* spp. and *Delphinodon dividum* are closely related (cf. Kellogg, 1927a, 1928: 67–69; Slijper, 1936:556), and both have been classified in the subfamily Kentriodontinae (Barnes, 1978). The periotic with the holotype of *Delphinodon dividum* (see True, 1912; pl. 25, figs. 6, 7) has many characters in common with the isolated periotic (LACM 41041) from Kern County. Notable among these are the large fossa for the head of the malleus, the globose anterior process which is bent medially, and the small, spherical cochlear portion. The periotic of *D. dividum* is somewhat similar in overall shape to periotics of *Kentriodon obscurus* and *K. pernix,* but differs by not having the cochlear portion as broad anteroposteriorly, by having the anterior process bent more medially, and by having the cochlear portion separated from the anterior process by a much deeper fissure. The isolated periotic from Kern County (LACM 41041) differs from the holotype of *D. dividum* by being smaller, having a relatively smaller posterior articular facet for the bulla, and by having a relatively smaller and narrower internal acoustic meatus. The latter character may be primitive in comparison with *D. dividum.* We believe this isolated periotic from the Round Mountain Silt is congeneric with *Delphinodon dividum* and represents an earlier, more primitive species.

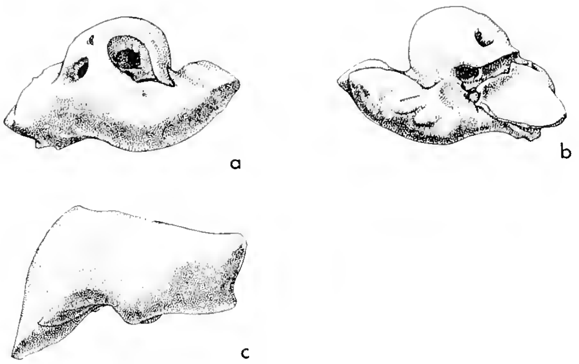

Figure 11. cf. *Kentriodon* sp., right periotic, UCMP 83605 from UCMP locality V-6953; **a,** cerebral or dorsal view; **b,** tympanic or ventral view; **c,** lateral view; all natural size.

A very closely related, if not identical, species is represented by a periotic from correlative rocks in Japan. Okazaki (1976:37–38, text-fig. 6, pl. 11, figs. 1a–c (where the scale is incorrect)) has identified that periotic, collected from the late Early or early Middle Miocene Nataki Formation, as a rhabdosteid dolphin, *Eurhinodelphis* sp. B. We do not concur with that generic allocation because the periotic described by Okazaki does not closely resemble periotics found in skulls of *Eurhinodelphis* spp. collected from the Calvert Formation in Maryland and Virginia (USNM collections). Instead, we believe the periotic from Japan very closely resembles the periotic of *Delphinodon dividum,* and the one from California that we identify here as aff. *Delphinodon dividum,* although it apparently is considerably larger than the latter. We conclude that the specimen from the Nataki Formation should

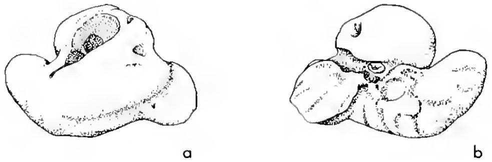

Figure 12. aff. *Delphinodon dividum* True, 1912, left periotic, LACM 41041 from LACM locality 6602; **a,** cerebral or dorsal view; **b,** tympanic or ventral view; both natural size.

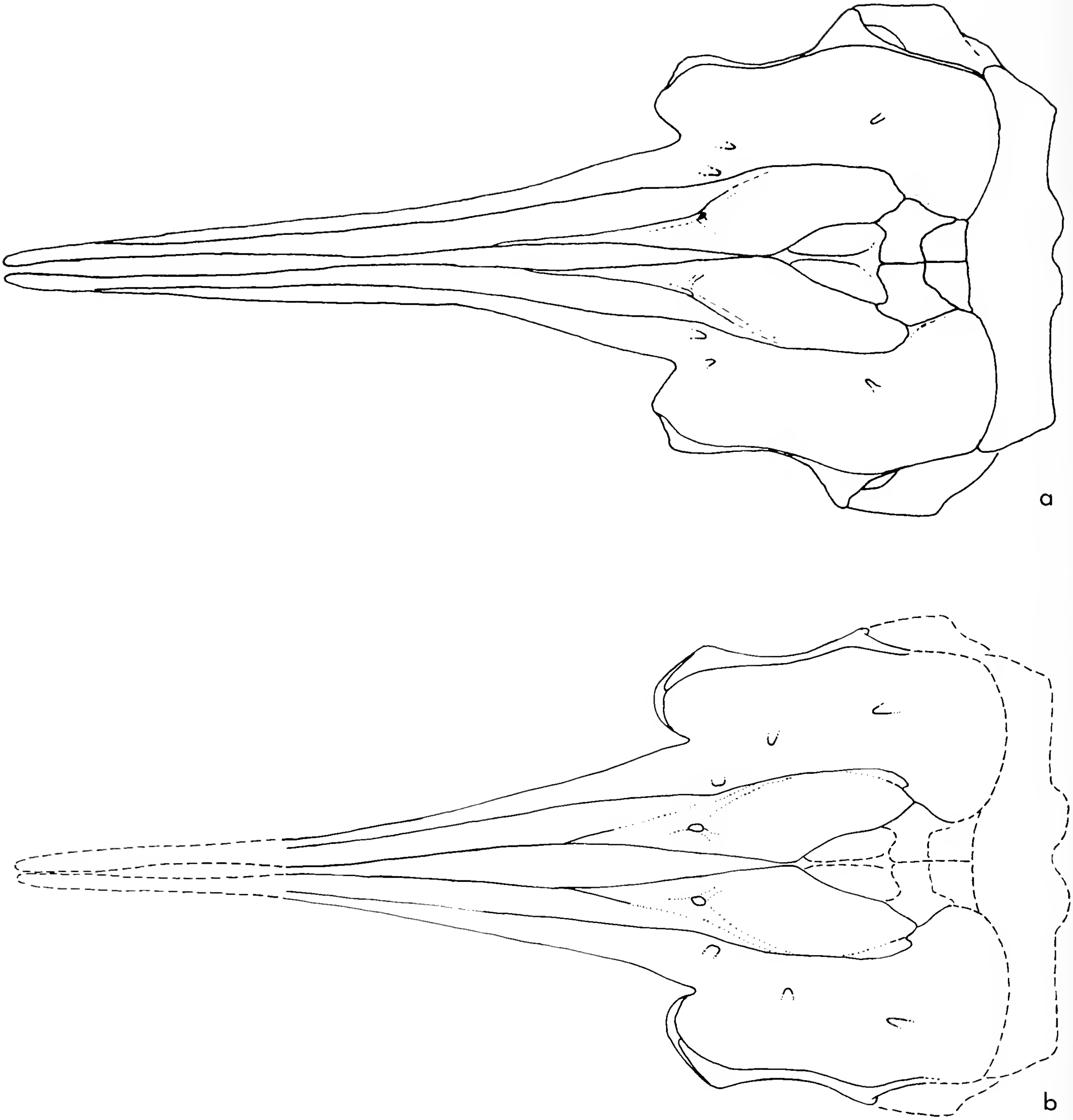

Figure 13. Reconstructions of dorsal views of skulls of *Kentriodon* Kellogg, 1927; **a,** *Kentriodon pernix* Kellogg, 1927, based on the holotype, USNM 8060, and the referred specimen, USNM 10670; **b,** *Kentriodon obscurus* (Kellogg, 1931), based on the referred specimen, LACM 21256, with outline of the rostral extremity and brain case from *K. pernix;* both at different scales, but reduced to the same brain case length (antorbital notches to condyles). (**a** from Kellogg, 1927: pls. 2, 6, and Barnes, 1978: fig. 14, c; **b** from our Fig. 2.)

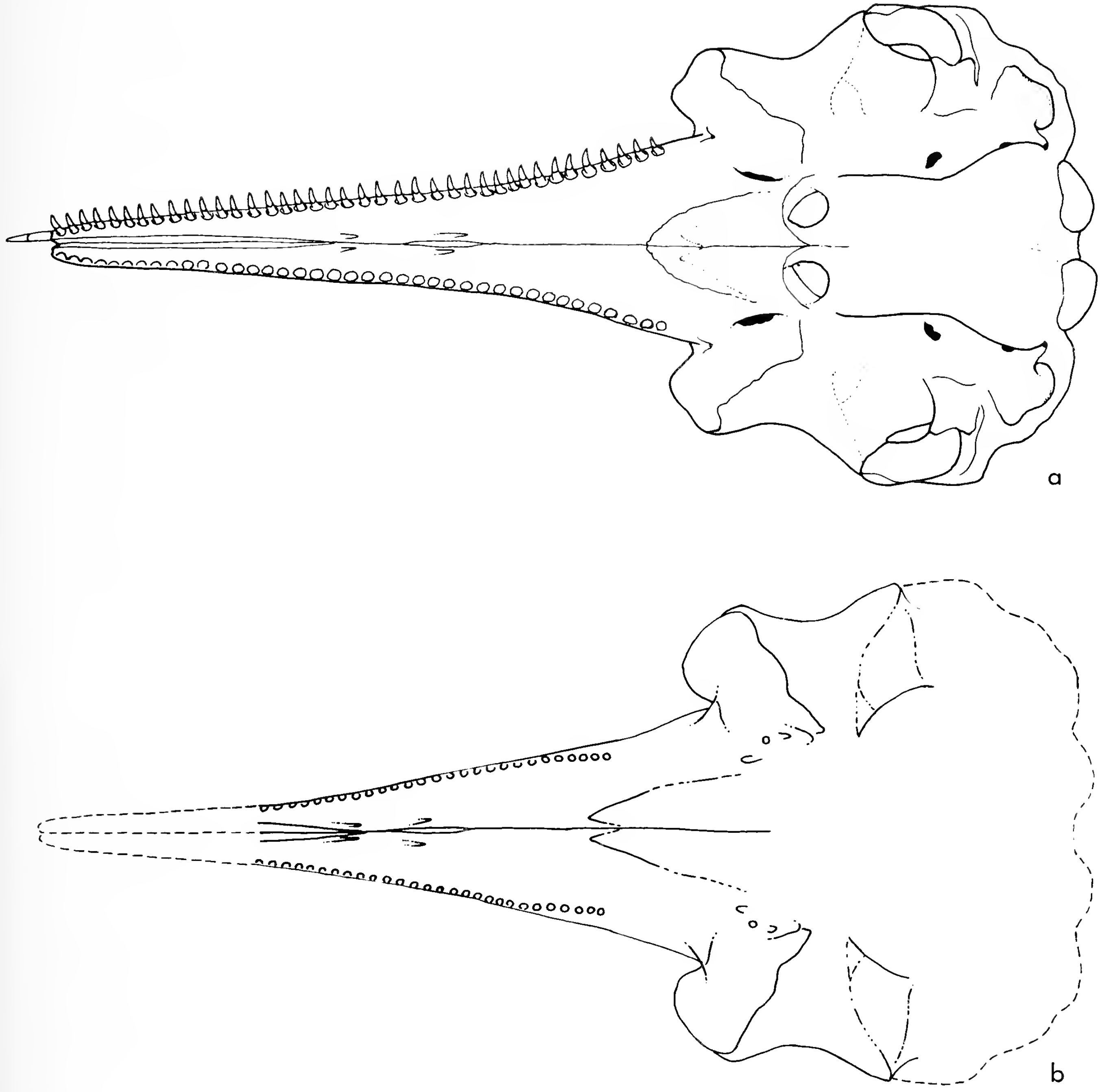

Figure 14. Reconstructions of ventral views of skulls of *Kentriodon* Kellogg, 1927; **a**, *Kentriodon pernix* Kellogg, 1927, based on the holotype, USNM 8060, and the referred specimen, USNM 10670, with the dentition omitted on one side so that the size and number of alveoli may be seen; **b**, *Kentriodon obscurus* (Kellogg, 1931), based on the referred specimen LACM 21256, with outline of the rostral extremity and brain case from *K. pernix;* both at different scales, but reduced to the same brain case length. (**a** from Kellogg, 1927: pls. 4, 5, 7 and 8; **b** from our Fig. 6.)

be re-identified as Kentriodontinae, aff. *Delphinodon dividum.*

DISCUSSION

RELATIVE ABUNDANCE OF *KENTRIODON OBSCURUS* IN THE SHARKTOOTH HILL BONEBED

A list of 15 odontocetes in the Sharktooth Hill Bonebed given by Barnes (1976:327, table 3) included 11 named species and four possibly undescribed species. *Grypolithax pavida* may now be deleted from that list because it is a synonym of *K. obscurus.* Each of the 14 remaining species is recognized by periotics. Some of the species in polytypic genera that are known only by periotics may be questionably valid (Barnes, 1976:327). The abundant sperm whale, *Aulophyseter morricei,* with quite distinctive periotics, is known by other skeletal elements. The platanistoid "*Squalodon*" *errabundus* also has distinctive periotics and is known from other skeletal elements, however, it is relatively rare in the bonebed, and we (unpublished data) have been able to collect or locate only 31 of the highly unique periotics of that species. Similarly, the distinctive periotics of the kentriodontid *Liolithax kernensis* total only 42 in number (Barnes, 1978). Only *Platylithax robusta,* known solely by the holotype, and the other four unidentified odontocete species are rarer in samples than *Kentriodon obscurus.* The total sample of *K. obscurus* amounts to only one skull and 31 periotics, and on this evidence the species ranks as one of the rarest odontocetes in the Sharktooth Hill Bonebed. The remaining hundreds of periotics in museum collections can be identified as belonging to species of the genera *Loxolithax* Kellogg, 1931, *Oedolithax* Kellogg, 1931, *Lamprolithax,* or *Nannolithax* Kellogg, 1931.

ZOOGEOGRAPHY

Fossil Kentriodontidae have been reported from the North Atlantic, the South and North Pacific, and the Paratethys regions. All the species included by Barnes (1978:26) in this family were Middle or Late Miocene in age. Fordyce (1980: 328) has subsequently reported a kentriodontid from Late Oligocene rocks of New Zealand. The fossils from early Middle Miocene rocks in California identified as cf. *Kentriodon* sp. and aff. *Delphinodon dividum* in this paper constitute the earliest records for the family in the North Pacific region. These, along with the sample we regard as *Kentriodon obscurus* from the Sharktooth Hill Bonebed, the kentriodontids from Japan, and Late Miocene species from California (Barnes, 1976) suggest that a considerable diversity of species in this family inhabited the North Pacific Ocean during the Miocene. This diversity equals that known for kentriodontids during the Middle and Late Miocene in the North Atlantic and Paratethys regions (see Barnes, 1978:26). The family might have been cosmopolitan during the Miocene, but there are as yet no kentriodontids recognized from the South Atlantic realm or from the eastern South Pacific. It would be premature to speculate on the place of origin of the family, even though the oldest known occurrence is in the South Pacific.

Barnes (1976:338) noted that the then available paleontologic literature suggested a pattern of generic cosmopolitanism among larger fossil late Tertiary cetaceans and one of generic endemism within major northern ocean basins among the smaller fossil odontocetes. Among the nine currently recognized genera of Kentriodontidae (cf. Barnes, 1978: 26), more than one-half (i.e. *Liolithax* Kellogg, 1931, *Kentriodon, Delphinodon* Leidy, 1869, *Pithanodelphis* Abel, 1905, and *Lophocetus* Cope, 1868) are now known by species in both the North Atlantic and the North Pacific regions. For the Kentriodontidae, it now appears that within ocean basins a pattern of endemism at the species level rather than the generic level prevailed.

PHYLOGENETIC RELATIONSHIPS

Kentriodon is the most primitive genus yet assigned to the subfamily Kentriodontidae. For example, *Kentriodon* lacks such derived characters as the elevated cranial vertex and enlarged nasal bones of *Pithanodelphis,* and the short rostrum, bulbous braincase and rounded facial margins of *Delphinodon dividum.* The cranial morphology of *Kentriodon* suggests that its origin might have been among more primitive species in the subfamily Kampholophinae. *Kentriodon* shares with the kampholophine species *Liolithax pappus* and *Kampholophos serrulus* such primitive characters as a narrow, elongate rostrum, high tooth count, low cranial vertex, and a concave margin of the facial region above the orbit. *Kentriodon* is more derived, however, than either of those species, by having facial surfaces of the frontal and the maxilla that are spread more over the dorsal opening of the temporal fossa. The extent of this spreading, however, had not progressed to the stage seen in the derived kentriodontine genera *Delphinodon, Leptodelphis* Kirpichnikov, 1954, *Microphocaena* Kudrin and Tatarinov, 1965, *Pithanodelphis* and *Sarmatodelphis* Kirpichnikov, 1954.

There are possibly relationships between Kentriodontinae and primitive modern Delphinidae, such as species in the subfamily Steninae (*sensu* Mead, 1975), and this has been discussed previously by True (1912), Kellogg (1927), and Barnes (1978). Similarities exist in overall cranial proportions, shape of the mandible, and size and numbers of teeth, but kentriodontines are more primitive by having symmetrical cranial vertices, less extensive air sinuses and unfused cervical vertebrae.

The two essentially synchronous species, *Kentriodon pernix* and *K. obscurus,* have different combinations of both primitive and derived characters (see Table 1). For example, *K. pernix* is more derived than *K. obscurus* by having the premaxillary foramina located more posteriorly (Fig. 13), and the posterior part of the palate less convex on either side of the pterygoid sinuses. *Kentriodon obscurus,* on the other hand, is more derived by having shorter postorbital processes of the frontals, smaller teeth (Fig. 14), medial premaxillary surface in front of the nares not inclined, a longer anterior extension of the palatine bones on the palatal surface and of the pterygoid air sinuses within the pterygoid hamuli, and a larger postorbital lobe of the pterygoid air sinus. The derived character states listed in Table 1 are equally spread between the two species. The polarity of these characters was determined by comparisons with species in the more primitive odontocete families, Squalodontidae and Agorophiidae.

Kentriodon pernix and *K. obscurus* might have evolved from a common ancestor, and the discoveries of the older fossils of kentriodontines in California certainly indicate that such *Kentriodon*-like dolphins lived prior to Middle Miocene time in the North Pacific Ocean.

CONCLUSIONS

A fossil delphinoid genus, *Kentriodon* Kellogg, 1927, that is uncommon in northwest Atlantic Middle Miocene rocks, occurs in contemporaneous rocks on the eastern margin of the North Pacific Ocean. A few fossils from the North Pacific margin identified as this genus or related genera of small dolphins have been briefly cited in previous literature, and it is shown here that the genus *Grypolithax* Kellogg, 1931, originally based on specimens from the Middle Miocene Sharktooth Hill Bonebed in California, is synonymous with *Kentriodon*. Based on isolated fossil periotics, Kellogg (1931) had named two species in *Grypolithax, G. obscura* Kellogg, 1931, and *G. pavida* Kellogg, 1931. These are the only species that have ever been assigned to *Grypolithax* and we regard them as synonymous. *G. obscura* has page priority, is the senior synonym of *G. pavida,* and is the type species of the genus. Because *Grypolithax* is not valid, the most appropriate binomen for the species from the Sharktooth Hill Bonebed is *Kentriodon obscurus* (Kellogg, 1931). We refer periotics and a partial skull to this species. The only other named species of *Kentriodon* is the type species, *K. pernix* Kellogg, 1927, from the Calvert Formation in Maryland.

Among possibly as many as 14 species of odontocetes found in the Sharktooth Hill Bonebed, *K. obscurus* is not abundant and is one of the rarest species. Only one of the rarer ones, *Platylithax robusta* Kellogg, 1931, has been named previously in the scientific literature. The other four have not been named, although Barnes (1976) has called attention to their presence. Only by increasing the total sample size will we be able to eventually recognize the rarer species in the Sharktooth Hill Local Fauna and learn their anatomy.

Middle Miocene fossils of *Kentriodon* have now been reported from Maryland and California in the U.S.A., and apparently also from Japan. The earliest reported kentriodontine fossils from the eastern North Pacific region are two isolated periotics we have identified as cf. *Kentriodon* sp. from the early Middle Miocene part of the Round Mountain Silt, lower stratigraphically than the Sharktooth Hill Bonebed. *Kentriodon* may have been a cosmopolitan genus in the Middle Miocene, but there is yet no published fossil evidence from the southern hemisphere to prove this.

Each of the two known species of *Kentriodon* has a different suite of primitive and derived characters, and the two are probably derived from a common ancestor.

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LITERATURE CITED

Abel, O. 1905. Les odontocètes du Boldérien (Miocène supérieur) d'Anvers. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 3(2):1–155.

Addicott, W.O. 1972. Provincial middle and late Tertiary molluscan stages, Temblor Range, California. Pages 1–26 *in* E.H. Stinemeyer, ed., Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium, Society of Economic Paleontologists and Mineralogists. 364 pp.

Barnes, L.G. 1976. Outline of eastern North Pacific fossil cetacean assemblages. Systematic Zoology 25(4):321–343.

———. 1978. A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odontoceti). Natural History Museum of Los Angeles County Science Bulletin 28:1–35.

Berggren, W., and J.A. Van Couvering. 1974. The late Neogene. Biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences. Palaeogeography, Palaeoclimatology and Palaeoecology 16(1/2):i–xi, 1–216.

Boenninghaus, G. 1904. Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung. Eine biologische Studie. Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere 19:189–360, pls. 12–13.

Clark, W.B., G.B. Shattuck, and W.H. Dall. 1904. The Miocene Deposits of Maryland. Pages xxi–xxxii *in* W.B. Clark, ed., Maryland Geological Survey—Miocene, Baltimore, The Johns Hopkins Press.

Cope, E.D. 1868a (for 1867). (Descriptions of *Eschrichtius cephalus, Rhabdosteus latiradix, Squalodon atlanticus* and *S. mento.*) Proceedings of the Academy of Natural Sciences, Philadelphia 19:131–132.

———. 1868b (for 1867). An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States. Proceedings of the Academy of Natural Sciences, Philadelphia 19:138–156.

Denker, A. 1902. Zur Anatomie des Gehörorgans der Cetacea. Anatomische Hefte 19(2):423–448, pls. 14–15.

Evernden, J.F., D.E. Savage, G.H. Curtis, and G.T. James. 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. American Journal of Science 262:145–198.

Fordyce, R.E. 1980. Whale evolution and Oligocene southern ocean environments. Palaeogeography, Palaeoclimatology and Palaeoecology 31:319–336.

———. 1981. Systematics of the odontocete whale *Agorophius pygmaeus* and the family Agorophiidae (Mammalia: Cetacea). Journal of Paleontology 55(5):1028–1045.

Fraser, F.C., and P.E. Purves. 1960. Hearing in cetaceans. Evolution of the accessory air sacs and the structure and function of the outer and middle ear in Recent cetaceans. Bulletin of the British Museum (Natural History), Zoology 7(1):1–140, frontispiece, pls. 1–53.

Gazin, C.L., and R.L. Collins. 1950. Remains of land mammals from the Miocene of the Chesapeake Bay region. Smithsonian Miscellaneous Collections 116(2):1–21.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the United States Geological Survey 179:1–868.

Kasuya, T. 1973. Systematic consideration of Recent toothed whales based on the morphology of tympano-periotic bone. Scientific Reports of the Whales Research Institute 25:1–103, pls. 1–28.

Kellogg, A.R. 1925. The relationships of the Tertiary cetaceans of Jugo-Slavia to those of eastern North America. Spomenice U Pocast Prof. Dr. Gorjanovic-Krambergera, Zagreb, pp. 1–8.

———. 1927a. *Kentriodon pernix,* a Miocene porpoise from Maryland. Proceedings of the United States National Museum 69(19):1–55, pls. 1–14.

———. 1927b. Study of the skull of a fossil sperm-whale from the Temblor Miocene of Southern California. Contributions to Paleontology, Carnegie Institution of Washington Publications 346:1–24, pls. 1–9.

———. 1928. The history of whales—their adaptation to life in the water. Quarterly Review of Biology 3(1, 2): 29–76, 174–208.

———. 1931. Pelagic mammals from the Temblor Formation of the Kern River region, California. Proceedings of the California Academy of Sciences, Ser. 4, 19(12): 217–397.

———. 1955. Three Miocene porpoises from the Calvert Cliffs, Maryland. Proceedings of the United States National Museum 105:101–154, pls. 1–21.

Kellogg, A.R., and F.C. Whitmore, Jr. 1957. Mammals. Pages 1021–1024 *in* H.S. Ladd, ed., Treatise on marine ecology and paleoecology. Volume 2, Paleoecology. Geological Society of America Memoir 67:i–x, 1–1077.

Kirpichnikov, A.A. 1954. Dva novykh roda del'finov iz sarmata SSSR. (Two new genera of dolphins from Sarmatian of U.S.S.R.) Trudy Paleontologicheskogo Instituta, Akademia Nauk S.S.S.R. 47:181–190, pls. 1–3.

Kudrin, L.N., and K.A. Tatarinov. 1965. O miotzenovykh del'finakh zapadnoi Ukrainy. (On the Miocene delphinids from the western Ukraine.) Paleontologicheskii Zhurnal 1965(4):68–74.

Lawrence, B., and W.E. Schevill. 1956. The functional anatomy of the delphinid nose. Bulletin of the Museum of Comparative Zoology, Harvard College 114(4):103–151.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Journal of the Academy of Natural Sciences of Philadelphia, new series 7:1–472.

Mead, J.G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). Smithsonian Contributions in Zoology 207:i–iv, 1–72.

Miller, G.S., Jr. 1923. The telescoping of the cetacean skull. Smithsonian Miscellaneous Collections 76(5):1–71.

Mitchell, E. 1965. History of research at Sharktooth Hill, Kern County, California. Kern County Historical Society (Bakersfield, California), Special Publication, vi + 45 pp.

———. 1966. The Miocene pinniped *Allodesmus*. University of California Publications in Geological Sciences 61: 1–46, pls. 1–29.

———, and R.H. Tedford. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bulletin of the American Museum of Natural History 151(3):201–284.

Okazaki, Y. 1976. Miocene long-snouted porpoises from the Mizunami Group, central Japan. Bulletin of the Mizunami Fossil Museum 3:25–40, pls. 9–11.

Ray, C.E. 1976. Geography of phocid evolution. Systematic Zoology 25(4):391–406.

Rensberger, J.M. 1969. A new iniid cetacean from the Miocene of California. University of California Publications in Geological Sciences 82:1–34, pls. 1–4.

Repenning, C.A., and R.H. Tedford. 1977. Otarioid seals of the Neogene. United States Geological Survey Professional Paper 992:i–vi, 1–93, pls. 1–24.

Savage, D.E., and L.G. Barnes. 1972. Miocene vertebrate geochronology of the west coast of North America. Pages 124–145 *in* E.H. Stinemeyer, ed., Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium, Society of Economic Paleontologists and Mineralogists. 364 pp.

Shikama, T., Y. Hasegawa, and H. Otsuka. 1973. Geological range of mammals in the Japanese Neogene. Memoirs of the Geological Society of Japan 8:137–141 (in Japanese, English abstract).

Simpson, G.G., A. Roe, and R.C. Lewontin. 1960. Quantitative Zoology. Revised Edition. Harcourt, Brace and World, Inc., New York, pp. i–vii, 1–440.

Slijper, E.J. 1936. Die Cetaceen. Vergleichend-anatomisch und systematisch. Capita Zoologica 6:i–xv, 1–590.

———. 1958. Walvissen. D.B. Centen's Uitgeversmaatschappij, Amsterdam. 524 pp.

True, F.W. 1912. Description of a new fossil porpoise of the genus *Delphinodon* from the Miocene Formation of Maryland. Journal of the Academy of Natural Sciences of Philadelphia, Ser. 2, 15:165–194, pls. 17–26.

Weaver, C.E. et al. 1944. Correlation of the marine Cenozoic formations of western North America. Geological Society of America Bulletin 55:569–598; pl. 1.

Wood, H.E. et al. 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of America Bulletin 52:1–48, pl. 1.

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SYSTEMATICS OF *FISSURELLA* IN THE PERUVIAN AND MAGELLANIC FAUNAL PROVINCES (GASTROPODA: PROSOBRANCHIA)

James H. McLean

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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SYSTEMATICS OF *FISSURELLA* IN THE PERUVIAN AND MAGELLANIC FAUNAL PROVINCES (GASTROPODA: PROSOBRANCHIA)

James H. McLean[1]

ABSTRACT. Fifty-eight names have been proposed for the large and abundant species of *Fissurella* in the Peruvian and Magellanic faunal provinces. Fieldwork in Peru and Chile and to a lesser extent in Argentina, has produced large collections. Following study of these collections, as well as most of the type specimens, I reduce the number of species to 13, three of which have geographic subspecies.

Peruvian-Magellanic species of *Fissurella* Bruguière, 1789, are members of the nominate subgenus, in which the shell has an inner layer of crossed lamellar aragonite and a thick outer layer of prismatic calcite. In contrast, most tropical species of *Fissurella,* which are in the subgenus *Cremides* H. and A. Adams, 1854, have a shell composed entirely of aragonite. The outer layer of calcite is evidently an adaptation to cold water in the Peruvian-Magellanic species.

Three species groups in *Fissurella* (*sensu stricto*) are recognized. The group of *Fissurella peruviana* Lamarck, 1822, is smaller-shelled and has a thinner calcitic layer than species in the other groups; this group includes the type species *F. nimbosa* Linnaeus, 1758, in the southern Caribbean (the only tropical member of the subgenus) and *F. volcano* Reeve, 1849, in California and Baja California.

The group of *F. maxima* Sowerby, 1833, is characterized by strong primary and secondary ribs (at least in juvenile stages) and also includes *F. latimarginata* Sowerby, 1835, *F. cumingi* Reeve, 1849, and *F. costata* Lesson, 1831, in the Peruvian Province, and *F. picta* (Gmelin, 1791), *F. radiosa* Lesson, 1831, *F. oriens* Sowerby, 1835, and *F. nigra* Lesson, 1831, in the Magellanic Province. The group of *F. limbata* Sowerby, 1835, is characterized by broad primary ribs and lack of secondary ribs; it includes *F. crassa* Lamarck, 1822, *F. bridgesii* Reeve, 1849, and *F. pulchra* Sowerby, 1835, all in the Peruvian Province.

Geographic subspecies are here recognized for three species broadly distributed in the Magellanic Province: *F. picta picta* (Gmelin, 1791) in southern Chile, and *F. picta lata* Sowerby, 1835, in central Chile; *F. radiosa radiosa* Lesson, 1831, in southern Chile, *F. radiosa tixierae* Métivier, 1969, in the vicinity of the Gulf of San Matias in Argentina; *F. oriens oriens* Sowerby, 1835, in southern Chile, and *F. oriens fulvescens* Sowerby, 1835, in central Chile.

Three species, *F. cumingi, F. bridgesii,* and *F. pulchra,* have been poorly understood by previous authors and are newly defined here.

Distributions of the Peruvian and Magellanic species overlap in south-central Chile, where 12 of the 13 species occur.

This account includes observations on shell epibionts and borers, and reviews the sparse literature on the biology of these species.

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RESUMEN. Hasta ahora habían sido propuestos 58 nombres para las grandes y abundantes especies de *Fisssurella* de las provincias biogeográficas Peruana y Magallánica. Trabajos de terreno en Perú y Chile, y en menor intensidad en Argentina, han proporcionado importantes colecciones. Realizado el estudio de estas colecciones y de muchos de los ejemplares tipo, se reduce a 13 el número de especies, tres de las cuales poseen subespecies geográficas.

Las especies de *Fissurella* de las provincias Peruana y Magallánica son integrantes del subgénero *Fissurella* Bruguière, 1789 (*sensu stricto*), en las cuales la concha tiene una capa interna compuesta de aragonita laminar cruzada y una capa más externa de calcita prismática. En cambio, muchas especies de *Fissurella* que pertenecen al subgénero *Cremides* H. y A. Adams, 1854, tienen la concha compuesta íntegramente de aragonita. La capa más externa de calcita es considerada como una adaptación de las especies de las provincias Peruana y Magallánica a aguas frías.

Se reconocen tres grupos de especies. Un primer grupo de *Fissurella peruviana* Lamarck, 1822, de concha más pequeña y cuya capa de calcita es más delgada que en las otras especies de los demás grupos. Este grupo comprende la especies tipo *F. nimbosa* Linnaeus, 1758, del sur del Caribe (único miembro tropical del subgénero) y *F. volcano* Reeve, 1849, de California y Baja California.

Un segundo grupo de *F. maxima* Sowerby, 1833, caracterizado por la presencia de gruesas costillas primarias y secundarias (al menos en los estados juveniles). Comprende también a *F. latimarginata* Sowerby, 1835, *F. cumingi* Reeve, 1849, y *F. costata* Lesson, 1831, de la provincia Peruana y a *F. picta* (Gmelin, 1791), *F. radiosa* Lesson, 1831, *F. oriens* Sowerby, 1835, y *F. nigra* Lesson, 1831, de la provincia Magallánica.

El tercer grupo de *F. limbata* Sowerby, 1835, está caracterizado por la presencia de costillas primarias anchas y ausencia de costillas secundarias. Comprende también a *F. crassa* Lamarck, 1822, *F. bridgesii* Reeve, 1849, y *F. pulchra* Sowerby, 1835, todas de la provincia Peruana.

Se reconocen las siguientes subespecies geográficas para tres especies ampliamente distribuídas en la provincia Magallánica: *F. picta picta* (Gmelin, 1791) del sur de Chile y *F. picta lata* Sowerby, 1835, de la zona central de Chile; *F. radiosa radiosa* Lesson, 1831,

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[1] Malacology Section, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.

Figure 1. A *Fissurella* "shell pile," consisting of large specimens of *F. latimarginata, F. cumingi,* and *F. maxima* at Los Molles, Aconcagua Province, Chile, October 15, 1975. The specimens had presumably been taken by shallow diving in the vicinity and the shells discarded. All shells were covered with the algal mat, which completely obscures the color pattern.

del sur de Chile y *F. radiosa tixierae* Métivier, 1969, de las cercanías del golfo de San Matías en Argentina; *F. oriens oriens* Sowerby, 1835, del sur de Chile y *F. oriens fulvescens* Sowerby, 1835, de Chile central.

Las especies *F. cumingi, F. bridgesii* y *F. pulchra,* que han sido escasamente tratadas por autores anteriores, son definidas nuevamente.

Se observa una sobreposición en la distribución de las especies de las provincias Peruana y Magallánica en la zona central-sur de Chile, donde 12 de las 13 especies se encuentran presentes.

En el presente trabajo se incluye, además, observaciones sobre los epibiontes y organismos perforadores de las conchas y se revisa la esparcida literatura que trata sobre la biología de algunas de estas especies.

INTRODUCTION

The *Fissurella* species of the cool waters of Peru, Chile, and southern Argentina are large and abundant, comprising a major element of the mollusk fauna of the west coast of South America. They are extensively used for food and are known locally as "lapas" (Fig. 1). The importance of the fishery is second only to that of *Concholepas,* the "loco," the large limpetlike thaidid gastropod of the region. Despite this importance, the taxonomy of the South American species of *Fissurella* has been poorly understood.

It has been recognized that a large number of highly variable, sympatric species occur in the region. Some 58 names for Recent species have been introduced in the literature. Widely varying estimates of the number of actual species have been given: Pilsbry (1890) recognized about 20 species; Ziegenhorn and Thiem (1925) treated 11 species and three "varieties"; Riveros-Zuñiga (1951) recognized 26 species and three "varieties"; Dell (1971) listed 11 possible species; and finally Ramirez-Boehme (1974) gave a key to 30 species and two "varieties."

The collection of mollusks from Iquique, Chile, reported upon by Marincovich (1973), and deposited in the Natural History Museum of Los Angeles County, included five species of *Fissurella.* Although this material introduced me to the subject, fieldwork of my own in Peru in 1972 and 1974, and in Chile for two months in 1975, and southern Argentina in 1978, enabled me to collect and observe the *Fissurella* species from many different localities. I have therefore been able to observe these mollusks throughout their entire geographic range from north-central Peru to southern Chile and Argentina.

The Magellanic Province of southern Chile and southern Argentina is also the center of distribution of another fissurellid group comprising the species *Fissurellidea megatrema* Orbigny, 1841, *F. patagonica* (Strebel, 1907), *Pupillaea annulus* (Odhner, 1932), and the shell-less *Buchanania onchidioides* Lesson, 1830. A report on these species has been published (McLean, 1984b).

In this work I offer a revised classification of the South American species of *Fissurella,* based on my field observations, study of the large collection now housed at the Los Angeles County Museum of Natural History, and study of type material borrowed from other museums. The classification cannot be exhaustive and does not offer a cladistic hypothesis of relationships. In the absence of anatomical, biochemical (electrophoretic), and other characters, that is beyond the scope of the present work. It is hoped that this paper will provide a basis for future work on the systematics and ecology of these species.

MATERIALS AND METHODS

Fieldwork

The collection upon which this report is chiefly based is now in the Los Angeles County Museum of Natural History. Some material from miscellaneous sources is represented in the collection, but the bulk of it resulted from nine major expeditions as follows:

1. Peru: Isla San Lorenzo, Isla Chinchas, and Bahía Independencia. Allan Hancock Expeditions, January, 1935, and February, 1938, intertidal and dredging stations.
2. Chile: Iquique. Louie Marincovich, June–September, 1964, June–July, 1970, intertidal stations.
3. Argentina: Isla de los Estados (E of Tierra del Fuego). R/V HERO, April, 1971, and October, 1971, intertidal and dredging stations; collections received from the Smithsonian Oceanographic Sorting Center.
4. Peru: Pueasana, Laguna Grande, Isla Chincha Norte, Paracas, Asia. James H. MeLean, April, 1972, intertidal and diving stations.
5. Chile: south of Isla de Chiloe. Paul Dayton, on R/V HERO, October–November, 1972, intertidal and diving stations.
6. Chile and Argentina: Strait of Magellan and Isla de los Estados. Paul Dayton, on R/V HERO, May, 1973, intertidal and diving stations.
7. Peru: Isla Guanape, Ancon, and Isla San Lorenzo. James H. McLean, January, 1974, intertidal and diving stations.
8. Chile: Iquique, Antofagasta, Coquimbo, Los Molles, Montemar, Cartagena, Concepción, Mehuin, Pargua, Guabun, Pumalin, Islota Nihuel, Isla Laitec, Puerto Hambre, Punta Arenas. James H. McLean, October–November, 1975, intertidal and diving stations.
9. Argentina: Golfo Nuevo and Golfo San Jose. James H. McLean, on R/V HERO, July 1978, intertidal and dredging stations.

Other Collections Examined

Upon returning from Chile in 1975, I compared the field-collected specimens with as many of the types of species described by nineteenth-century authors as could be located for me in the British Museum (Natural History) and the Paris Museum. I have also studied the collections of *Fissurella* in the U.S. National Museum of Natural History, Washington, D.C., the Academy of Natural Sciences, Philadephia, and the American Museum of Natural History, New York. Other specimens were received on loan from the Museum of Comparative Zoology, Harvard, and the National Museum of New Zealand, Wellington. After conducting my fieldwork in Argentina in 1978, I examined the *Fissurella* material in the Museo Argentino de Ciencias Naturales, Buenos Aires, and the Museo Nacional de Historia Natural, Santiago. Records from these collections enabled further refinements in species distributions.

Preparation of Specimens

Although most of the field-collected specimens were either kept dry or the entire specimen preserved in alcohol, without cleaning the shell, the photographed specimens had to be cleaned of encrusting organisms. Shells were placed in full strength laundry bleach, which softens the algal mat and loosens other encrusting organisms so that the shell can be scraped clean with a knife or wire brush. Color was restored with a light application of mineral oil.

Shells of each species were embedded in plaster and cut with a diamond rock saw for the examination and photography of the shell layers. Scanning electron microscopy (SEM) was used for the examination of shell structure in a fragment of a small specimen of *F. latimarginata.* Radulae of large specimens of each species were air-dried for macrophotography; radulae of small specimens were prepared for both light microscopy and SEM.

Conventions

Figured specimens for each species are arranged by localities from north to south, including type specimens of nominate taxa and synonyms. All shell specimens are illustrated with the anterior at the top; lateral views are those of the left side of the shell. Measurements for the figured specimens are given in the captions, not repeated in the text. Measurements are given in this order: length, width, and height. Unless otherwise indicated, the figured specimens were collected in the intertidal zone. Latitude and longitude for the figured specimens from LACM stations are given in a locality list following the systematic section.

Abbreviations

Abreviations of institutions mentioned in the text are as follows:

AHF	Allan Hancock Foundation Collection (at LACM)
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
LACM	Los Angeles County Museum of Natural History, Los Angeles
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN	Museo Nacional de Historia Natural, Santiago
MNHNP	Museum National d'Histoire Naturelle, Paris
NMNZ	National Museum of New Zealand, Wellington

USNM United States National Museum of Natural History, Washington, D.C.

HISTORICAL REVIEW

The Strait of Magellan was probably the origin of the earliest collected shells of *Fissurella* to reach Europe. The first species to be known was the common Magellanic *F. picta*, which was well described and figured in the non-binomial work of Davila (1767), who called it "Un Lepas rare de Magellan" (Pilsbry, 1890:114). The name *Fissurella picta* dates from J.F. Gmelin (1791), whose knowledge of it came in part from Davila.

J.B.P.A. de Lamarck (1822) validated *F. crassa* and *F. peruviana* in his "Histoire naturelle des animaux sans vertébrés." Lamarck's types are preserved at the Geneva Museum (Mermod, 1950).

G.B. Sowerby (1825) introduced a synonym for *F. crassa*, but was later to recognize Lamarck's unfigured species.

G.P. Deshayes (1830) named two Chilean species in the "Encyclopédie Méthodique," but one of them was a synonym of *F. peruviana* and the other, *F. rudis*, although prior to *F. costata* Lesson, 1831, is preoccupied. Types are extant at the Paris Museum.

R.P. Lesson (1831), in his report on collections from the South American voyage of the "Coquille," described four species of *Fissurella* without illustrations, all from the southern and southernmost regions of Chile. The names for three of his species are now in use: *F. nigra*, *F. radiosa* and *F. costata*. One other, *F. obovalis*, remains a *nomen dubium*. Lesson's work has frequently been cited as published in 1830, but the pages that included the *Fissurella* descriptions are correctly dated 1831. Although some of Lesson's types have been recognized at the Paris Museum, P. Bouchet reports (personal communication) that he has been unable to locate any of the *Fissurella* types.

By 1831, six of the currently recognized species had been established. Eleven names had then been proposed, but very few of these taxa had been illustrated.

In 1835, no less than 13 names were introduced by G.B. Sowerby, based on specimens received from the British collector Hugh Cuming, who had lived in Valparaíso, Chile, from 1819 to 1831. Brief descriptions were given in the Proceedings of the Zoological Society of London for 1834. Dating for these species has frequently been cited as 1834, but the publication date for the pages involved is 1835. Illustrations were published simultaneously in the "Conchological Illustrations" (Sowerby, 1835b). Sowerby recognized some of the species described earlier by French authors; seven of his names remain useful: *F. maxima*, *F. latimarginata*, *F. limbata*, *F. oriens*, *F. pulchra*, *F. lata* (here *F. picta lata*), and *F. fulvescens* (here *F. oriens fulvescens*). The Sowerby types are preserved at the British Museum (Natural History).

By 1835, 11 of the 13 species I recognize from Chile had been named, and the total number of described taxa had reached 25.

R.A. Philippi (1845, 1845–46) proposed five names, but none of these has any current utility. One of these, *F. alba*, has been used by some authors, but is here regarded as a synonym of *F. oriens*. Unfortunately, the present whereabouts of Philippi's *Fissurella* types is unknown.

A.A. Gould (1846) introduced one name, here regarded as a synonym for *F. peruviana*. The holotype is in the United States National Museum.

Lovell Reeve (1849–50), in his monograph of *Fissurella* in the Conchologica Iconica, added two more of the species recognized here, *F. cumingi* and *F. bridgesii*, both of which have been enigmatic until now. However, he also introduced nine superfluous names, based on further splitting of Cuming's material. Some were described without locality. Reeve gave colored illustrations for all the previously recognized species but did not give any interior views of the shells, thereby not treating the broad margin, one of the most useful characters. Also, he did not always figure the same specimen illustrated by Sowerby, a factor contributing to confusion in some cases. The Reeve types are housed in the British Museum (Natural History).

An attempt at summarizing the recognizable species in Chile was made by L.H. Hupé, 1854, who added Spanish translations of original descriptions of earlier species, and included some of his own commentary, but gave no illustrations. Twenty-one species were recognized. One new taxon was introduced, the renaming of a preoccuppied name of Philippi.

Philippi (1857) proposed another name now having no value. In 1860 Philippi briefly treated eight species of *Fissurella* from Paposa (near Antofagasta) in his "Reise durch die Wueste Atacama . . . ."

G.B. Sowerby II's treatment of *Fissurella* in the "Thesaurus Conchyliorum" (1862) was scarcely an advance over that of Reeve. Specimens illustrated were not always those of Sowerby or Reeve. One additional synonym was named. Little new information was given, nor was opportunity taken to reduce the number of names. The figures were smaller than those given by Reeve, and there were no interior views.

A.T. de Rochebrune and J. Mabille (1885) proposed three taxa from the southernmost region, none of which were compared to established species; the names are now regarded as junior synonyms. Two of the three type specimens are housed in the Paris Museum; the whereabouts of the other is unknown.

H.A. Pilsbry's (1890) treatment of *Fissurella* in the "Manual of Conchology" was an admirable effort at summary and review. For most taxa he provided English translations of text by German and French authors and copied original illustrations for all taxa, whether recognized as valid or placed in synonymy. Synonyms were allocated as far as possible. Approximately 20 were treated as good species. However, the specimens available to Pilsbry were limited, and many questions remained unanswered. Only one unnecessary new species was introduced, the holotype of which is preserved at the Academy of Natural Sciences, Philadelphia.

J.C. Melvill and R. Standen (1898, 1907, 1914) listed and gave notes on mollusks from the Falkland Islands. The *Fissurella* species were briefly treated.

H. Strebel (1907) treated the Magellanic and Patagonian *Fissurella*. For three of the species that I consider to inhabit this southern area, he recognized six, but introduced no synonyms. A year later, Strebel (1908) listed *F. exquisita* from Paulet Island, Antarctic Peninsula, a record that needs further verification. Unfortunately, the Strebel Collection was destroyed in World War II (Dance, 1966:302).

W.H. Dall (1909) listed 18 species of *Fissurella* in his checklist of mollusks from the Peruvian faunal province. Those pertaining to the Magellanic area were omitted. Some of Dall's records are now clearly erroneous: *F. crassa* at the Galapagos Islands and both *F. maxima* and *F. picta* at Manta, Ecuador. The records from Manta had previously been cited by Stearns (1891).

A. Ziegenhorn and H. Thiem (1925) reported upon a collection made in Chile by L.H. Plate. From a collection of only 15 specimens, they discussed and illustrated 11 species. They omitted three species that I recognize and treated two others as "varieties," but their scheme is the best effort available in the literature. Some external features of the animal were mentioned, and good illustrations of the shells were given, but no interior views. Among the subsequent authors, only Odhner (1932) and Dell (1971) cited their work.

I. Perez-Farfante (1943) mentioned only *F. picta* in her account of Atlantic Fissurellidae. She made this species the type of her new subgenus, *Balboaina,* which I here synonymize with *Fissurella, sensu stricto.*

The "Catalogo descriptivo de fisurelidos Chilenos" of F. Riveros-Zuñiga (1951) was compiled almost entirely from the literature. Text from previous authors was translated into Spanish. Illustrations were single exterior views, most of which were copied from other sources. Twenty-six species and three varieties were recognized. Three of the common Peruvian Province species were erroneously cited from Fuerte Bulnes, near Punta Arenas in the Strait of Magellan.

A.R. Carcelles (1950), Carcelles and S.I. Williamson (1951), and Carcelles (1953), produced a series of faunal checklists for the Patagonian, Magellanic, and Antarctic regions, in which *Fissurella* species were listed.

Pérez-Farfante (1952) proposed the subgenus *Carcellesia,* with the new type species *F. doellojuradoi,* which I regard as a synonym of *F. oriens.* The subgeneric name is here regarded as a synonym of *Fissurella, sensu stricto.*

B. Métivier (1969) named *F. tixierae* from the Golfo Nuevo, Argentina, a name here treated as a geographic subspecies of *F. radiosa* Lesson. The type specimen is preserved at the Paris Museum.

G.M. Peña (1970) included six species (five that I recognize) in his list of the intertidal mollusks of Peru, and cited a number of his own collecting localities for each.

R.K. Dell (1971) illustrated many Sowerby and Reeve syntypes from the Cuming Collection in the British Museum in his report on mollusks from the Royal Society Expedition to southern Chile. His collection, however, was not sufficiently complete to enable a full revision, and his list of 11 "possible species" differs considerably from that adopted here.

L. Marincovich (1973) figured the five most abundant species from Iquique in northern Chile but did not discuss their synonymy. The Marincovich collection is preserved at the Los Angeles County Museum of Natural History.

J. Christiaens (1973) did not treat the Chilean species in his review of the tropical *Fissurella* species; however, he proposed the subgenus *Corrina* for *F. alba* Philippi, a species here placed in the synonymy of *F. oriens. Corrina* is here regarded as a synonym of *Fissurella, sensu stricto.*

J. Ramirez-Boehme (1974) gave a key that included 30 different species (plus two varieties) of *Fissurella* from Chile. Some of the taxa recognized in his key have never been illustrated and have been considered indeterminate by other authors. He also introduced four synonymous names in *Fissurella* (along with 21 "new species" names for acmaeid limpets). All were figured in watercolor. Types are preserved at the Museo Nacional de Historia Natural, Santiago.

In July, 1978, I distributed copies of a preliminary draft of this manuscript to a number of Chilean biologists whom I had met in 1975. That version differed from this primarily in recommending the replacement of *F. rudis* Deshayes, 1830, for *F. costata* Lesson, 1831. However, Deshayes' name is preoccupied, so the better known name of Lesson is reinstated here. I am gratified to see that my present classification scheme has been adopted by Chilean biologists, and am grateful for the help they have provided in making this account the more complete.

Recent papers on the biology of *Fissurella* species are those of Acuna (1977), Bretos (1978, 1979, 1980, 1982, 1983), Jara and Moreno (1984), Moreno and Jaramillo (1983), and Moreno et al. (1984).

STRUCTURE

Internal Anatomy

Anatomy in the Fissurellidae has been treated by Boutan (1885), Illingworth (1902), Tobler (1902), Ziegenhorn and Thiem (1925), and Odhner (1932). The latter two accounts included references to Chilean species of *Fissurella.* Fretter and Graham (1962) gave a number of useful drawings of fissurellid anatomy. The reader is referred to these works for details.

Although some incidences of hermaphroditism are known in fissurellids (see Fretter and Graham, 1964), to my knowledge, *Fissurella* species are gonochoristic, having separate sexes. There are no apparent external sexually dimorphic features, although the testis of males is beige-colored and the ovary of females is bright green. The gonads discharge through the right kidney, which therefore has a reproductive as well as an excretory function. The Fissurellidae are unusual among archaeogastropods in having a highly reduced left kidney, which is nearly vestigial. In contrast, the left kidney is a prominent papillary sac in the archaeogastropod families Pleurotomariidae, Haliotidae, and Trochidae. These families also differ in having the spiral caecum appendage to the stomach and a well-developed hypobranchial gland attached to the mantle skirt, structures that are lacking in the Fissurellidae.

Anatomy in the Fissurellidae is so unlike that of the Pleurotomariidae, Haliotidae, and Trochidae, that the affinity is

Figure 2. External anatomy of *Fissurella picta*. Two views of same preserved specimen removed from shell, the mantle skirt cut above the head to the excurrent siphon and folded back to show the paired gills in the mantle cavity. Bahía York, Isla de los Estados, Argentina. LACM 71-177, shell length 75.4 mm. Left, anterior view, showing radular ribbon protruding from mouth. Right, dorsal view.

distant from these groups. I have argued (McLean, 1984a) in support of the theory that the Fissurellidae were derived from the extinct Paleozoic Bellerophontacea. The bilateral symmetry of the Fissurellidae would therefore not be secondarily derived, as has been assumed by most authors, but primitive.

External Anatomy

Structures of the head are the snout, which terminates in a broad oral disc (Fig. 2), and cephalic tentacles, the eyes at the bases of the tentacles. The cephalic tentacles extend forward when the animal is active.

The body is attached to the shell by a horseshoe-shaped shell muscle, which is open anteriorly, corresponding to the mantle cavity above the head. The animal may be detached from the shell by severing the shell muscle. Structures within the mantle cavity (Fig. 2) may then be observed by cutting the thin mantle roof tissue above the head. This exposes a pair of large, bipectinate gills, which fill most of the space in the mantle cavity on either side. The gills are attached by a long ventral (efferent) membrane and a short dorsal (afferent) membrane. The anus opens close to the foramen. Water currents enter above the head, pass the gills, and exit through the foramen of the shell, sweeping the fecal material out at the same time. The currents are propelled by bands of cilia on the gill filaments. Left and right kidney openings are positioned near the anus.

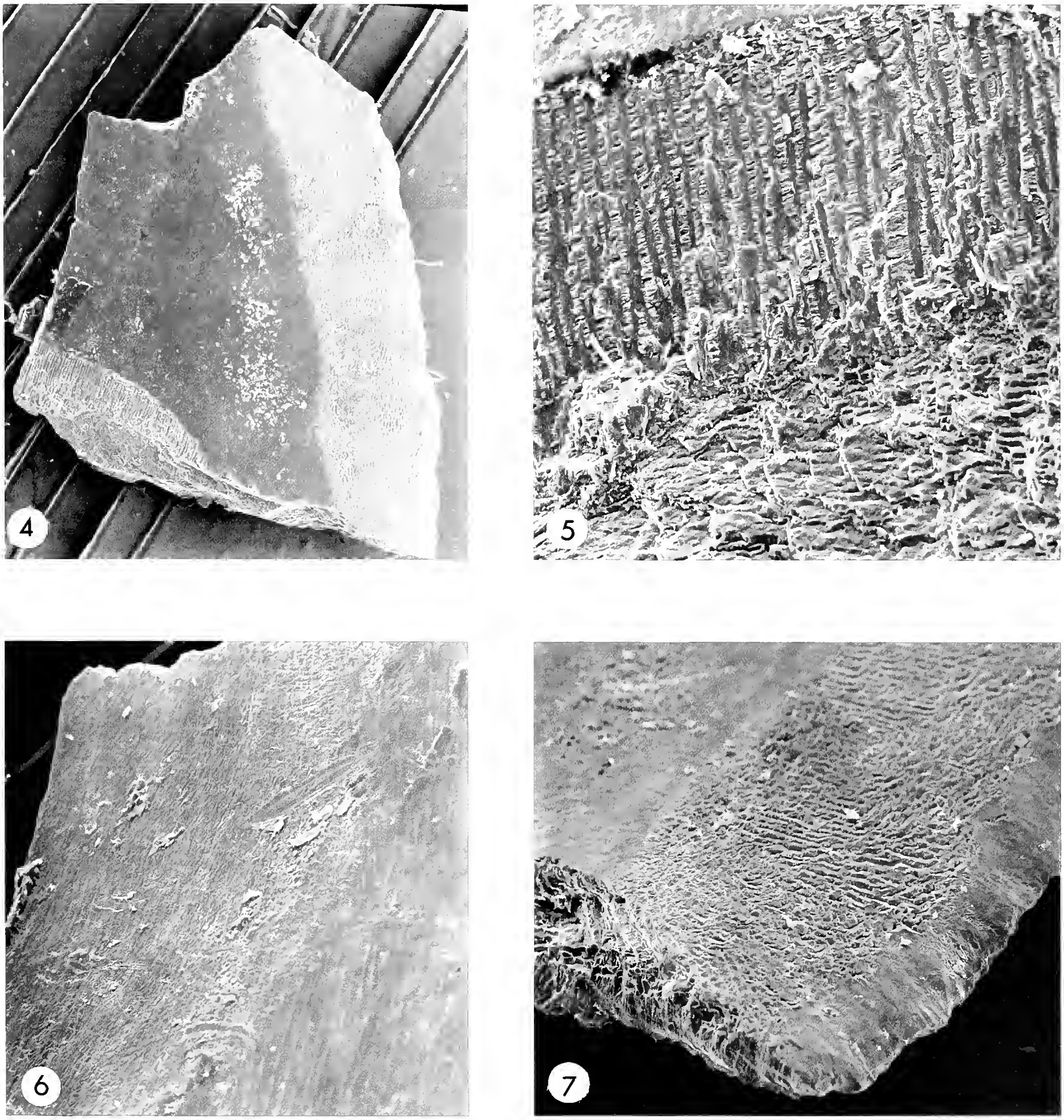
In living *Fissurella,* the shell edge is enveloped by the mantle fold, which secretes and protects the growing edge of the shell and has sensory papillae scattered on its surface. The mantle fold is color-banded to match the rayed pattern of the shell. The mantle fold is capable of expanding to cover the entire shell and foot sides. The foramen is also bordered by mantle folds that have papillae and a pigment pattern similar to that of the mantle at the shell margin. The diameter of the excurrent opening in the mantle skirt varies under differing conditions of exposure to air or water.

Figure 3. *Fissurella oriens,* SEM view of juvenile shell 1.9 mm in length, showing coiled protoconch and early foramen. Islota Nihuel, Chiloe Province, Chile. LACM 75-42.

The pigmented side of the foot has a single row of short, stubby epipodial tentacles, extending anteriorly to the head. These tentacles are poorly developed. The elaborate mantle lobes probably have more of a sensory function than do the epipodial tentacles. In other archaeogastropod families, particularly the Haliotidae, the epipodium is well developed, forming several rows of tentacles on a separate fold called the epipodial lobe.

Radula

The radula consists of rows of chitinous teeth on a long ribbon (shown projecting through the mouth in Fig. 2). The entire radular ribbon may be as much as ⅓ the length of the shell. The teeth rows are rhipidoglossate, with a narrow rachidian (central tooth), four pairs of lateral teeth shaped like the rachidian, a pair of large, four-cusped outer lateral teeth, a pair of uncusped lateromarginal plates, and a large number of marginal teeth. The lateromarginal plates separate the large outer laterals from the "books" of marginal teeth. The fissurellid radula is markedly asymmetrical (Hickman, 1981, 1984), with teeth on the left side of the ribbon higher or more anteriorly placed than those on the right, extending forward of the rachidian, which itself is asymmetrical. This pronounced asymmetry enables the large outer laterals to interlock like the teeth of a zipper when the ribbon is folded and retracted at the close of the feeding stroke. The teeth are folded in the same way while developing in the radular sac.



Figures 4 through 7. Shell structure of *Fissurella latimarginata*. SEM views of single fragment from young specimen, courtesy H.A. Lowenstam. LACM 64-16, Iquique, Chile. (**4**) Interior view of shell fragment, the broad, beveled interior margin (calcitic layer of exterior) of shell at right (length at margin 2.14 mm), and the smooth interior aragonitic layer in center and left. Fractured area at lower left exposes the crossed lamellar structure of the aragonitic layer and the platy calcitic layer below. ×30. (**5**) Enlargement of lower left area of shell fragment, showing the smooth interior at top, the fractured surface of crossed lamellar aragonite below, and the transition between the latter and the fractured platy calcitic layer at the lower edge of the frame. ×200. (**6**) Enlargement of upper left corner of shell fragment. Vertical lines are the lamellae of the smooth interior aragonitic layer. Curved lines represent the successive positions of the expanding muscle attachment area. ×120. (**7**) Enlargement of lower right corner of fragment, showing the smooth growing edge (calcitic layer), the undulations reflecting the external sculpture of radial ribs. The broad, beveled margin has an irregular surface (for mantle contact) between the smooth edge and the smooth aragonitic surface at the left. ×80.

The large outer laterals are the functional teeth; the rachidian and inner laterals are so small that their role is minimal.

Shell Morphology

The apical perforation, or foramen, is the most striking shell feature. It enlarges as the shell grows; shell material is resorbed by the mantle tissue that surrounds the foramen. Young shells have a coiled protoconch, but this is obliterated by the expanding foramen and is generally present only in juvenile specimens of up to two mm in length (Fig. 3). Although the postprotoconch stage of *Diodora* has a selenizone (slitband), this is lacking altogether in developing stages of *Fissurella* (McLean, 1984a).

Prominent features of the shell interior are the horseshoe-shaped muscle sear, open in front, and the apical callus, a broad flat area surrounding the foramen. The two round terminations of the muscle scar are connected by a line that marks the anterior attachment zone of the mantle skirt.

Shell Structure

Most fissurellids have the shell composed entirely of the aragonitic form of calcium carbonate (Bøggild, 1930; MacClintock, 1963, 1967). Bøggild (1930) noted that the Chilean *Fissurella crassa* also has an outer layer composed of the calcitic form of calcium carbonate. Other species treated here were not mentioned by Bøggild, but all have a similar two-layered shell (Figs. 4–7). The shell structure of radial ribs and the pigmentation is confined to the outer layer. This layer has a waxen, translucent appearance. A periostracum is lacking.

In the Peruvian and Magellanic species, it is the outer calcitic layer that comprises the broad, pigmented interior margin of the shell. This layer is secreted by the mantle lobe only at the growing edge. In contrast, the opaque white aragonitic inner layer is deposited throughout the interior and thickens with growth. The interior aragonitic layer is thick only in the apical region, where it has greatly augmented the thin calcitic layer of the early shell. Away from the apical area, the inner layer becomes thinner, its depth only one-third to one-fifth the thickness of the calcitic layer; it is lacking altogether at the shell edge (margin).

The prismatic structure of the calcitic layer is not readily apparent under low magnification; however, the structure of the opaque white aragonitic layer can be seen under the dissecting microscope. It shows a series of lines running parallel to the shell margin, a typical feature of "concentric cross-lamellar" shell structure. The lamellae may be seen throughout the interior of the shell, including the muscle scar and the apical callus (Fig. 6).

Tropical species of *Fissurella* have shells composed entirely of aragonite and lack the distinctively colored inner shell margin. This difference between the tropical species (Fig. 30) and the cooler-water species is here treated as a subgeneric distinction.

In molluscan species with both calcite and aragonite deposited in separate shell layers, the ratio of calcite to aragonite deposition varies with temperature. A greater percentage of calcite deposition takes place at colder latitudes and seasonally, during winter months (Lowenstam, 1954, 1964; Vermeij, 1978). Lowenstam (1954) noted a greater percentage of calcite deposition in species of *Mytilus* and *Littorina* as latitude increased. This is apparent in specimens of *Fissurella picta* from different latitudes. In *F. picta* from the Strait of Magellan at 53°37′ S (Fig. 145) the aragonitic layer is noticeably thinner than in *F. picta* from 42°42′ S (Fig. 144). The greater calcitic deposition in cold water helps to explain why these species are so prolific at high latitudes, where they reach a much larger size than do their tropical counterparts. The calcitic layer of the South American species is evidently an adaptation to cold water.

Calcite is more stable than aragonite, and fossil calcitic shells are generally better preserved. This is evident in the specimen of the Pliocene *F. concolor* Philippi, 1887, from Antofagasta (Fig. 17). Only the calcitic outer layer remains; the aragonitic interior is completely missing. However, specimens in old shell piles indicate that when exposed to subaerial weathering, the calcitic layer fractures and separates, whereas the aragonitic layer tends to remain intact.

BIOLOGY AND ECOLOGY

Habitat

As in other limpet families with large numbers of sympatric species, each of the Peruvian-Magellanic *Fissurella* species has a unique habitat or niche.

All tropical species of *Fissurella* are limited to the intertidal zone, but some of the Peruvian-Magellanic species extend into the subtidal zone. *Fissurella peruviana, F. pulchra,* and *F. oriens* may occur more abundantly in the sublittoral than in the lower intertidal zone. *Fissurella maxima, F. cumingi,* and *F. latimarginata* occur commonly from the lower intertidal zone to a depth of about 5 m. The intertidal occurrence of these species is limited to areas protected from strong wave exposure.

The remaining species are intertidal and do not occur in the sublittoral zone. The highest occurring species is *Fissurella crassa,* which is tightly wedged in crevices when exposed at low tide. *Fissurella limbata* and *F. costata* live exposed to surf in the lower intertidal zone, *F. limbata* on horizontal surfaces, and *F. costata* on vertical surfaces. *Fissurella nigra* occurs on the undersides of large rocks in protected tide pools at mid-tidal to lower intertidal levels.

Fissurella bridgesii has a unique habitat. It occurs on rocks near sandy areas, unlike the others, which avoid proximity to sand.

Fissurella picta has a more ubiquitous occurrence. It is rare at its northern limit, where it is sympatric with other species, but to the south of the southern limit of most of the other species it occurs from the mid-tidal to lower intertidal zone under various conditions of exposure, filling niches that are occupied by other species in the north.

Feeding

Little is known of the feeding habits of Peruvian and Magellanic *Fissurella.* Many genera of fissurellids feed upon sponges and detritus (Fretter and Graham, 1976), but Ward (1966a) has shown that the tropical species *F.* (*Cremides*) *barbadenisis* (Gmelin, 1791) feeds upon algae. Bretos (1978) indicated that *F. crassa* feeds upon such green algae as *Ulva* and *Enteromorpha.*

At Mehuin in southern Chile, *Fissurella picta lata* is a nocturnal herbivore, feeding upon the red alga *Iridaea boryana* and the green alga *Ulva rigida* (Jara and Moreno, 1984; Moreno and Jaramillo, 1983; Moreno et al., 1984).

Information on the diets of the other South American species is needed.

Reproduction and Growth

Bretos (1983) treated reproduction in *F. maxima,* finding that spawning occurred in late November–December (late spring) and again in July–August (winter). The breeding cycle of the tropical *F. barbadensis* was treated by Ward (1966b). That species is known to have a pelagic phase of two to three days duration.

Bretos (1978, 1980) studied the growth rate of *F. crassa,* finding that growth is rapid in early spring and late summer, slower in late spring, autumn, and winter. Harvestable sizes were reached in 2 to 4 years. Two growth rings were formed each year and were considered reliable indicators of growth for the first 6 years, after which growth was slowed and the rings could not be identified. *Fissurella maxima* was also determined to form two growth rings each year (Bretos, 1982). Growth in *F. latimarginata* was studied by Acuna (1977).

The El Nino event of 1982–1983 had a major effect on the *Fissurella* populations in northern Chile. According to J. Tomicic (personal communication), all large *Fissurella* species near shore were killed during the austral summer of 1982–1983. However, in November, 1983, fast growing juveniles were reported as abundant.

Epibiotic Associations

Fissurella shells offer a surface for colonization by many species of algae and invertebrates. Many shells are so encrusted that color patterns are obscured (Fig. 1). Only those species that occur high in the intertidal zone (*F. crassa*), or predominantly on the undersides of large rocks in the lower intertidal (*F. nigra* and *F. pulchra*), have shells that stay relatively free of encrusting organisms.

Species of the shallow sublittoral zone (*F. latimarginata, F. cumingi,* and *F. maxima*) generally have a thick algal mat consisting of dense tufts of finely branched red algae, which reaches a height of 5 mm above the shell (Figs. 1, 8). This algal growth is absent on the rocky substrate because grazing by the black urchin *Tetrapygus niger,* and presumably by the *Fissurella* species, leaves the rock barren except for encrusting coralline algae.

Although the algal mat on the shells of a living *Fissurella* would be a source of food for other individuals of *Fissurella* as well as the urchins, they evidently do not tolerate grazing by their own kind or by the urchins, because the algal mat is usually intact. I observed thick algal mats on most shells seen in the course of diving, those in shell piles on the shore, and those sold in markets. The chiton *Chaetopleura peruviana* is able to graze successfully on the algal mat of shells (Fig. 8).

Balanus psittacus is frequently found on subtidal *Fissurella* shells, and *B. flosculus* occurs on shells in exposed intertidal habitats, particularly on *F. costata* and *F. limbata.*

The mussel *Semimytilus algosus* may form aggregations on specimens of *F. latimarginata* (Fig. 74).

Epibiotic growths on *Fissurella* shells provide a protective advantage, making it more difficult for boring organisms to penetrate the shell. Those specimens of *F. latimarginata* that have lost the algal mat are usually deeply eroded. The advantage of epibionts to chamid bivalves was discussed by Vance (1978).

Epibiotic *Scurria parasitica*

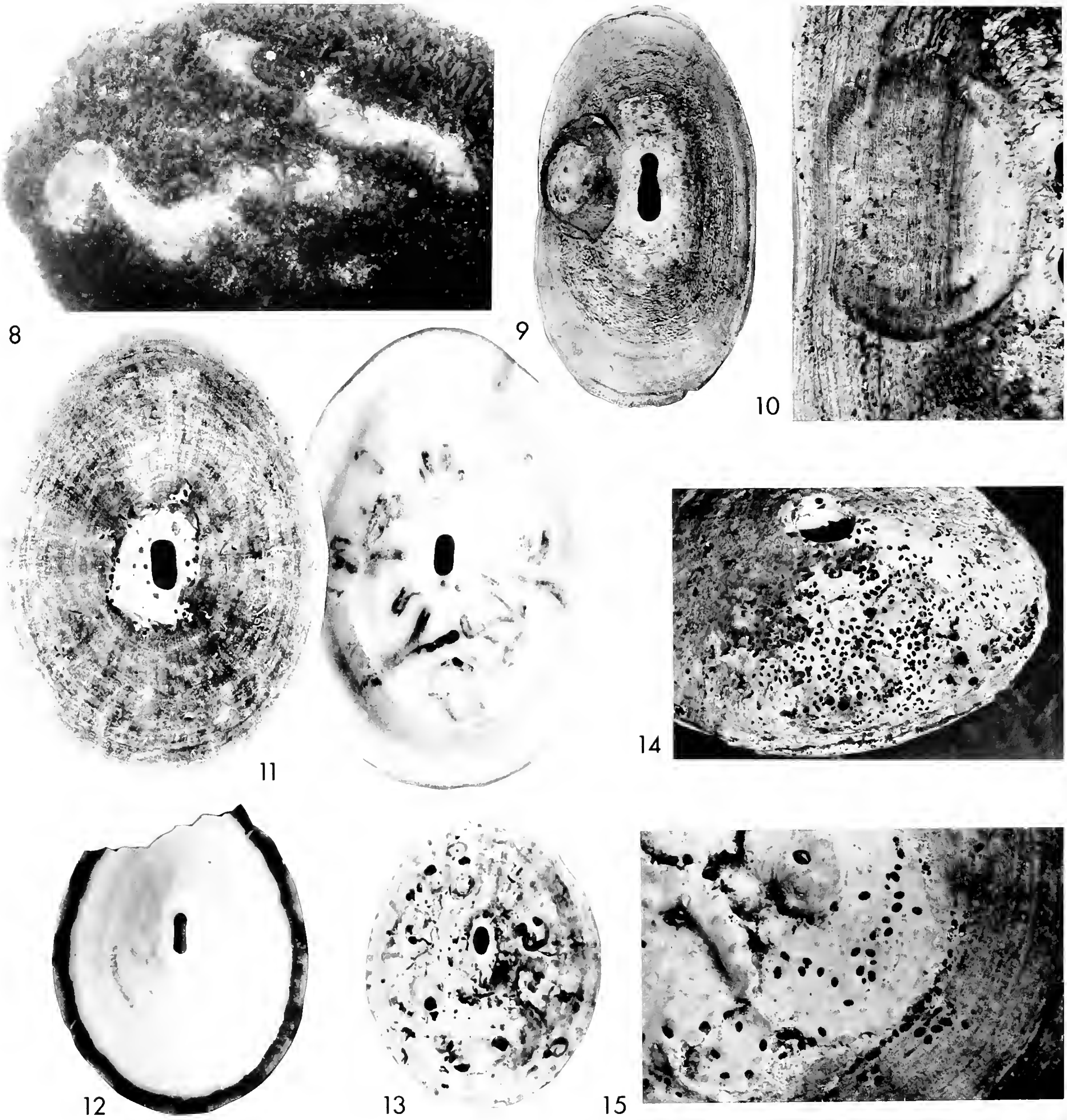
Most individuals of *F. crassa* and *F. limbata,* two species that only occur in the intertidal zone, have a single (or rarely two) *Scurria parasitica,* an acmaeid limpet, attached to "home scars" on the shell (Figs. 9, 10). This limpet occurs also on shells of *Scurria viridula* and the chitons *Enoplochiton niger* and *Acanthopleura echinata* (see Marincovich, 1973) and rarely on other species of intertidal *Fissurella.* I am aware of no studies on its biology.

Lindberg (1976), Dwyer and Lindberg (1981), and Lindberg and Dwyer (1983) described the home-scar depression of the Californian acmaeid *Collisella scabra* on the shells of the mussel *Mytilus californianus* and the acmaeid limpet *Lottia gigantea,* noting the similarity of the scar to that formed by *Scurria parasitica* on chitons. These epibiotic limpets produce deep scars on their host shells (Fig. 10), in which there is an outer depression corresponding to the shell margin, and an inner depression to correspond to the breadth of the foot. The outer depression provides a seal that helps to prevent desiccation and dislodgment. Microscopic examination of the home scars shows the presence of radular scraping marks, which indicates that enlargement of the scar is an activity unassociated with feeding. Lindberg and Dwyer (1983) also found evidence of shell dissolution by acidic mucopolysaccharides secreted by the foot and carbonic anhydrase by the mantle edge.

The feeding range of the limpets studied by Lindberg and Dwyer (1983) was restricted to the shells of the host mollusks. This is probably true for *S. parasitica* on shells of *F. limbata* and *F. crassa.* Scar-bearing *Fissurella* shells do not have other encrusting organisms and are always deeply eroded.

Shell Borers

Cirratulid polychaetes of the genus *Dodecaceria* (identified both by K. Fauchald and J.C. Castilla) commonly burrow into *Fissurella* shells, riddling and weakening them (Fig. 11). The polychaete tubes open at the exterior surface, where they are ordinarily concealed by the algal mat. The inside diameter of the tube reaches 1.3 mm. The burrows are visible on the shell interior, but do not break the surface except in gerontic shells. Gibson (1978) briefly discussed Chilean species of



Figures 8 through 15. Shell epiphytes, shell grazers, shell borers. **(8)** Dense mat of red algae on exterior of *F. latimarginata,* with chiton *Chaetopleura peruviana* and grazing trails made by the chiton. LACM 75-29, Los Molles, Aconcagua Province, Chile, shell length 106 mm. **(9)** Epizoic limpet *Scurria parasitica* on *F. crassa.* LACM 90796, Iquique, Chile, shell length 57.5 mm. **(10)** Scar of *S. parasitica,* showing inner and outer depression of scar. Same specimen, length of scar 13.1 mm. **(11)** Shell of *F. latimarginata* infested with borings by cirratulid polychaete *Dodecaceria* sp., exterior view of cleaned shell showing openings to burrows; interior view showing trace of burrows. LACM 75-29, Los Molles, Aconcagua Province, Chile, shell length 115 mm. **(12)** Shell of *F. cumingi* removed from stomach of clingfish *Sicyases sanguineus,* showing breakage pattern caused by this predator. LACM 75-31, Islota Concon, Valparaíso Province, Chile, shell length 50.8 mm. **(13)** Shell of *F. costata* with excavated depressions made by vermetid gastropod *Dendropoma* sp. LACM 75-27, beach-worn specimen, Bahía El Teniente, Coquimbo Province, Chile, length 50 mm. **(14)** Shell of *F. cumingi* with burrows of barnacle *Cryptophialus minutus.* MACN 9027-11, specimen studied by Tomlinson (1969), locality unknown, shell length 83.7 mm. **(15)** Exterior surface of *F. limbata* showing burrows of *Cryptophialus.* LACM 75-19, Los Colorados, Antofagasta Province, Chile, length of field 21 mm.

Dodecacaeria. However, the systematics of the group remains poorly known.

K. Fauchald (personal communication) has also identified the spionid polychaete *Polydora* sp. as a borer in *F. latimarginata.*

Polychaete burrows in *Fissurella* shells provide shelter for young specimens of the bivalve *Hiatella solida,* which may then bore further into the shell, as has been reported in shells of *F. nigra* by Gallardo and Osorio (1978).

Acrothoracican barnacles (burrowing barnacles) penetrate the shells of Chilean *Fissurella* species (Figs. 14, 15). Tomlinson (1969:88) reported the species *Cryptophialus minutus* Darwin, 1854, in a shell of *Fissurella maxima.* The specimen examined by Tomlinson (actually *F. cumingi*) is illustrated here (Fig. 14). I have found this pattern of burrows in a specimen of *F. limbata* from Antofagasta (Fig. 15) and in *F. latimarginata* from a number of localities.

Burrows of a vermetid gastropod, *Dendropoma* sp., have been noted on specimens of *F. costata* (Fig. 13), forming one-whorled depressions nearly flush with the surface of the host shell, but not penetrating to the interior.

Parasites

Bretos and Jiron (1980) reported that digenetic trematodes of the genus *Proctoeces* Odhner, 1911, family Fellodistomidae, were present in the gonads of eight species of *Fissurella* in northern Chile. Percentages of infected individuals in each species ranged from 14% to 97%. The effect of this parasitism on reproduction in the host species is unknown.

Seastar Predators

The seastar *Heliaster helianthus* is a voracious predator upon many species of mollusks in the lower intertidal zone (Paine and Palmer, 1978; Castilla, 1981). However, *Fissurella* has a highly effective escape response. *Fissurella* respond to initial contact with *Heliaster* by first raising the mantle fold above the edge of the shell, preventing the seastar's tube feet from making contact with the shell; thereupon they move rapidly out of reach. A collector with a seastar in hand may dislodge tightly wedged specimens without using a tool. The raising of the mantle to cover most of the shell surface is similar to the response of the north Pacific fissurellid *Diodora aspera* to various seastar predators (Margolin, 1964).

Fissurella costata is the only species that fails to show an escape response to *Heliaster.* It remains tightly appressed. Its foramen, the smallest among the larger species, is evidently too small for penetration by *Heliaster.*

The overall effect of *Heliaster* on populations of various species of *Fissurella* probably is not significant. Large individuals can move fast enough to escape and the small, less motile ones stay out of reach in crevices, or on the undersides of rocks.

In southern Chile, the asteroid *Meyenaster gelatinosus* is a major predator on many mollusks (Dayton et al., 1977). *Fissurella* and other gastropods escape predation from this seastar in surging water by allowing the water motion to move them away.

Vertebrate Predators

Non-human vertebrate predators that include *Fissurella* species in their diets in central Chile are the Chilean sea otter *Lutra felina,* the seagull *Larus dominicanus,* the oyster catcher *Haematopus ater,* and the clingfish *Sicyases sanguineus* (see Castilla, 1981).

The Chilean sea otter, the "nutria de mar," has a restricted and localized distribution, but where it occurs, the effect of this carnivore is significant. It feeds upon *Sicyases, Concholepas, Fissurella* species, the acmaeid limpets *Scurria* species and at least three species of crabs. Castilla and Bahamonde (1979) gave a more complete account of the ecology of *Lutra felina.*

According to Castilla (1981), *Haematopus ater* feeds upon *Concholepas, Scurria* species and *Fissurella* species; *Larus dominicanus* feeds upon *Concholepas,* crabs, herbivorous snails, *Fissurella* species, chitons, *Scurria* species, and mussels.

Sicyases feeds on a wide variety of invertebrates and algae on vertical walls in the surf-exposed intertidal zone (Paine and Palmer, 1978). Those authors reported small specimens of several species of *Fissurella,* and even one relatively large specimen of *F. cumingi* (Fig. 12), in clingfish stomachs. Most of the *Fissurella* shells were broken at one end, presumably by the strong teeth of this predator. Many shells cast up on beaches are broken in a similar way, suggesting that *Sicyases* is a major predator on *Fissurella.* A study of the breakage pattern in beach-worn shells would be useful to further document the feeding of *Sicyases.*

Fissurella costata is well adapted to habitats where *Sicyases* occurs. It attaches tightly, making it difficult for the clingfish to get hold of the shell. Other species of *Fissurella* have poor defense against *Sicyases* because the shell edge normally is raised and the mantle and foot exposed. *Sicyases* may be such an effective predator that it completely removes other species that stray into its habitat.

Human Predation and Economic Importance

Man is the chief predator upon *Fissurella.* Large individuals of all species are used for food throughout Chile and Peru. I found six species for sale in the municipal market at Iquique: *F. crassa, F. maxima, F. latimarginata, F. cumingi, F. limbata,* and *F. bridgesii.* They are collectively know as "lapas" and are not sorted by species when sold. Although the fishery for the lapa is on a small scale compared to that of the "loco," *Concholepas,* it amounts to a significant predation pressure on the larger-shelled species. Those sold in the market are kept intact in the shell. However, the shorelines in Chile have numerous piles of discarded shells (Fig. 1). According to figures from the Chilean Servicio Nacional de Pesca (SERNAP), 451,000 tons of *Fissurella* species were harvested in 1982 (C.A. Moreno, personal communication).

In populated areas, human predation on *Fissurella* is significant. Moreno et al. (1984) found few specimens of *F.*

picta lata over 4 cm in length in the vicinity of Valdivia. Much larger sizes occurred in areas where human access was restricted. Where the *Fissurella* were experimentally removed from the habitat, there were dramatic increases in the algal cover of *Iridaea boryana*, its chief food source. This alga is also harvested in Chile. Human predation on *Fissurella* therefore helps to ensure a good harvest of the alga.

Fishermen in Chile know each species by a common, descriptive name (Bretos, personal communication). The names in use in northern Chile are mentioned in the species accounts.

SYSTEMATIC CHARACTERS

Useful shell characters include: size; outline in dorsal view; sculpture—the strength and spacing of the radial ribs; color pattern; interior shell margin—the thickness and pigmentation pattern; and foramen—the size, shape, and placement. Other shell characters such as the muscle scar and the internal callus show few significant differences and are therefore not treated unless they have unusual features. The organisms that encrust the surface of shells can provide important ecological information, but shells must be cleaned in order to see the sculpture and color pattern.

Juvenile shells are commonly very different from mature shells and are therefore separately described in this account.

Features of external anatomy such as color of the cephalic tentacles and development of mantle lobe papillae and tubercles on the foot are specific characters that may enable identification of species.

The morphology of the large outer lateral tooth of the radula provides a specific character.

The most useful specific characters are discussed in greater detail as follows.

Size and Shape

The anterior end of the shell is narrower than the posterior. The muscle scar opens anteriorly. All shells are illustrated here with the anterior at the top; the lateral view shows the left side.

The outline in most species is elongate-oval. *Fissurella costata, F. picta lata,* and *F. peruviana* are generally rounder than other species. *Fissurella latimarginata, F. cumingi,* and *F. pulchra* are wedge-shaped, having a relatively narrow front end and tapered sides.

Shells seldom lie flat in one plane. In most species, the sides are slightly elevated relative to the ends. This is particularly true of such highly motile species as *F. maxima,* and enables a better fit on rounded rock surfaces. Species that commonly nestle in crevices or have a habitual site of home attachment may instead have elevated ends for a better fit. Both extremes are possible in *F. nigra* and *F. oriens.* Some specimens of these species have both elevated sides and elevated ends, so that the shell rests on four corners.

Shell height is fairly constant in some species and variable in others. Species with relatively low shells (length 3.2 to 5.9 times height) include *F. crassa, F. bridgesii,* and *F. pulchra.* Those that vary from low to medium in height (length 2.8 to 4.5 times height) include *F. maxima, F. latimarginata, F. costata, F. radiosa,* and *F. oriens. Fissurella peruviana* varies from extremely low to high (length 1.5 to 4.8 times height).

In some species, the shell may be steeply conical in young stages and abruptly become more flattened at later stages. This commonly happens in *F. oriens, F. costata,* and *F. limbata.*

Fissurella nigra may grow by increasing the shell height while contracting the length and width, especially in gerontic specimens. This makes the slopes convex and the shell margin very thick. This growth form has not been observed in other species.

Sculpture

Shell sculpture is relatively consistent within most species. The radial ribs produced in the earliest growth stages are called the primary ribs and those arising between the primary ribs at later growth stages are called the secondary ribs. Secondary ribs attain the size and prominence of the primary ribs in *F. latimarginata, F. cumingi,* and *F. oriens.* Primary ribs are stronger than the secondary ribs at all growth stages in *F. picta, F. radiosa, F. costata, F. maxima,* and *F. peruviana. Fissurella crassa, F. pulchra,* and *F. bridgesii* generally have smooth shells in mature stages, although their young stages have rounded primary ribs, but no secondary ribs.

Color Pattern

Color patterns in all species have definite limits of variation, extensive in some, limited in others. Most species have a pattern of dark-colored rays on a lighter ground color. Least variable in color pattern are *F. maxima, F. limbata,* and *F. pulchra.* Such strongly rayed shells as those of *F. picta, F. radiosa, F. cumingi,* and *F. oriens* have ground colors ranging from light to dark gray or tan and correspondingly darker rays. White shells occur only in *F. oriens.* The most variable species, having both rayed forms and uniformly colored forms, are *F. peruviana, F. latimarginata, F. radiosa,* and *F. oriens.*

In addition to the radial rays, all species may have concentric growth bands of varying color intensity. Changes in the coloration of growth bands have been correlated with changes in diet in such herbivorous archaeogastropods as *Haliotis* (Olsen, 1968a, 1968b). Changes in supply of food or a shift in the algal composition of the diet can probably be correlated with changes in the banding of *Fissurella* shells. Concentric color changes are most pronounced in *F. picta, F. radiosa,* and *F. oriens,* the three species that range to the high southern latitudes where ecological conditions are most extreme. Bretos (1978, 1980) has shown that there are seasonal growth rings in *F. crassa.*

Shells exposed to weathering fade. The dark purple or gray rays change to red, particularly in *F. maxima* and *F. picta lata.*

Interior Margin

The interior margin or border, composed of the calcitic layer of the shell, generally has several bands or zones, visible also in cut or broken pieces of the shell. Color differences in the margin are useful specific characters. The width of the margin changes with growth. In young, rapidly growing shells, it is relatively broad; in mature shells it is proportionately narrower, and in old shells it may be nearly obliterated by the encroachment and thickening of the inner aragonitic layer. It is consistently narrow in all growth stages of *F. radiosa* and *F. peruviana.* In most species the margin or growing edge is flat, but in *F. maxima* it is convex, and in *F. crassa* the entire edge is rounded.

In some species the margin of the shell is uniformly pigmented across its full width, in others the pigment is concentrated near the surface or deeper within the layer. Only in *F. nigra* is the outermost zone darker than the inner zone. In *F. latimarginata* and *F. pulchra* the outer edge is lighter and in *F. limbata* the outer edge is much lighter and contrasts sharply with the inner zone. Color rays are confined to the outermost layers of the margin in *F. limbata* and *F. maxima,* but extend the full width of the margin in *F. cumingi* and *F. oriens.*

Foramen

The relative size and the configuration of the foramen changes with growth. In young shells it is elongate, broad in the middle and constricted in two places on the sides. The foramen can be described as tripartite, and the side walls as bidentate if the three-lobed aspect is especially conspicuous. In most species the foramen changes from tripartite in young stages to oval in mature stages. In some species its size in mature specimens varies greatly; it may become very large in some old shells of *F. oriens.* In *F. peruviana,* the tripartite aspect of the foramen is lost at a very early stage, and the foramen becomes oval. *Fissurella costata* has a particularly small foramen at all growth stages. *Fissurella limbata* is unusual in retaining an elongate foramen in mature sizes. *Fissurella crassa* also retains an elongate foramen that is constricted in the middle, although the young shells are bidentate like those of other species.

In most species the position of the foramen is slightly posterior to the midpoint of the shell, but in *F. nigra* and *F. radiosa* it is more markedly so.

Juvenile Shell

The earliest juvenile shells of all species are more elevated and conical than later stages. Primary ribs appear at an early stage. In forms with a rayed pattern, the elevated ribs are light-colored and the interspaces are dark-rayed. Juveniles of many species have a pair of broad white rays extending laterally, more prominently than the other light-colored rays. This pattern is especially evident in the juveniles of *F. latimarginata,* in which the light rays persist until the shell is 10 or 20 mm in length. In *F. nigra, F. crassa, F. peruviana, F. cumingi,* and *F. maxima,* the two light rays are seen only in juveniles of less than 5 mm length. Some have characteristic early colorations unlike the adults. Young *F. nigra* are light-colored rather than black; *F. oriens, F. maxima,* and *F. peruviana* are reddish when young; *F. limbata* has a zigzag pattern of lines; *F. maxima* and *F. cumingi* have speckled patterns.

External Anatomy

The relative size of the animal in proportion to its shell is a useful comparison for at least those species at either extreme; the animals of most species are relatively large and just barely containable within the shell. The extremes are *Fissurella crassa* and *F. bridgesii,* which have flat shells that cannot contain the animal, and *Fissurella costata* and *F. peruviana,* which have high conical shells, the animal easily contained within the shell.

In most species, the cephalic tentacles are dark, reddish on the inner side and yellowish at the tips. *Fissurella nigra* is the only species that shows only shades of gray and black on the tentacles as well as on the mantle and foot.

The mantle lobe has three edges, here called the inner, the upper, and the lower. The inner lobe lacks papillae and is in direct contact with the growing margin of the shell. The upper lobe extends up over the edge of the shell, and the lower lobe extends down. The edges of the upper and lower lobes have finely branched papillae. The papillae of the upper lobe are generally more strongly developed than those of the lower edge. The area between, which is greatly expandable, is usually vertically banded to match the pattern of rays on the shell. This area may also show dark pigment in concentric grooves. The edge of the lower lobe of *F. latimarginata* is a striking orange color, the only species so marked, making it readily recognizable.

In all species the side of the foot is rugose or pustular. Coloration is mottled, the tips of the pustules or tubercles lighter in color. Overall coloration of the foot is brown or gray in most species; however, the foot of *F. cumingi* has a distinctive strawberry-red color and that of *F. costata* has a pale pinkish-brown color.

Epipodial tentacles extend along the foot sides. They are short and stubby but are slightly more prominent that the ordinary tubercles on the foot side. They are particularly prominent in *F. oriens.*

Radula

There are few specific differences in the rachidian and inner lateral teeth in *Fissurella,* although those of *F. pulchra* (Figs. 266, 267) are somewhat unusual in having longer overhanging cusps. The larger outer laterals, however, show interspecific differences, as will be noted in comparing the illustrations for the radula of *F. nimbosa* (Figs. 21, 25), *F. picta* (Figs. 138, 142, 143), *F. peruviana* (Figs. 43, 44), *F. oriens* (Figs. 193, 194), and *F. pulchra* (Figs. 266, 267).

NAMES, ALLOCATIONS, AND KEY CHARACTERS

Names and Allocations

Fifty-eight names have been proposed for Recent species of *Fissurella* from the Peruvian Faunal Province, which encompasses central Peru to central Chile, and the Magellanic Fau-

Table 1. Names proposed for Recent species of *Fissurella* from the Peruvian and Magellanic faunal provinces, with allocations as discussed in this paper.

affinis Sowerby, 1835 = *F. peruviana*
alba Philippi, 1845 = *F. oriens oriens*
arenicola Rochebrune and Mabille, 1885 = *F. oriens oriens*
atrata Reeve, 1850 = *F. picta picta*
australis Philippi, 1845 = *F. oriens oriens*
bella Reeve, 1849 = *F. latimarginata*
biradiata Sowerby, 1835 = *F. latimarginata*
bridgesii Reeve, 1849
clypeiformis Sowerby, 1825 = *F. crassa*
clypeus Sowerby, 1835 = *F. peruviana*
cheullina Ramirez-Boehme, 1974 = *F. oriens oriens*
chilensis Sowerby, 1835 = *F. costata*
concinna Philippi, 1845 = *F. maxima*
costata Lesson, 1831
crassa Lamarck, 1822
cumingi Reeve, 1849
darwinii Reeve, 1849 = *F. radiosa radiosa*
depressa Lamarck, 1822 = *F. crassa*
doellojuradoi Pérez-Farfante, 1952 = *F. oriens oriens*
dozei Rochebrune and Mabille, 1885 = *F. radiosa radiosa*
exquisita Reeve, 1850 = *F. radiosa radiosa*
flavida Philippi, 1857 = *F. oriens oriens*
fulvescens Sowerby, 1835 = *F. oriens fulvescens*
galericulum Reeve, 1850 = *F. latimarginata*
grandis Sowerby, 1835 = *F. nigra*
grisea Reeve, 1849 = *F. radiosa*
hedeia Rochebrune and Mabille, 1885 = *F. oriens oriens*
hondurasensis Reeve, 1849 = *F. maxima*
lata Sowerby, 1835 = *F. picta lata*
latimarginata Sowerby, 1835
limbata Sowerby, 1835
maxima Sowerby, 1835
mexicana Sowerby, 1835 = *F. oriens oriens*
multilineata, limbata var., Ziegenhorn and Thiem, 1925 = *F. limbata*
muricata Reeve, 1850 = *F. picta picta*
navidensis Ramirez-Boehme, 1974 = *F. picta lata*
nigra Lesson, 1831
nigra Philippi, 1845, not Lesson, 1831 = *F. radiosa radiosa*
oblonga Ramirez-Boehme, 1974 = *F. oriens oriens*
obovalis Lesson, 1831 = ?
occidens Gould, 1846 = *F. peruviana*
oriens Sowerby, 1835
papudana Ramirez-Boehme, 1974 = *F. peruviana*
peruviana Lamarck, 1822
philippiana Reeve, 1850 = *F. radiosa radiosa*
philippii Hupé, 1854 = *F. radiosa radiosa*
picta Gmelin, 1791
polygona Sowerby II, 1862 = *F. radiosa radiosa*
pulchra Sowerby, 1835
punctatissima Pilsbry, 1890 = *F. latimarginata*
radiosa Lesson, 1831
rubra, costata var., Ziegenhorn and Thiem, 1925 = *F. costata*
rudis Deshayes, 1830, not Roeding, 1798 = *F. costata*
solida Philippi, 1845 = *F. maxima*
stellata Reeve, 1850 = *F. cumingi*
subrotunda Deshayes, 1830 = *F. peruviana*
tixierae Métivier, 1969 = *F. radiosa tixierae*
violacea Rathke, 1833 = *F. nigra*

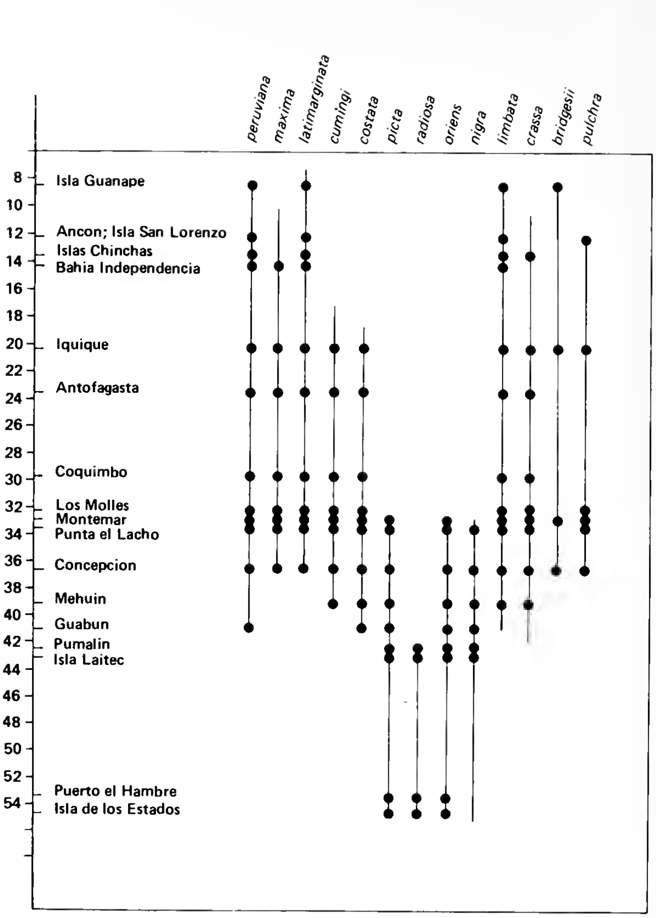


Figure 16. Distribution of *Fissurella* species in Peru, Chile, and southern Argentina by degrees south latitude. The identified place names are major LACM localities, some comprising several stations. The dots indicate that specimens are represented in the LACM collection. Lines without dots indicate distributions taken from other sources (see text).

nal Province, which includes southern Chile and southern Argentina. These names are listed alphabetically in Table 1, followed by my allocation. In the text that follows, I discuss the limits of variation for each species, but do not use variety or form names, even though some may be based upon readily recognizable variants. Geographic subspecies are discernible in three species of the Magellanic Faunal Province: *F. picta, F. radiosa,* and *F. oriens.* Trinomial designations are therefore used for these three species.

Difficulty in determining the taxa of such early authors as Lesson (1831) and Philippi (1845, 1857) has been due to a lack of illlustrations. I have not succeeded in locating the type specimens of these two authors. Nevertheless, using evidence from the original descriptions and type localities, I feel confident of the allocation of all names, except for *F. obovalis* Lesson, which is unassigned.

Chart of Key Characters

Attempts to prepare a dichotomuous key have not been successful because of the extreme variability of some of the species. Instead, the key characters are summarized in Table 2.

DISTRIBUTION AND ZOOGEOGRAPHY

Distributions of the 13 species of the subgenus *Fissurella* known from Peru, Chile, and Argentina are shown by latitude in Figure 16.

Nine species occur in the warm-temperate Peruvian Province, which extends from central Peru to central Chile: *F. peruviana, F. maxima, F. latimarginata, F. cumingi, F. costata, F. limbata, F. crassa, F. bridgesii,* and *F. pulchra.* Their northern and southern distributional records differ, but all nine are present between Iquique and Concepción, Chile (20° S to 37° S).

Four species are primarily members of the cold-temperate Magellanic Province, which includes southern Chile and southern Argentina: *F. picta, F. radiosa, F. oriens,* and *F. nigra.* Their distributions also differ, but all are present between 43° S and 54° S.

Except for *F. radiosa,* three of the four Magellanic species extend north in Chile to overlap with the distributions of the Peruvian species. The region of overlap is that between Valparaíso and Concepción, from 33° S to 37° S, in which 12 of the 13 species occur. At some point to the south of Concepción, four of the Peruvian Province species (*F. maxima, F. latimarginata, F. pulchra,* and *F. bridgesii*) drop out. I did not find them at Mehuin, Valdivia Province (39° S). Stuardo (1964) noted a transition zone between the two provinces from 38° S to 43° S. The transition zone noted here is therefore considerably to the north of that reported by Stuardo.

The number of *Fissurella* species occurring between Valparaíso and Concepción is significantly greater than the number known either to the north or the south. Distributions of species in other families should be considered to determine whether this transition area has a higher number of species than either of the two provinces treated separately.

The northernmost occurrence of the Peruvian Province species of *Fissurella* is at Isla Guanape, Peru (8°33′ S), where I have found *F. latimarginata, F. limbata, F. bridgesii,* and *F. peruviana.* I found none in January, 1974, in the transitional region between the Peruvian Faunal Province and the tropical Panamic Faunal Province at the Lobos Afueras Islands in northern Peru.

None of the species is known from the offshore islands of central Chile, Isla San Felix or Islas Juan Fernandez, either from literature records or recent expedition material from ANTON BRUUN cruises. A number of common Chilean mollusks are known from these islands. The absence of *Fissurella* correlates with the brief planktonic larval stage and resulting poor colonizing potential of fissurellids and other archaeogastropod larvae.

Fissurella picta, F. radiosa, and *F. oriens* are abundant at the southern limits of their distributions, where they undoubtedly extend to Cape Horn. These three species also occur at the Falkland Islands, which region is included in the Magellanic Faunal Province. They do not, however, occur at South Georgia or any of the subantarctic islands east of the Falklands (Powell, 1951). Strebel (1908:79) reported *F. exquisita* [here = *F. radiosa*] at Paulet Island, Antarctic Peninsula, a record that should not be accepted without further confirmation.

The Magellanic Faunal Province extends north through the Patagonian region of Argentina to the Gulf of San Matias, but only one of the Magellanic species, *F. radiosa,* occurs to the north of Tierra del Fuego in Argentina. It has a subspecies, *F. radiosa tixierae,* in its northernmost extent in Argentina. Absence of the other three species in Chubut and Santa Cruz Provinces of Argentina may be due to the vastly different ecological conditions. In Argentina, the tidal range is extreme, broad tidal flats are exposed, and inshore sediments often consist of fine beach sand. In southern Chile, the tidal range is less extensive, inshore waters are deep and clear, and beaches are few.

FOSSIL RECORD

There is little information in the literature about the fossil record of *Fissurella* in Peru and Chile. Ihering (1907) particularly noted the abundance of *Fissurella* in the Recent and the complete lack of the genus in the lower Tertiary of Chile and Patagonia.

In the most recent report on the mollusks of the Pliocene and Pleistocene formations of Chile (Herm, 1969), none of the *Fissurella* species was given formal systematic treatment. Herm listed five characteristic Pleistocene species: *F. microtrema* Sowerby, 1833 [undoubtedly *F. peruviana,* rather than the tropical *F. microtrema*], *F. costata, F. crassa, F. lata* [*F. picta lata* here], and *F. concinna* [*F. maxima* here]. In his list of Pliocene species he noted only: "*Fissurella,* div. sp."

One species has been described from fossil material: *F. concolor* Philippi, 1887, from Pliocene beds of Mejillones, north of Antofagasta, Chile. I have received specimens identified as this species from E. Martinez, collected from two of the Pliocene localities near Antofagasta detailed by Herm: the Cerro Costino locality south of Antofagasta, and the Hornito locality north of Antofagasta. Specimens (Fig. 17) agree with Philippi's description in having three smaller ribs between each of the larger ribs. The overall shape and profile is similar to that of *F. maxima,* but the primary ribs are stronger than those of *F. maxima.* The interior aragonitic layer is missing entirely from the specimens, in agreement with the principle that calcitic structures are best preserved in fossils.

A fragmentary specimen of another species from the Cerro Costino locality has also been received from E. Martinez. This species (Fig. 18) has some affinity to *F. crassa.* In the absence of additional specimens, I am unable to further treat the fossil record of the group.

Fissurella, sensu stricto, is one of the youngest genera in the Fissurellidae, traced only to the Pliocene (Herm, 1969). Except for the Caribbean type species, it is an eastern Pacific genus, well represented in the Peruvian and Magellanic faunal provinces, and with a single species ranging from California to Baja California, Mexico (Fig. 19). The type species may have become established in the Caribbean during the

Table 2. Chart of key characters.

	Size	Height	Mature sculpture	Outline of base
F. peruviana	small 25–40 mm	low to high	medium ribs, strong primaries	oval to elongate
F. maxima	large 80–135 mm	medium	strong ribs, strong primaries	elongate oval
F. latimarginata	large 70–115 mm	low to medium	fine ribs	tapered oval
F. cumingi	large 80–100 mm	medium	medium ribs	tapered oval
F. costata	medium 50–80 mm	low to medium	strong ribs, strong primaries	oval
F. picta picta	large 65–95 mm	medium	strong ribs, strong primaries	elongate oval
F. picta lata	medium 50–80 mm	medium to high	strong ribs, strong primaries	oval
F. rad. radiosa	small 40–55 mm	low to medium	medium ribs, strong primaries	tapered elongate
F. rad. tixierae	small 25–45 mm	medium	medium ribs, strong primaries	tapered elongate
F. oriens oriens	medium 40–70 mm	low to medium	fine, broad ribs	elongate oval
F. o. fulvescens	medium 45 mm	low	fine, broad ribs	elongate oval
F. nigra	large 70–110 mm	medium	fine, weak ribs	elongate oval
F. limbata	large 60–90 mm	medium	undulations	elongate oval
F. crassa	medium 60–90 mm	low	undulations	elongate oval
F. bridgesii	large 65–90 mm	low	irregular striae	tapered oval
F. pulchra	medium 35–75 mm	low	undulations	tapered oval

period in which the Central American seaway provided free access between the western Atlantic and eastern Pacific during the Miocene and early Pliocene (see Woodring, 1965, 1966).

FORMAT FOR SPECIES ACCOUNTS

Description. Shell descriptions treat the following characters in order: the size range (length in mm) of examples considered to be mature, the relative height, the outline in dorsal view, whether the sides or ends are raised, strength of the radial ribs, the color pattern, the shell layers, the interior margin, and the position and shape of the foramen. Dimensions for shell length, width, and height are given in that order in the captions for the figured specimens, not duplicated in the text. For specimens with uneven basal margins, shell height is the maximum elevation when the shell rests upon a plane surface.

Juvenile Shell. A separate description.

Mantle and Foot. Anatomical characters include the relative size of the body and shell, the relative prominence of papillae on the upper and lower edges of the mantle lobe, coloration of the cephalic tentacles, the color of the foot-side and the relative prominence of the foot-side tubercles.

Habitat. The intertidal or subtidal occurrence, conditions of exposure, and the epibiotic associations.

Distribution. The northernmost and southernmost verified record, the latitude coordinates for these records, and the source of the record. The source is the museum catalog number if the specimen has been examined, or an author and date, if the record is based on a published account considered to be correctly identified. This is followed by commentary about its possible occurrence beyond the verified limits and corrections of previous records now considered to be inaccurate.

Table 2. Continued.

Shell color	Shell margin	Mature foramen	Foot side color
red, gray, white rayed or solid	narrow showing rays	oval	gray-brown mottled
reddish brown rays on white	broad, rays on outer edge	oval	dark brown mottled
solid purple gray	broad, solid reddish brown	elongate oval	black with yellow outer edge of mantle
reddish rays on dark yellow	broad, rays show on full width	elongate oval	reddish brown mottled
gray rays on yellow	broad, rays show on full width	elongate oval, small	pinkish gray mottled
split gray rays on light ground	broad, rays strong on outer edge	elongate	light brown-black mottled
split gray rays on light ground	broad, rays strong on outer edge	elongate	brown-black mottled
gray or reddish rays on white	narrow, showing rays	elongate	gray-brown mottled
gray or reddish rays on white	narrow, showing rays	elongate	gray-brown mottled
red to gray rays on light ground	medium width, showing rays	elongate oval	pinkish brown mottled
reddish rays on dark yellow gr.	medium width, showing rays	elongate oval	not seen
solid gray, rays faint	broad, gray, dark at edge	elongate oval beveled	gray mottled
purple rays on dark yellow	broad, purple, white at edge	elongate	light gray mottled
solid brown, faint rays	brown upturned	very long, constricted	mantle brown banded foot gray mottled
gray brown, rays faint	broad, solid reddish brown	elongate oval	brown-black mottled
rays and speckles on pinkish brown	broad, reddish brown	elongate	light pinkish mottled

Number of Lots Examined. The total number of lots and the number in each of the following museum collections: LACM, AMNH, ANSP, MACN, MNHN, and USNM. These counts also provide an indication of the relative abundance of each species.

Taxonomic History. Indicates whether authors have understood the species with the limits now recognized, or if the present treatment is a departure from past classifications.

Abundance and Use. The fishery use and potential of each species, and the common name, as provided by M. Bretos.

Characteristics and Variability. The first statement under this heading is a brief description meant to convey the most characteristic features of the species, followed by an assessment of the variability, and whether variation may be correlated with geographic distribution.

Affinity and Comparisons. As assessment of the affinity to the most closely related species and the chief means of distinguishing the species from similar forms. Remarks about affinity are inferences. Future work may support or contradict these suggestions.

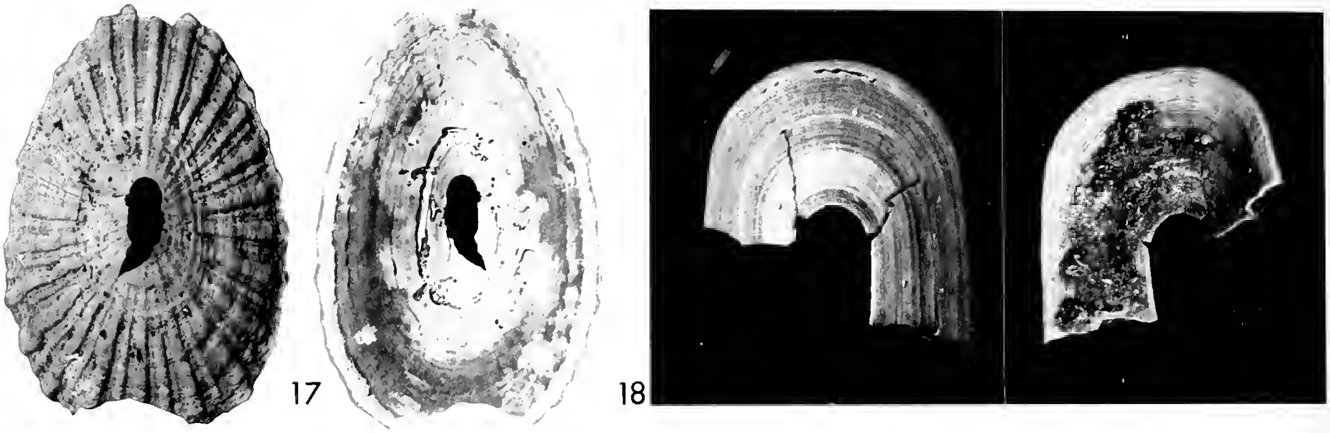
Synonymy and Types. Reasons for the assignment of each taxon; the type locality, measurements, and repository of type specimens. Lectotypes are designated for lots consisting of more than one original specimen.

SYSTEMATICS

Family Fissurellidae Fleming, 1822

I recognize two subfamilies in the Fissurellidae: the Emarginulinae, which I further subdivide into tribes (McLean, 1984b, and other work in progress), and the Fissurellinae.

The Fissurellinae are the youngest members of the family,



Figures 17 and 18. Fossil specimens of *Fissurella* spp. of Pliocene age, Cerro Costino, 12 km S of Antofagasta, Chile (23°45′ S, 70°26′ W), collected by E. Martinez. Specimens have lost the interior aragonitic layer. **(17)** *F. concolor* Philippi, 1887. LACM 90797, 60.6 × 40.8 × 9.5 mm. **(18)** *Fissurella* sp., cf. *F. crassa*, LACM 90798, 25.2 × 24.4 × 8.6 mm (specimen incomplete).

appearing in the Cenozoic; the Emarginulinae arose in the Mesozoic, with a burst of radiation in the Jurassic.

Subfamily Fissurellinae Fleming, 1822

DIAGNOSIS. Apex of mature shell wholly absorbed by the foramen; foramen bordered inside by a ring of callus that is not truncated or excavated posteriorly. Selenizone not present in juvenile stage. Shell muscle and muscle scar lacking inturned hooked processes. Rachidian tooth of radula narrow at the tip, its base broad, no larger than the adjacent laterals; the massive fifth lateral usually with four cusps; marginals numerous.

The subfamily Fissurellinae differs from the subfamily Emarginulinae in radular characters and in the morphology of the shell muscle. In the Emarginulinae the rachidian tooth is rhomboidal in shape (whether broad or narrow) and the enlarged fifth lateral has only two prominent cusps; in the Fissurellinae the rachidian tooth is narrow at the tip and the enlarged fifth lateral has four cusps (except three in *Amblychilepas*, one very small). Also, the muscle scar and corresponding shell muscle of the fissurelline genera lack the hook-shaped process of such emarginuline genera as *Puncturella* and *Diodora*. Early stages of emarginuline genera have a selenizone that may be lost in mature stages, but the selenizone is not present at any stage in the Fissurellinae.

Other genera in the subfamily Fissurellinae are *Amblychilepas* Pilsbry, 1890, and *Macrochisma* Sowerby, 1839, both of which are limited to the Indo-Pacific, and have animals too large to be contained in the shell.

Genus *Fissurella* Bruguière, 1789

DIAGNOSIS. Shell conical, sculpture chiefly radial; foramen nearly central.

Two subgenera of *Fissurella* are here recognized: *Fissurella, sensu stricto,* with a two-layered shell, the outer layer composed of calcite, the inner layer of aragonite, and *Cremides* H. and A. Adams, 1854, in which the shell is composed entirely of aragonite (Fig. 30). This is the first time that the subgenera have been so defined. As discussed above, it has not previously been noted that the shell margin is indicative of a two-layered shell rather than merely a color difference.

Figure 19. Distribution of *Fissurella, sensu stricto,* in North and South America.

Recent authors (e.g., Keen, *in* Knight et al., 1960) have regarded *Fissurella, sensu stricto,* as monotypic, and have placed the tropical species lacking the shell margin in *Cremides* and the South American species having the shell margin in *Balboaina* Pérez-Farfante, 1943. In the present treatment, the scope of the subgenus *Cremides* remains unchanged, but *Balboaina* is synonymized with *Fissurella, sensu stricto.*

Cremides has a fossil record from the Oligocene (Keen, *in* Knight et al., 1960), whereas *Fissurella, sensu stricto,* dates from the Pliocene.

Subgenus *Fissurella* Bruguière, 1789

Fissurella Bruguière, 1789:xiv (genus without named species). Type species, by subsequent monotypy of Lamarck, 1799: *Patella nimbosa* Linnaeus, 1758.

Balboaina Pérez-Farfante, 1943:2. Type species, by original designation, *Fissurella picta* (Gmelin, 1791).

Carcellesia Pérez-Farfante, 1952:31. Type species, by original designation, *Fissurella* (*Carcellesia*) *doellojuradoi* Pérez-Farfante, 1952 [= *F. oriens* Sowerby, 1835].

Corrina Christiaens, 1973:93. Type species, by original designation, *Fissurella* (*Corrina*) *alba* Philippi, 1845 [= *F. oriens* Sowerby, 1835].

DIAGNOSIS. Shell moderately large, composed of pigmented, outer calcitic layer that forms broad margin on inner side; interior aragonitic layer relatively thin except in apical area, extending to shell margin only in some fully mature specimens. Mantle papillae well developed; foot side tubercles well developed, epipodial tentacles short and stubby.

The species of *Fissurella, sensu stricto,* total 15: the 13 species of Peru and Chile treated in detail here, plus the Caribbean type species *F. nimbosa* (Figs. 20–25) and the Californian *F. volcano* Reeve, 1849 (Figs. 26–29). The distribution of *Fissurella, sensu stricto,* is shown in Figure 19.

Generic Synonymy. Bruguière's introduction of the name without reference to species has caused some confusion over the type designation. Although many authors have followed Pilsbry (1890) in the usage of *F. picta* as the type species, more recent authors have followed Wenz (1938) in citing *F. nimbosa,* by subsequent monotypy of Lamarck (1799).

Fissurella nimbosa (Figs. 20–25) is unlike all other tropical species of the genus. Pilsbry (1890) described the interior of *F. nimbosa* as having a "black line around the edge." He also observed that the species "has more the aspect of the Chilean species than that of the West Indian," a comment overlooked by subsequent authors. *Fissurella nimbosa* is the only species with the two-layered shell that has a tropical distribution. It differs from all the Peruvian and Magellanic species in having a green suffusion to the interior, a character shared with the Californian *F. volcano* (Figs. 26–29).

Pérez-Farfante (1943) did not notice that young shells of *F. nimbosa* have a well-defined dark margin. The shell she figured (1943, pl. 1, figs. 1, 2) is mature, with the aragonitic layer obliterating the dark border. She considered *Fissurella* to be a monotypic subgenus consisting only of *F. nimbosa* for reasons not clearly stated, but presumably because *F. nimbosa* is larger and more conical than most of the tropical speeies. She therefore missed the affinity of *F. nimbosa* with the Peruvian and Chilean species and proposed the subgenus *Balboaina* for those species with the dark border.

In my opinion, *F. nimbosa* is sufficiently similar to other species having the two-layered shell that it can not be separated from them on a subgeneric level. It is premature to offer a final opinion about the subgeneric division of the group, and I am, therefore, following a conservative course in uniting those with the calcitic layer. Further evidence about the affinity of the species with the calcitic outer layer needs to be offered from other lines of investigation, for example, electrophoresis. Until convincing arguments can be advanced to separate the Chilean species from *F. nimbosa* and *F. volcano,* I am treating *Balboaina* as a synonym of *Fissurella, sensu stricto.*

Pérez-Farfante's original diagnosis of *Balboaina* included the following provisions: "Margin of the shell entirely in one plane, simple, not crenulated . . . ." Neither of these traits is true for the majority of the southern species. Those species having radial ribbing are in fact finely crenulate at the margin, and most are raised at the sides.

Two other subgeneric names have been proposed: *Carcellesia* Pérez-Farfante, 1952, and *Corrina* Christiaens, 1973. Both names are based on type species that are here regarded as synonyms of *F. oriens. Carcellesia,* type species *F. doellojuradoi* Pérez-Farfante, 1952, was based upon a single aberrant example of *F. oriens* with prominently raised ends. *Corrina.* tvpe species *F. alba* Philippi, 1845, was intended to apply to thin-shelled forms lacking sculpture. I consider *F. alba* a synonym of *F. oriens,* based upon the scarce white-shelled form of the species. Christiaens also included in *Corrina* the South African species *F. mutabilis* Sowerby, 1835, but that species has no dark margin and is therefore unrelated. *Fissurella oriens* is a readily recognizable species in which the sculpture is weak, but I find no reason to single it out as representing a subgenus. Consequently, both names are relegated to the synonymy of *Fissurella, sensu stricto.*

Species Groups. Pilsbry (1890) placed the species having a "distinct dark marginal border inside" in four groups of species based on shell characters. I recognize a somewhat similar scheme of three groups within the subgenus *Fissurella, sensu stricto,* based on the presence or absence of complex radial sculpture and the relative thickness of the calcitic and aragonitic shell layers. Affinity among the species within each group is inferred, but this should be tested by future workers.

1. Aragonitic layer as thick as calcitic layer .... Group of *F. peruviana*
   Aragonitic layer markedly thinner than calcitic layer 2
2. Sculpture of primary and secondary ribs .... Group of *F. maxima*
   Sculpture of broad primary ribs only .... Group of *F. limbata*

Group of *Fissurella peruviana*

Relatively small-shelled species in which the thickness of the aragonitic layer equals or approximates that of the external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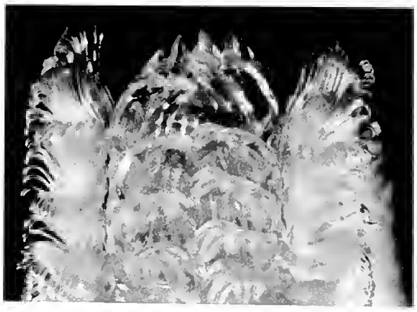
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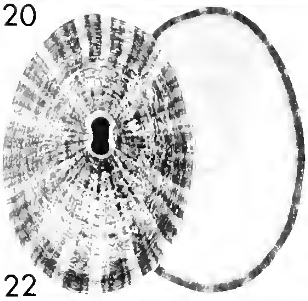
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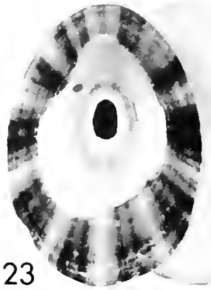
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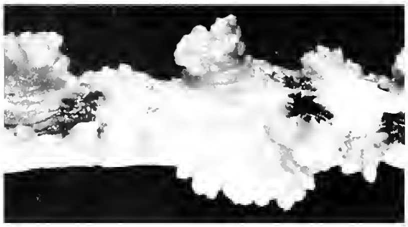
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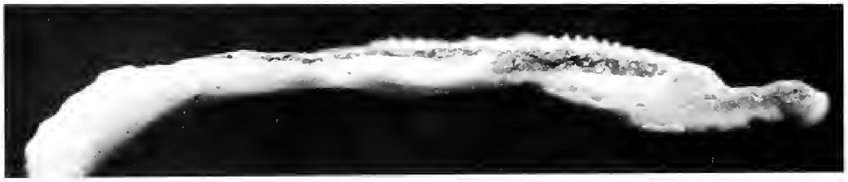
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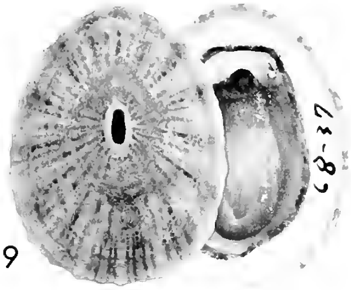
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Figures 20 through 30. Shells, radulae, mantle lobes, and cut shells of *Fissurella nimbosa* (Linnaeus, 1758), *F. volcano* Reeve, 1849, and *F.* (*Cremides*) *virescens* Sowerby, 1835. **Figures 20 through 25.** *F. nimbosa.* **(20)** Cut shell, showing thin, dark calcitic layer. LACM 76-30, Puerte La Cruz, Venezuela, length of cut edge 20.5 mm. **(21)** Radular ribbon. Same locality, width of ribbon, 1.4 mm. **(22)** Shell, Frigate Bay, St. Christopher, U.S. Virgin Islands. LACM 76-25, 27.0 × 24.9 × 8.1 mm. **(23)** Shell, Cabo Blanco, Isla Margarita, Venezuela, showing partial loss of the external calcitic layer and wear obliterating the dark margin in beach-worn shell. LACM 76-28, 37.9 × 26.2 × 14.0 mm. **(24)** Mantle edge, Frigate Bay, St. Christopher, U.S. Virgin Islands. LACM 76-25, length 3.5 mm. **(25)** SEM view of radula. LACM 76-30, Puerte La Cruz, Venezuela, width of field 0.8 mm. **Figures 26 through 29.** *Fissurella volcano.* **(26)** Cut shell, showing thin calcitic layer. LACM 66-1, Santo Tomas, Baja California, Mexico, length of cut edge 20 mm. **(27)** Mantle edge. AHF 1595-47, Río Santo Tomas, Baja California, calcitic layer; the shell margin (calcitic layer) narrow at all growth stages and in mature specimens often obliterated by encroachment of the aragonitic layer. Radial sculpture of primary and secondary ribs, which remain pronounced at all growth stages.

This group differs from both the group of *F. maxima* and the group of *F. limbata* in its relatively smaller size and in having a thicker aragonitic layer and a relatively thin and narrow calcitic layer.

In addition to *F. peruviana*, this group includes the type species of *Fissurella, F. nimbosa* (Linnaeus, 1757), of the tropical Caribbean faunal province (Figs. 20–25), and *F. volcano* Reeve, 1849, of the warm temperate Californian Faunal Province (Figs. 26–29). None of the species extends into the cold temperate Magellanic Faunal Province.

Although *F. radiosa* has an unusually narrow margin, as do the members of this group, it does not have a sufficiently thick aragonitic layer to suggest that it is related to these species.

In having a relatively thick aragonitic layer, this group of species represents the connecting link between the tropical species lacking the calcitic layer (subgenus *Cremides*), and the South American species with thick calcitic layers (subgenus *Fissurella, sensu stricto*).

Fissurella peruviana Lamarck, 1822

Figures 31–50

Fissurella peruviana Lamarck, 1822, 6(2):15; Orbigny, 1841: 74; Delessert, 1841, pl. 24, fig. 7; Reeve, 1849, pl. 5, figs. 26a–d; Hupé, 1854:241; Philippi, 1860:181; Sowerby II, 1862:185, figs. 38–41; Pilsbry, 1890:155, pl. 33, figs. 41–45, pl. 42, figs. 57–59; Dall, 1909:178, 242; Mermod, 1950: 713, fig. 22; Riveros-Zuñiga, 1951:130, fig. 35; Peña, 1970: 156; Dell, 1971:190; Christiaens, 1973:86; Ramirez-Boehme, 1974:31 [key].

Fissurella subrotunda Deshayes, 1830:135; Deshayes *in* Lamarck, 1836, 7:602; Orbigny, 1841:74 [under *F. peruviana*]; Reeve, 1849, pl. 5 [under *F. peruviana*].

Fissurella affinis "Gray," Sowerby, 1835a:125; Sowerby, 1835b:4, fig. 44; Sowerby II, 1862:185, figs. 46, 179; Christiaens, 1973:83.

Fissurella clypeus Sowerby, 1835a:128; Sowerby, 1835b:4, fig. 44; Reeve, 1850, fig. 76; Sowerby II, 1862:185, fig. 63; Pilsbry, 1890:156, pl. 60, fig. 82, pl. 31, fig. 20; McLean *in* Keen, 1971:901; Christiaens, 1973:83 [under *F. asperella*].

Fissurella occidens Gould, 1846:156; Gould, 1852:364, pl. 31, figs. 473a, b; Pilsbry, 1890:155 [under *F. peruviana*]; Johnson, 1964:118 [holotype, USNM 5863].

Fissurella papudana Ramirez-Boehme, 1974:18, 31 [key], pl. 2, figs. 5a, b, c.

Shell. Relatively small (25–40 mm mature length); variable in height from low to high conical; variable in outline from broadly oval to elongate and uneven; plane of margin also varying and probably conforming to an attachment site. Sculpture of fine, often imbricate, radial ribs, primary ribs remaining strong. Color highly variable, including some that are solid dark red to reddish gray, some that are faintly rayed, and some with rays of brown and white; lateral rays of elongate specimens often curving forward. Margin relatively narrow at all growth stages, reflecting pattern of rays through full thickness of calcitic layer. Cut shells show aragonitic layer slightly thicker than calcitic layer. Foramen elongate and tripartite in earliest stages but quickly becoming oval in juvenile shells and broadly oval in mature shells.

Juvenile Shell. Strongly sculptured, conical; frequently reddish with two lateral white rays. Mature specimens with brown and white rays have a red ring in the calcitic layer surrounding the foramen, a remnant of the juvenile red phase.

Mantle and Foot. Fully retractable in the shell. Mantle banded to match the rays of the shell. Mantle lobe relatively narrow, upper and lower edges with branched papillae. Foot side brown to black, with numerous, projecting, light-tipped tubercles.

Habitat. Lower intertidal zone to 20 m, but most abundant in the sublittoral zone. Scattered individuals occurring at low tide, nestled in crevices on the sides of rocks, the shell outline moulded to fit the site of attachment. Occurring at greater depths than any other of the species in northern Chile. At Mejillones (23°02′ S) it was the only species that I saw at 10–20 m on a sloping rocky bottom dominated by the mussel *Aulacomya ater*.

Distribution. Chiclayo, Peru (6°47′ S) (LACM, collector unknown; also reported at Chiclayo by Peña, 1970), to Guabun, northwestern tip of Isla de Chiloe, Chile (41°50′ S) (LACM 75-40, McLean). I have found specimens at most localities between Isla Guanape, Peru (8°32′ S), and Río Biobio, Concepción Province, Chile (36°48′ S), but did not find it at Mehuin, Valdivia Province.

Number of Lots Examined. 118 (LACM 52, AMNH 11, ANSP 11, MACN 3, MNHN 17, USNM 24).

Taxonomic History. *Fissurella peruviana* has been reasonably well understood by authors, at least with reference to its occurrence in Peru. Its presence in Chile has not been adequately discussed; Riveros-Zuñiga (1951) merely listed previous authors who cited records from Chile. A low form of this species with irregular outline is common in Chile (Figs. 36, 37, 39–42) and was illustrated by Riveros-Zuñiga (1951), misidentified as *F. stellata* Reeve, 1850. This form was twice named by Sowerby in 1835 and again by Ramirez-Boehme in 1974. Christiaens (1973) considered *F. affinis* Sowerby to be a good species, but there is little justification for such a

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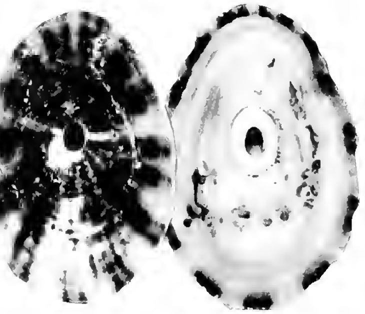
Mexico, length 5 mm. **(28)** Shell, White's Point, Los Angeles County, California. LACM 69-37, 28.7 × 20.0 × 11.7 mm. **(29)** Shell, same locality, 27.2 × 21.0 × 8.3 mm. **(30)** *Fissurella* (*Cremides*) *virescens*, cut shell, calcitic layer lacking, La Cruz de Juanacaxtl, Nayarit, Mexico. LACM 71-33, length of cut edge 23.7 mm.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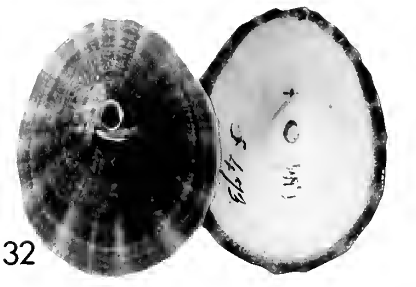
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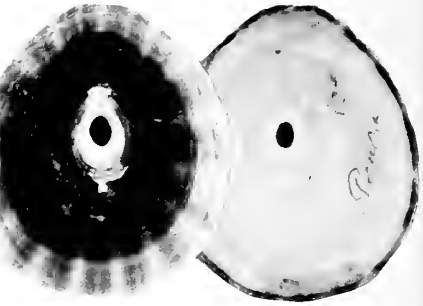
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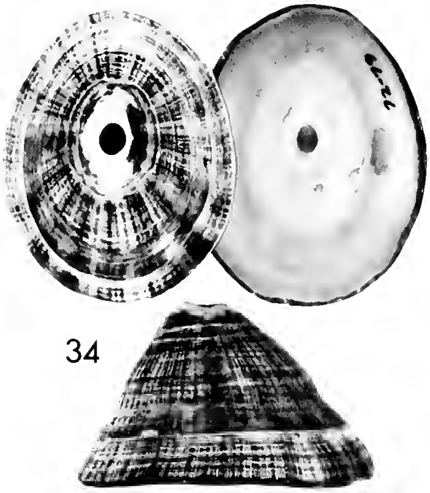
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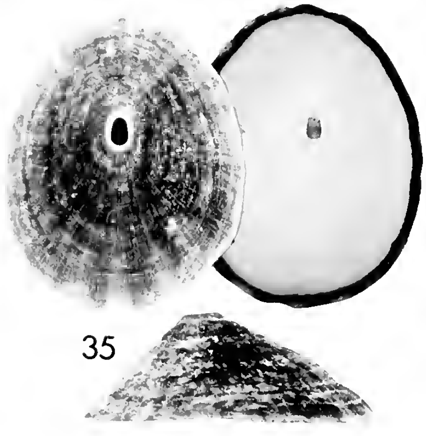
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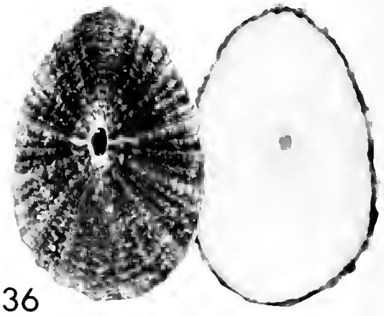
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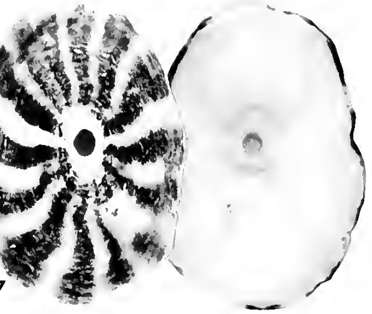
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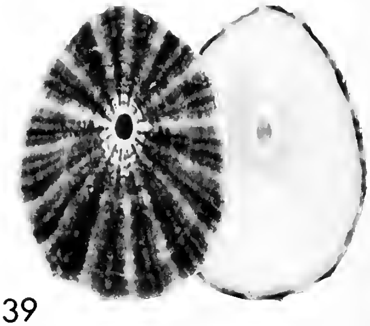
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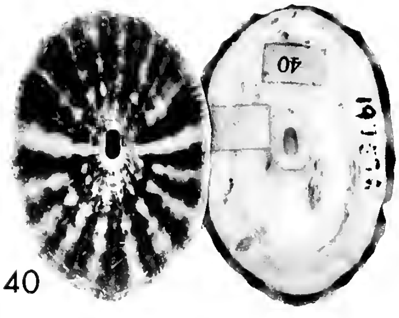
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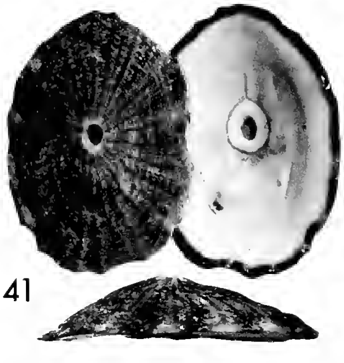
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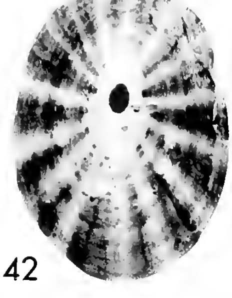
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Figures 31 through 42. *Fissurella peruviana* Lamarck, 1822. Mature shells. (**31**) 3–5 m, Isla Guanape, Peru. LACM 74-3, 45.1 × 23.5 × 12.8 mm. (**32**) Holotype, *F. occidens* Gould. Callao, Peru. USNM 5863, 35 × 27 × 19 mm. (**33**) Lectotype, *F. subrotunda* Deshayes. "Peru." MNHNP, 31.3 × 27.4 × 16.8 mm. (**34**) Paracas, Ica Province, Peru. LACM 72-79, 31.5 × 24.0 × 17.8 (beach shell). (**35**) Laguna Grande, Ica Province, Peru. LACM 72-77, 31.2 × 25.9 × 11.5 mm (beach shell). (**36**) Iquique, Chile. LACM 64-16, 24.0 × 16.7 × 7.6 mm. (**37**) view, as discussed below. The broad distribution and the extent of intraspecific variation in *F. peruviana* have not previously been understood.

Abundance and Use. Because of its chiefly sublittoral habitat, *F. peruviana* seems to be uncommon, although beach-worn shells are common throughout the range. This is the smallest species of *Fissurella* in Peru and Chile and therefore has little importance as a food resource. According to M. Bretos, the species has no common name in northern Chile, perhaps because it is considered the juvenile form of such species as *F. maxima.*

Characteristics and Variability. *Fissurella peruviana* is characterized by its small size, imbricate radial ribs, oval foramen, narrow margin, and relatively thick aragonitic layer. In lateral profile it varies from low to extremely conical; in outline it varies from broadly oval to elongate and irregular. Its color varies from uniformly dark reddish to gray or rayed with brown and white. It is the most variable species of *Fissurella* in the Peruvian Faunal Province.

Specimens from Peru tend to be more conical and more uniformly colored, whereas those from central Chile tend to be flatter and are more likely to be rayed with brown and white. However, I am not convinced that a geographic distinction can be drawn. I have noticed that the more conical forms occur on rocks adjacent to sandy bottoms, whereas the flattened forms with irregular outlines are found on rocky bottoms away from sand. At Iquique and Antofagasta the flattened irregular forms occur, but I have found some highly conical forms associated with the scallop beds north of Antofagasta at Bahia Morena. Conical specimens have also been seen from the Concepción vicinity. The recognition of geographic subspecies is therefore not justified.

Affinity and Comparisons. *Fissurella peruviana* differs from all other Peruvian and Magellanic species in having a relatively thick aragonitic layer and in having the oval foramen well developed at an early stage. Yet these differences do not seem sufficient to regard it as unrelated to those species with well-defined primary and secondary ribs in the group of *Fissurella maxima.* Of those species, it has the most in common with *F. costata,* with which it shares overall shape and the small, oval foramen. It more closely resembles *F. volcano* from California, which is also relatively small, with a narrow margin and proportionately thick aragonitic layer. *Fissurella peruviana* differs from *F. volcano* in having a more oval foramen and in lacking the green tinge of the interior and pink-bordered callus of *F. volcano. F. volcano* is an intertidally occurring species and *F. peruviana* is characteristically sublittoral.

When compared to young specimens of other Peruvian and Chilean species, *F. peruviana* can be distinguished by its narrow margin and oval foramen. Small specimens may be distinguished from the juveniles of *F. maxima* in having the foramen more oval and the margin not rounded. The primary ribs are not as strongly developed as those in young stages of *F. costata, F. picta lata,* or *F. radiosa.*

Synonymy and Types. *Fissurella peruviana* Lamarck, 1822, is one of the three earliest-named species of the region. Lamarck's specimens were from the "coasts of Peru," and some of the specimens were said by Lamarck to be less conical than others. Unfortunately, the first illustration of Lamarck's species (Delessert, 1841) may be a specimen of some other species, as suggested by Pilsbry (1890), Mermod (1950), and Christiaens (1973). Mermod (1950) discussed two Lamarckian specimens in the Geneva Museum collection considered to be original. "Specimen no. 2" discussed by Mermod fits the present concept of *F. peruviana* and is inscribed by the hand of Lamarck, according to Mermod. I am not able to determine the identity of "specimen no. 1," which is apparently the specimen figured by Delessert. Inasmuch as Lamarck indicated that there were several specimens, I hereby designate "specimen no. 2" as the lectotype, which is in accord with the original intent of the author. The lectotype (see Mermod, 1950, fig. 22-2) represents the high conical form of *F. peruviana* with a nearly circular foramen; length 20, width 25, height 16 mm.

I have examined 8 syntypes and the original mounting board of *F. subrotunda* Deshayes, 1830, received on loan from the Paris Museum. Lengths are 35.6, 31.3, 30.3, 30.0, 25.7, 22.7, and 20.7 mm. The original measurements were 32 mm in length and 28 mm in width; the second largest specimen is here designated the lectotype (Fig. 33); it is 31.3 mm in length and 27.4 mm in width and is probably the measured specimen. Type material, from "Perou," apparently has not previously been illustrated. All specimens are dark reddish rayed, moderately conical, and with an oval basal outline. No comparisons were originally made with *F. peruviana;* Orbigny (1841) relegated the name to the synonymy of *F. peruviana.*

Type material of *F. affinis* Sowerby, 1835, has not been located. Reeve (1849) regarded it as an elongate, flattened form of *F. peruviana.* Sowerby II (1862) doubtfully recognized it as a species "in order to avoid the extreme inconvenience of including opposite characters under the same name . . . ." Christiaens (1973) maintained it as a species, but in my opinion the original figure in the "Conchological Illustrations" represents the extreme flattened form of *F. peruviana,* which occurs throughout the range of the species in Chile. Several localities were mentioned originally: "Insulas Mexillones et Lobos, Iquiqui, and Valparaíso."

The holotype of F. *clypeus* Sowerby, 1835 (Fig. 40), was said to have come from "Sanctam Elenam," presumably the Santa Elena Peninsula, Ecuador. This name has baffled sub-

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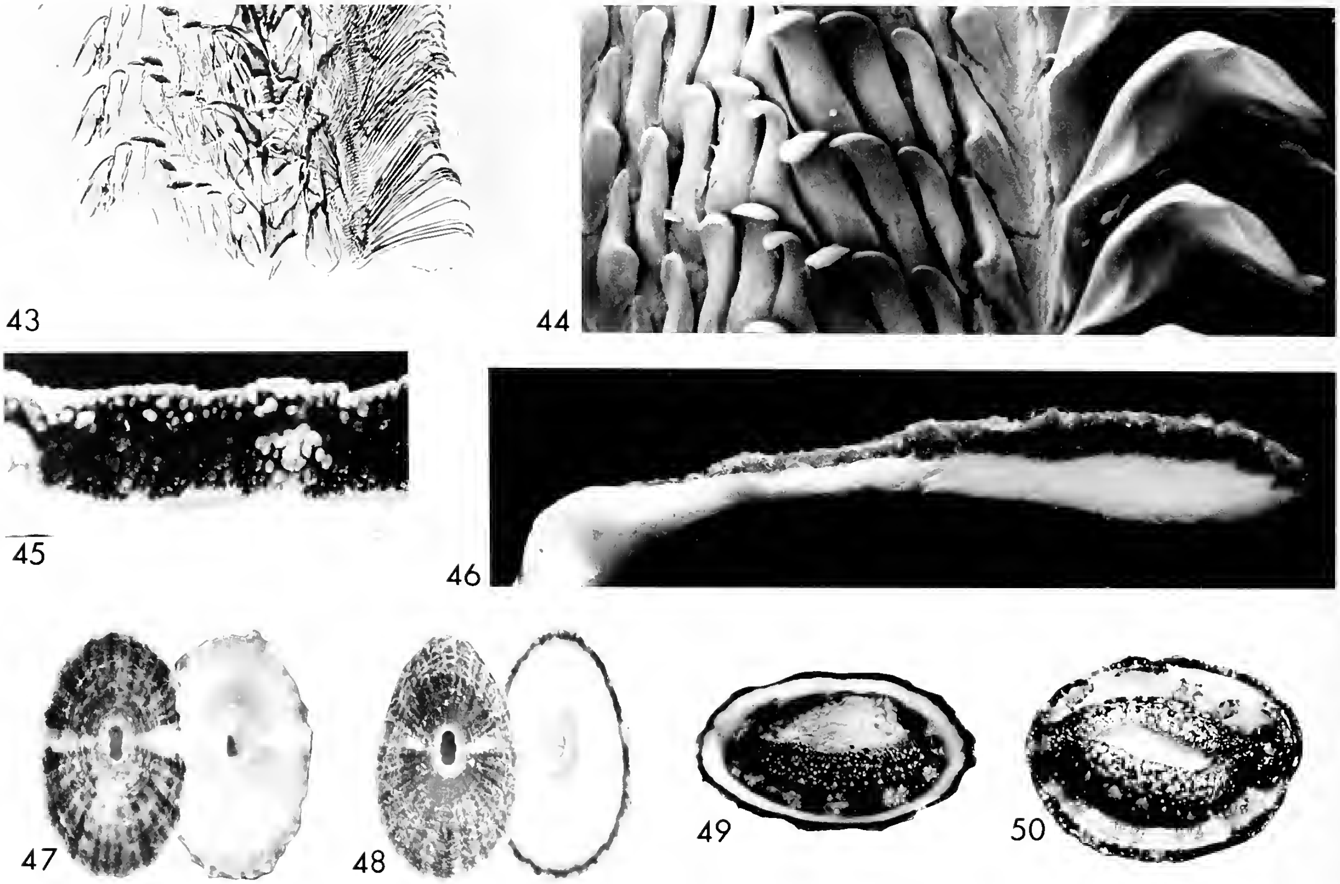
Iquique, Chile. LACM 75-12, 23.6 × 16.4 × 7.4 mm (beach shell). **(38)** 2–4 m, El Rincon de Mejillones, Antofagasta Province, Chile. LACM 75-23, 32.0 × 29.8 × 15.0 mm. **(39)** 2–5 m, Antofagasta, Chile. LACM 75-20, 27.0 × 18.8 × 17.6 mm. **(40)** Holotype, *F. clypeus* Sowerby. Locality doubtful. BMNH 197578, 28.0 × 18.9 × 5.8 mm. **(41)** Holotype, *F. papudana* Ramirez-Boehme. Papudo, Aconcagua Province, Chile. MNHN 200374, 36 × 26 × 10 mm. **(42)** Guabun, Chiloe Province, Chile. LACM 75-40, 27.3 × 19.7 × 7.9 mm (beach shell).



Figures 43 through 50. *Fissurella peruviana* Lamarck, 1822. Radula, mantle lobe, cut shell, juvenile shells, and intact specimens. **(43)** Radula, light microscope preparation. Montemar, Valparaíso Province, Chile. LACM 75-30, width of ribbon 0.4 mm. **(44)** Radula, SEM. 7–20 m, Mejillones, Chile. LACM 75-21, width of field 1 mm. **(45)** Mantle edge. 1–2 m, Playa Hermosa, Ancon, Peru. LACM 74-21, length 4 mm. **(46)** Cut shell. Los Colorados, Antofagasto, Chile. LACM 75-19, length 21 mm. **(47)** Juvenile shell. Same locality. 4.5 × 2.7 × 1.5 mm. **(48)** Juvenile shell. 3–5 m, Isla Guanape, Peru. LACM 74-3, 9.0 × 5.3 × 2.4 mm. **(49)** Body of preserved specimen. Antofagasta, Chile. LACM 75-15, shell length 25.1 mm. **(50)** Living specimen. Same locality, same specimen.

sequent authors, especially because a view of the internal margin has never been given and the foramen has been figured to be much longer that it actually is. In my opinion it is the flattened form of *F. peruviana,* as was suspected by Sowerby II (1862), and the shell more likely came from Chile. The Ecuadorian locality is well to the north of the northern limit of *F. peruviana,* and the flattened form of the species is particularly common in Chile. The foramen of the specimen is slightly longer than normal. Pilsbry (1890) copied the Reeve figure, but his figure 82, said to be a copy of the Sowerby figure, is not that, which has contributed to the confusion.

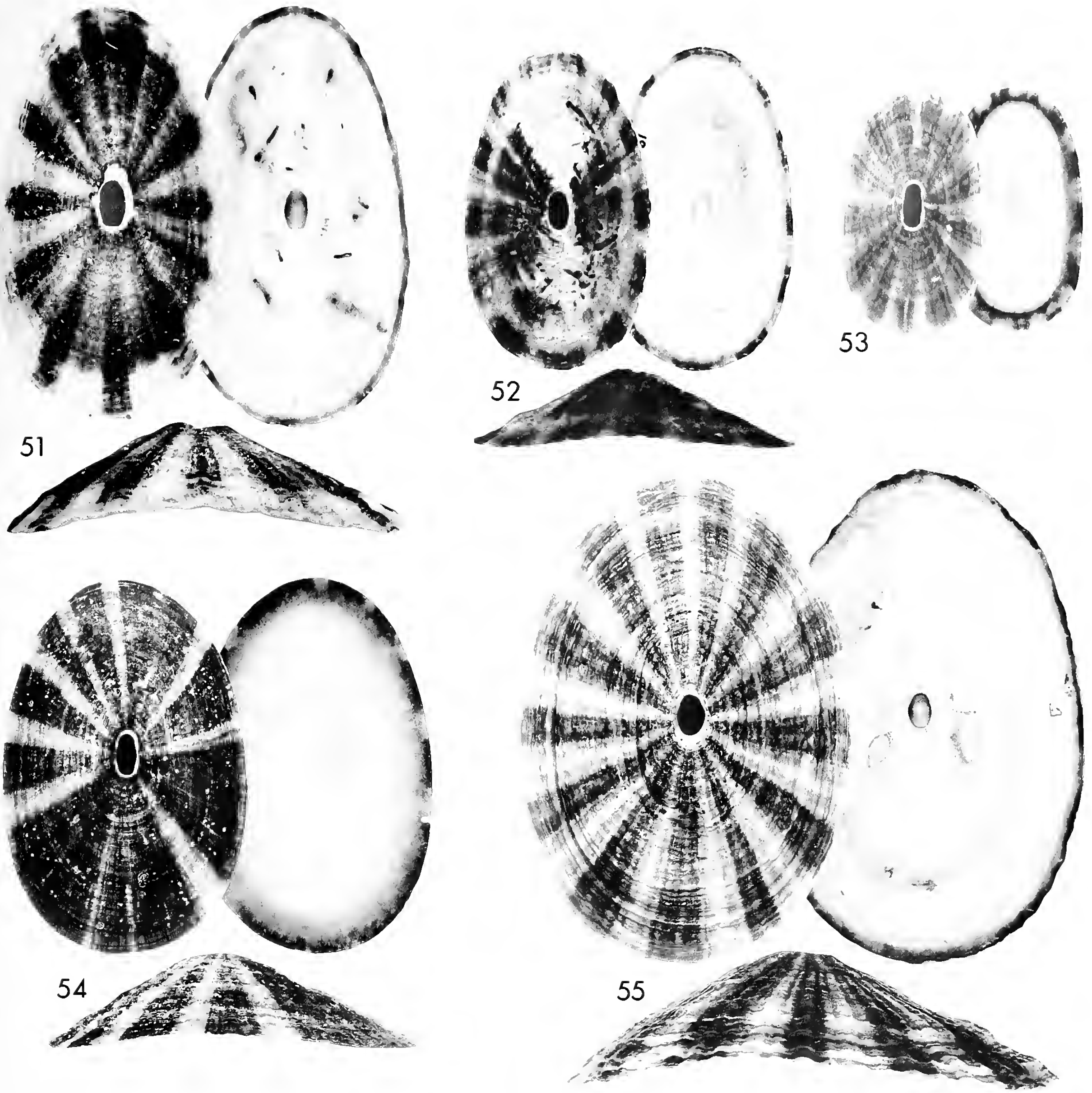
The holotype of *F. occidens* Gould, 1846, is USNM 5863, length 35 mm (Fig. 32). There are two paratypes, MCZ 155766 (Johnson, 1964). The type locality is Callao, Peru. The holotype represents the high-conical, reddish rayed form so abundant in Peru.

Fissurella papudana Ramirez-Boehme, 1974, was described without comparisons to other species. The type locality was Papudo, Aconcagua province, Chile. The holotype (Fig. 41), MNHN 200374, is an example of the flattened form of F. *peruviana,* with a narrow margin, irregular outline, oval foramen, and brown and white rays.

Group of *Fissurella maxima*

Relatively large-shelled species in which the thickness of the exterior calcitic layer of the shell greatly exceeds that of the interior aragonitic layer. All species have strong radial sculpture, at least in the early stages. Sculpture consists of primary ribs and weaker secondary ribs that arise between the primary ribs. Mature shells may retain the distinction between primary and secondary ribs, or all the ribs may attain a similar strength, whether coarse or very fine.

There are eight species in the group of *F. maxima,* four in the Peruvian Provice and four in the Magellanic Province. Most of the species in this group are highly variable and eurytopic, tolerant of a broad range of conditions of intertidal



Figures 51 through 55. *Fissurella maxima* Sowerby, 1835. Mature shells. **(51)** Bahia Independencia, Peru. AHF 380-35, 84.0 × 47.7 × 23.0 mm. **(52)** Lectotype, *F. hondurasensis* Reeve. Locality unknown. BMNH 1976139, 56.6 × 32.5 × 13.5 mm. **(53)** Iquique, Chile. LACM 64-16, 26.0 × 14.4 × 5.8 mm. **(54)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 73.9 × 47.4 × 18.0 mm. **(55)** Holotype, *F. maxima* Sowerby. Valparaíso, Chile. BMNH 197569, 128.8 × 85.4 × 34.7 mm.

exposure. Most species, particularly those with high variability, have been overnamed, the synonyms applying to variant specimens.

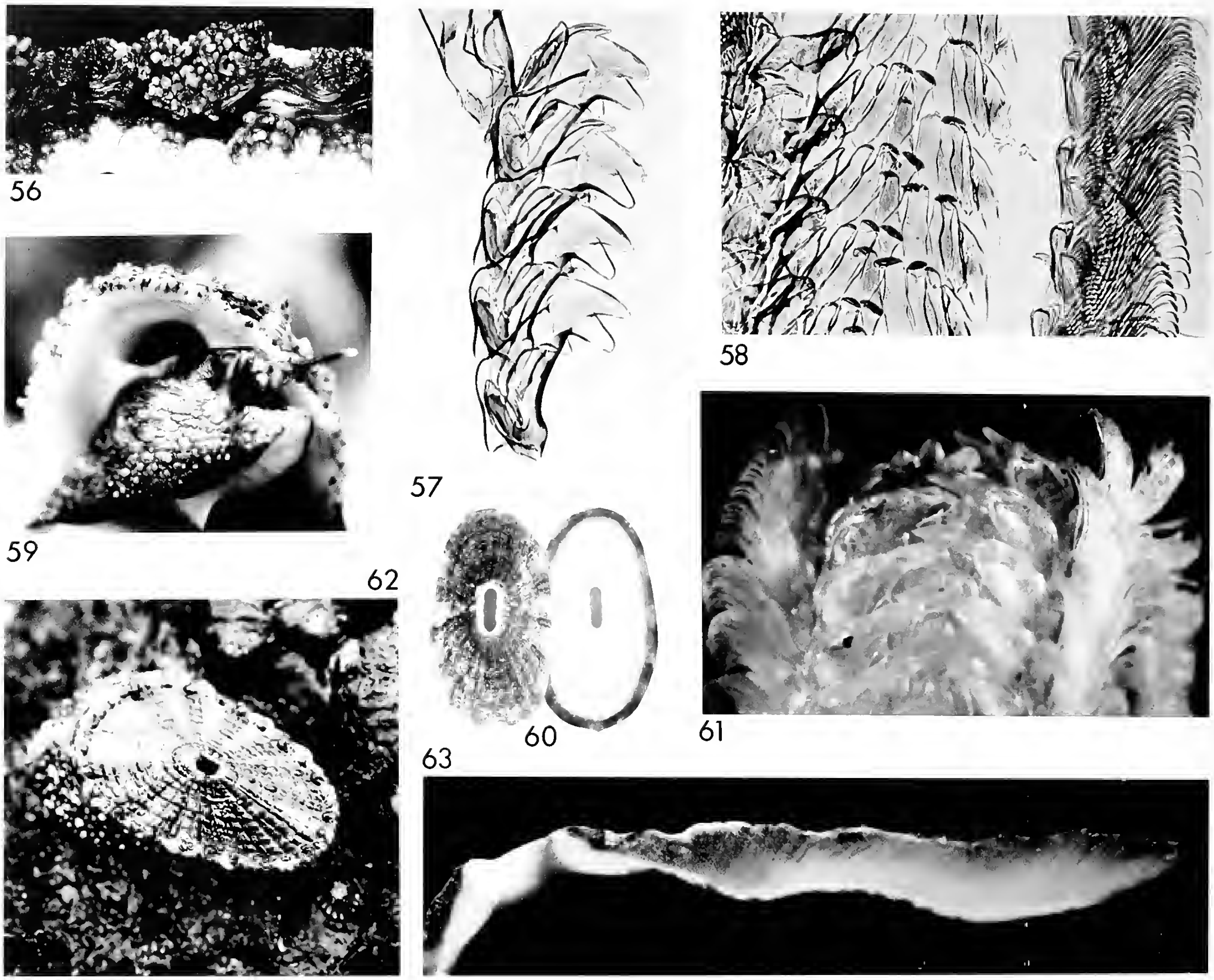
Only one species in this group, *F. nigra,* is stenotopic, with a narrow ecological tolerance, and low variability. It also differs from the other in having primary and secondary ribs pronounced only in juvenile stages.

Three of the four Magellanic species in this group have geographic subspecies.

Fissurella maxima Sowerby, 1835

Figures 51–63

Fissurella maxima Sowerby, 1835a:123; Sowerby, 1835b:3, fig. 18; Orbigny, 1841:475, pl. 64, figs. 4–7; Philippi, 1845:



Figures 56 through 63. *Fissurella maxima* Sowerby, 1835. Radula, mantle lobe, cut shell, juvenile shell, and living specimens. **(56)** Mantle lobe. Iquique, Chile. LACM 75-12, length 9 mm. **(57)** Radular teeth, lateral view of large outer lateral teeth. Iquique, Chile. LACM 70-68, width of ribbon 0.4 mm, shell length 20.5 mm. **(58)** Radular ribbon, same specimen. Width of field 1.0 mm. **(59)** Living specimen, anterior end, showing head with cephalic tentacles and foot side. Iquique, Chile. LACM 75-12. **(60)** Juvenile specimen. Punta El Lacho, Santiago Province, Chile. LACM 75-32, 14.0 × 7.8 × 2.9 mm. **(61)** Radular ribbon, air-dried. Bahía San Juan, Peru. AHF 828-38, width of ribbon 2.5 mm, shell length 58.9 mm. **(62)** Living specimen on rock substrate, anterior at right. Pozo Toyo, Tarapaca Province, Chile. LACM 75-10. **(63)** Cut shell. Montemar, Valparaíso Province, Chile. LACM 75-30, length of cut edge 37 mm.

3, pl. 1, fig. 1; Reeve, 1849, pl. 4, fig. 22; Hupé, 1854:239; Philippi, 1860:180; Sowerby II, 1862:187, figs. 8, 9; Watson, 1886:33; Pilsbry, 1890:145, pl. 30, figs. 8, 9, pl. 33, figs. 46, 47; Dall, 1909:242; Ziegenhorn and Thiem, 1925: 11, pl. 1, figs. 8a, 8b, 9a, 9b; Peña, 1970:156; Riveros-Zuñiga, 1951:102, fig. 18; Dell, 1971:188, pl. 4, figs. 1–3; Marincovich, 1973:18, fig. 31; Ramirez-Boehme, 1974:31 [key].

Fissurella solida Philippi, 1845:142; Carcelles and Williamson, 1951: 256; Dell, 1971:193; Ramirez-Boehme, 1974: 31 [key].

Fissurella concinna Philippi, 1845:143; Philippi, 1846:66, pl. 2, fig. 5; Reeve, 1850, pl. 15, fig. 112; Hupé, 1854:245; Sowerby II, 1862:187, figs. 4, 178, 206; Rochebrune and Mabille, 1889:71; Pilsbry, 1890:146, pl. 32, figs. 32, 33, pl. 45, figs. 7, 8 [as var. of *F. maxima*]; Carcelles and Williamson, 1951:256; Peña, 1970:156; Dell, 1971:183; Ramirez-Boehme, 1974:30 [key].

Fissurella hondurasensis Reeve, 1849, pl. 7, fig. 48; Pilsbry, 1890:146, pl. 35, fig. 6.

Shell. Relatively large (80 to 135 mm mature length), low to medium in height, outline elongate-oval; sides of shell elevated. Radial ribs prominent, low and rounded, alternating in strength, crenulating margin. Ground color pale yellow; rays dark purple, broad, uninterrupted; primary ribs centered in each light and dark ray. Margin very broad in growing shells, narrow in mature shells, rounded at junction with aragonitic layer; margin zoned; outer zone narrow, showing color rays; inner zone broader, uniformly pale and translucent. Cut shells show pigment of rays concentrated at surface. Foramen nearly central, elongate in young shells, oval in mature shells.

Juvenile Shell. High conical, base elongate, margin rounded; ribs rounded, strong; color reddish, with two lateral white rays and scattered black flecks. After length of 6 mm shell becomes flatter, the primary ribs nodulous and much more prominent than the secondary ribs; the light and dark rayed pattern emerges and the black flecks are lost.

Mantle and Foot. Not fully retractable in shell; cephalic tentacles brown, tipped with yellow. Mantle lobe broad, banded with purplish-brown and light gray to match rays on shell; papillae of upper edge bulbous, finely branched, those of lower edge smaller. Side of foot brown; tubercles strongly developed, tips lighter colored.

Habitat. Partially exposed rocky areas at low tide to 4 m. Some individuals are free of encrusting algae and live on the under sides of large flat rocks at low tide, but most live in the open and are covered with a dense low growth of red algae. When exposed at low tide they are tightly wedged in crevices. Only rarely do specimens have attached *Scurria parasitica* on the shell.

Distribution. Huarmey, Peru (10°06′ S) (LACM 70-97, E del Solar), to Lirquen, Concepción Province, Chile (36°41′ S) (LACM 72-207, Univ. Concepción). The southermost range of *F. maxima* in Chile is not as extensive as that of most of the other common species of the Peruvian Faunal Province. I found no trace of it at Río Bio-bio, Concepción Province, Mehuin, near Valdivia, or Guabun on the northwest tip of Isla de Chiloe. More extreme records in the literature are rejected: Dall's (1909) record from Manta, Ecuador, and Riveros-Zuñiga's (1951) record from Fuerte Bulnes in the Strait of Magellan. Dell's (1971) records from Isla de Chiloe are based upon specimens of *F. picta lata.*

Number of Lots Examined. 128 (LACM 34, AMNH 25, ANSP 7, MACN 14, MNHN 30, USNM 18).

Taxonomic History. *Fissurella maxima* has been recognized by previous authors. Its three synonyms have not been considered important, although *F. concinna* Philippi has sometimes been given status as a narrow "form" of the species.

Abundance and Use. Common throughout its range and particularly abundant in central and northern Chile. It is one of the major species used for food, taken by shore collectors and divers in relatively shallow water. It is called the "lapa de huiros," because it frequently occurs near the brown algae *Lessonia,* known as "huiros."

Characteristics and Variability. Always strongly ribbed and having a consistent color pattern of dark purple rays, the most characteristic feature is the interior border, which is uniquely rounded and has two zones. The margin is always crenulated by the radial ribs, even in the largest specimens. It is not a highly variable species; color pattern and shell height are consistent. Width of the shell is the most variable feature; some specimens may be especially elongate (Fig. 51); oval specimens are rare. Largest specimens come from shell piles in central Chile; those from Peru are small. Elongate specimens are frequently those from Peru. However, I do not consider the geographic differences of sufficient importance to warrant recognition of subspecies.

Affinity and Comparisons. *Fissurella maxima* has features that represent an extreme; its rounded margin is not shared by other species. It most resembles *F. cumingi,* which has a similarly large mantle and foot, and similar size, height, and color pattern. *Fissurella maxima* differs in having a rounded margin, stronger sculpture, and more pronounced primary ribbing. It might also be confused with *F. picta lata,* but it is lower, more elongate, and has broader ribs than that species. Juveniles are reddish like those of *F. peruviana,* but differ in having an upturned margin, a more elongate foramen, and are more elongate.

Synonymy and Types. *Fissurella maxima* was described by Sowerby, 1835, from a specimen collected by Cuming at Valparaíso, Chile. The holotype, BMNH 197569 (Fig. 55), length 128.8 mm, matches the specimen figured by Sowerby (1835b). Reeve (1849) figured a different specimen; these two specimens have also been figured by Dell (1971, pl. 4, fig. 1, holotype; figs. 2, 3, Reeve specimen).

I have not located any type material of *F. solida* Philippi, 1845, from "Chile." It has not been illustrated. Philippi's description mentions what I interpret as the rounded internal border of *F. maxima* and states that he did not know the young of *F. maxima;* other features are in accord with *F. maxima,* so I am confident that the name should be relegated to the synonymy of *F. maxima.*

Type material of *F. concinna* Philippi, 1845, also from "Chile," has not been located. Philippi's figures have suggested to most authors that it is a small, laterally compressed form of *F. maxima.* As with *F. solida,* Philippi noted the rounded margin. Stunted, narrow specimens matching his figure are present in collections; those from central Peru (Fig. 51) may be predominantly narrow, but broader specimens occur at the same localities and it is doubtful that the name has any taxonomic utility. Rochebrune and Mabille (1889) used the name incorrectly for specimens from Tierra del Fuego (no doubt confusing it with *F. radiosa*); this accounts for the Fuegan records of the "variety" *concinna* repeated by subsequent authors.

Fissurella hondurasensis Reeve, 1849, supposedly (in error) from "Honduras," was correctly placed in the synonymy of *F. maxima* by Pilsbry (1890). There are four specimens with the original mounting board now labeled syntypes, BMNH 1976139, lengths 56.6, 36.8, 33.0, and 28.5 mm; the largest is here figured (Fig. 52) and designated the lectotype. All are young specimens, more thin-shelled and with narrower margins than usual, but the dark flecks of the juveniles of *F. maxima* are apparent, and I am confident of their identity with *F. maxima.* A fifth specimen originally mounted on the same board is a young specimen of *F. pulchra.*

Fissurella latimarginata Sowerby, 1835

Figures 64–79

Fissurella latimarginata Sowerby, 1835a:126; Sowerby, 1835b:3, fig. 69; Gray, 1839:148, pl. 39, fig. 8; Reeve, 1849, pl. 3, fig. 19; Hupé, 1854:242; Philippi, 1860:180; Sowerby II, 1862:185, figs. 6, 7, 12; Pilsbry, 1890:153, pl. 32, figs. 36–38; Dall, 1909:242; Ziegenhorn and Thiem, 1925:17, pl. 2, figs. 22a, 22b; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:125, fig. 33; Peña, 1970:156; Dell, 1971:187, pl. 3, figs. 12–14; Marincovich, 1973:17, fig. 29; Ramirez-Boehme, 1974:31 [key].

Fissurella biradiata Sowerby, 1835a:124; Sowerby, 1835b:3, figs. 23, 52; Orbigny, 1841:477; Reeve, 1849, pl. 3, fig. 20; Philippi, 1860:180; Sowerby II, 1862:185, figs. 1–3; Ziegenhorn and Thiem, 1925:17, pl. 2, fig. 23; Dell, 1971: 182, pl. 3, figs. 10, 11.

Fissurella latimarginata var. *biradiata,* Pilsbry, 1890:154, pl. 35, fig. 3, pl. 46, figs. 12–14; Riveros-Zuñiga, 1951:126, fig. 34; Ramirez-Boehme, 1974:31 [key].

Fissurella bella Reeve, 1849, pl. 3, fig. 21; Sowerby II, 1862: 185, fig. 25; Pilsbry, 1890:150, pl. 33, fig. 48; Riveros-Zuñiga, 1951:119; Dell, 1971:182, pl. 3, figs. 3, 4; Ramirez-Boehme, 1974:32 [key].

Fissurella galericulum Reeve, 1850, pl. 11, fig. 77.

Fissurella latimarginata var. *galericulum,* Ramirez-Boehme, 1974:31 [key].

Fissurella punctatissima Pilsbry, 1890:150, pl. 58, figs. 21–23; Dall, 1909:124; Riveros-Zuñiga, 1951:118, fig. 26; Dell, 1971:192.

Shell. Relatively large (70 to 115 mm mature length); low to moderately high; outline oval, markedly tapered anteriorly; base of shell in one plane or slightly elevated on sides. Sculpture of very fine, sharply raised radial ribs. Color uniformly dark purplish red to gray, except for two lighter rays extending laterally in young shells, fading away in mature shells; occasional specimens faintly rayed throughout. Margin very broad and flat in young shells, solid dark red, outer edge with narrow gray zone. Cut shells showing gray outer zone in calcitic layer; recent growth of outermost zone in some mature shells changing from gray to nearly colorless. Foramen very long and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Elongate and elevated, radial ribs faint, nearly black except for two lateral white rays. After shell length of 5 mm, new growth less conical, fine radial ribs stronger, and shell lighter in color, not yet showing gray outer zone to calcitic layer.

Mantle and Foot. Not fully retractable in shell; mantle lobe usually enveloping and capable of great expansion over edge of shell. Upper edge with finely branched tongue-shaped papillae that alternate with shorter papillae. Lower edge with closely spaced tongue-shaped papillae of lesser size. Mantle lobe and foot side black except for lower mantle edge, on which branched papillae are bright yellow-orange. The bright yellow color of the lower edge makes a very conspicuous ring that encircles the animal, a coloration not present in other species. Determination of living specimens is readily made on this feature alone; in preserved specimens it remains lighter colored that the rest of the mantle lobe.

Habitat. Lowermost intertidal zone in partially protected areas, and in the sublittoral to depths of 5 m, living exposed on the upper surfaces of rocks. At Antofagasta I found that the sublittoral population occurred along with a few specimens of *F. cumingi* and still fewer *F. maxima.* The rocky substratum there looked barren from urchin grazing, but all *Fissurella* shells had a thick algal mat.

Distribution. Chiclayo, Peru (6°47′ S) (Peña, 1950), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). I have found it abundantly as far north as Isla Guanape, Peru (8°32′ S), and at all stations throughout the range. It undoubtedly occurs further south than Concepción, but I did not find it at Mehuin, near Valdivia, or at Guabun at the northwest tip of Isla de Chiloe.

Number of Lots Examined. 82 (LACM 26, AMNH 18, ANSP 8, MACN 7, MNHN 10, USNM 13).

Taxonomic History. The normal color form of *F. latimarginata* has been understood by authors. Its synonyms are based upon color forms with the rayed pattern, except for Pilsbry's *F. punctatissima,* which was based upon a gerontic specimen.

Abundance and Use. *Fissurella latimarginata* is common throughout its range. It occurs widely in Peru, where few of the other species are known. It is one of the most important food species, more so than any other in northern Chile. The largest specimens are taken by divers. Its common name is the "lapa viuda," which means widow, for its black aspect.

Characteristics and Variability. *Fissurella latimarginata* is characterized by its generally uniform gray to reddish-brown color, fine but persistent ribs, and tapered anterior end. The lateral white rays that characterize juvenile shells of so many of the species are likely to persist through later growth stages in this species. The broad, dark internal border

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Figures 64 through 71. *Fissurella latimarginata* Sowerby, 1835. Mature shells. **(64)** 3–5 m, Isla Guanape, Peru. LACM 74-3, 41.9 × 27.1 × 11.7 mm. **(65)** Iquique, Chile. LACM 64-16, 87.9 × 64.2 × 20.7 mm. **(66)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 34.8 × 25.5 × 9.0 mm. **(67)** Los Molles, Aconcagua Province, Chile. LACM 75-29, 116.5 × 85.5 × 37.5 mm. **(68)** Lectotype, *F. latimarginata* Sowerby. Valparaíso or Iquique, Chile. BMNH 197572, 80.2 × 55.0 × 18.7 mm. **(69)** Syntype, *F. bella* Reeve. Cape Horn (probable error). BMNH 197567, 56.7 × 37.4 × 12.7 mm. **(70)** Lectotype, *F. galericulum* Reeve. Locality unknown. BMNH 1976138, 33.0 × 21.5 × 9.5 mm. **(71)** Holotype, *F. punctatissima* Pilsbry. Valparaíso, Chile. ANSP 50262, 88 × 66 × 22 mm.


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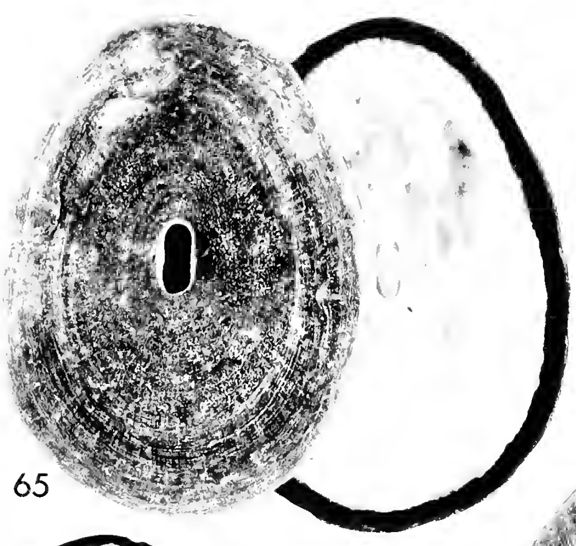
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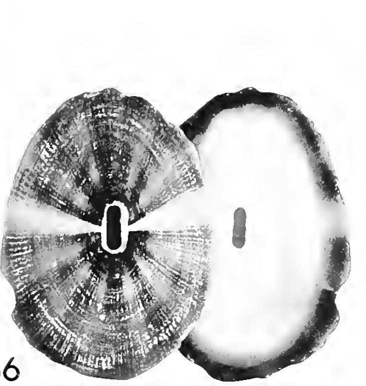
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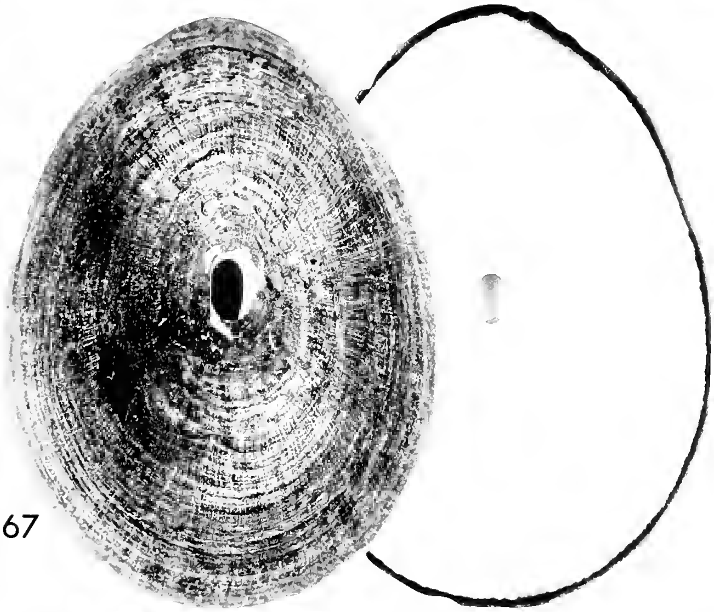
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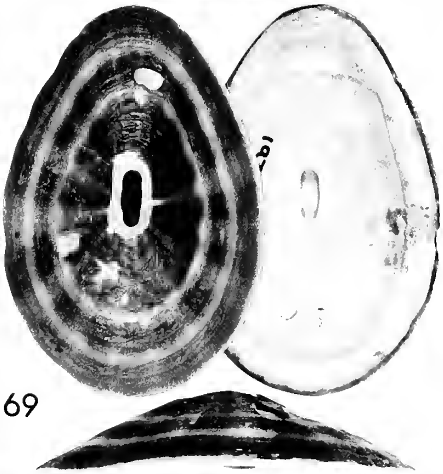
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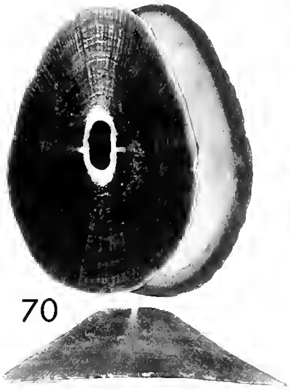
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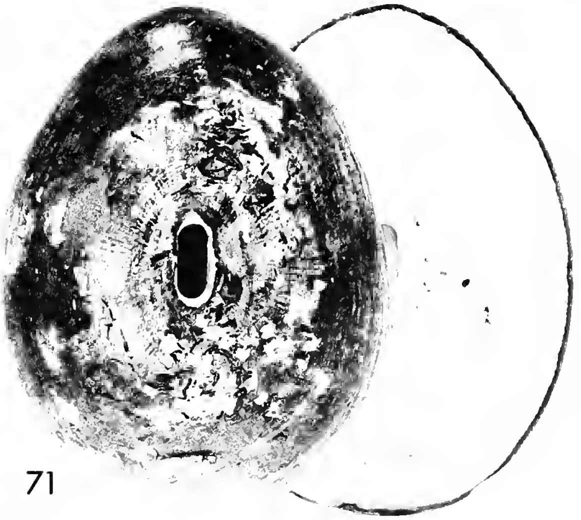
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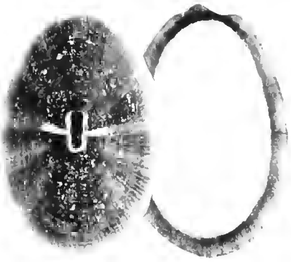
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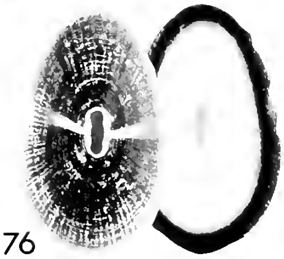
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Figures 72 through 79. *Fissurella latimarginata* Sowerby, 1835. Preserved specimens, mantle edge, juvenile shells, radula, and cut shell. **(72)** Living specimen, showing light colored lower mantle edge against dark foot side. Antofagasta, Chile. LACM 75-20. **(73)** Mantle lobe. Isla Guanape, Peru. LACM 74-2, length, 24 mm. **(74)** Preserved specimen with epizoic mytilids *Semimytilus algosus* on shell. 1–4 m, Isla San Lorenzo, Peru. LACM 74-24, 66.2 × 42.5 × 22.0 mm. **(75)** Juvenile shell. Los Colorados, Antofagasta Province, Chile. LACM 75-19, 16.0 × 10.5 × 3.9 mm. **(76)** Juvenile shell. Iquique, Chile. LACM 64-16, 13.8 × 3.5 × 3.6 mm. **(77)** Radula, air-dried. Antofagasta, Chile. LACM 75-20, width of ribbon 3.4 mm, shell length 85.0 mm. **(78)** Head of preserved specimen, showing mantle lobe and mouth. Isla Guanape, Peru. LACM 74-2, shell length 70.0 mm. **(79)** Cut shell, also showing algal mat. Los Molles, Aconcagua Province, Chile. LACM 75-29, length of cut edge 42 mm.

is characteristic, but it is a feature shared with other species. Living specimens are always recognizable by the bright yellow lower edge to the mantle lobe. Largest specimens seen were from central Chile; smaller specimens occur at both extremes of the range. Shell height varies extensively within populations. Specimens with patterns of rays like those of *F. cumingi* (Fig. 61) are uncommon but occur throughout the range. There are no geographic differences of sufficient importance to warrant recognition of subspecies.

Affinity and Comparisons. *Fissurella latimarginata* most resembles *F. cumingi,* having in common the size, proportions, and tapered anterior end. The unusual pattern of rays in variant specimens of *F. latimarginata* is similar to the normal pattern in *F. cumingi.* The sculpture of *F. latimarginata* is finer, sharper, and less beaded than that of *F. cumingi;* the rare color form of *F. latimarginata* may always be distinguished on this difference in sculpture. Shells of *F. latimarginata* may resemble those of *F. nigra* but are more sharply ribbed, have a reddish rather than gray interior border, and lack the inwardly tapered, white bordered foramen of *F. nigra.* A similar elaboration of the tongue-shaped papillae of the mantle lobe is known only in *F. bridgesii.* Both have broad margins and are dark colored with an incipient tendency to produce faintly rayed variants. *Fissurella latimarginata* may always be distinguished by its fine, sharp ribbing, which is lacking in *F. bridgesii.*

Synonymy and Types. There are six syntypes of *F. latimarginata* Sowerby, 1835, described from "Valparaíso and Iquique," Chile, four from one lot, BMNH 197572, lengths 80.2, 73.8, 61.7, and 51.1 mm, and two in BMNH 197573, lengths 56.3 and 27.3 mm. Both original mounting boards are penned with "Valparaíso and Iquique," so it is not known from which of the two localities each shell originated. The shells are clean and uniformly dark red, faintly, or not at all, showing the lateral white rays. The largest specimen is figured here (Fig. 68) and designated the lectotype; Dell (1971) figured the 73.8 mm specimen.

Type material of *F. biradiata* Sowerby was not received on loan from the British Museum. The type locality is Valparaíso, Chile. Figure 23 of the "Conchological Illustrations" shows a finely ribbed shell 41 mm long (presumed life-size) in which the only color pattern consists of the two lateral white rays. The type figure can therefore be relegated to the normal form of *F. latimarginata* without question. Figure 52 of the "Conchological Illustrations" is stated to be a "var." of *F. biradiata* from Iquique; this specimen is the one figured by Reeve (1849) and Dell (1971). Reeve's coloration shows it to be reddish brown and faintly rayed. Until I can examine the sculpture of that specimen I am unable to decide whether it is *F. cumingi* or the rare, rayed form of *F. latimarginata*, but the question is of minor importance because the type of *F. biradiata* is clearly recognizable as a specimen of *F. latimarginata.*

Fissurella bella Reeve, 1849, supposedly from Cape Horn, is represented by two syntypes, BMNH 197567, lengths 56.7 and 42.5 mm. The smaller specimen was figured by Reeve (here designated the lectotype) and the larger one by Dell (1971) and refigured here (Fig. 69). No author has recognized a species based on this name. Dell suggested an affinity with *F. pulchra,* but the absence of flecking rules that out. The narrowed anterior end and rayed pattern is shared only with the rare color form of *F. latimarginata* and normal *F. cumingi.* The shells appear to be acid-cleaned, the fine radial ribs are like those of *F. latimarginata* rather than *F. cumingi.* The margin in both shells is narrow, suggesting a degree of maturity that can be matched with *F. latimarginata* at extremes of its distribution, but not with similarly sized *F. cumingi.* I therefore identify the syntypes as the rare color form of *F. latimarginata.* The Cape Horn locality is therefore erroneous.

There are three syntypes of *F. galericulum* Reeve, 1850, BMNH 1976138, lengths 33.0, 31.0, and 30.5 mm, described with unknown locality. The largest (here designated the lectotype) is illustrated here (Fig. 70). It is clearly the normal white-rayed young stage of *F. latimarginata* and has been so recognized by previous authors.

Fissurella punctatissima Pilsbry, 1890, from Valparaíso, Chile, was considered by Pilsbry to differ from *F. latimarginata* in being more elevated and having a narrower internal margin. Shell proportions of the holotype (ANSP 50262, Fig. 71) and paratype (ANSP 61923) are within the normal range of variation and the narrow margin is that of mature examples of the species. The interior pitting, which suggested the name, is not unusual in large shells. Dell's records (1971) under this name are based upon specimens of *F. nigra.*

Fissurella cumingi Reeve, 1849

Figures 80–94

Fissurella cumingi Reeve, 1849, pl. 3, fig. 17; Hupé, 1854: 238; Sowerby II, 1862:187, figs. 5, 132; Carcelles and Williamson, 1951:256; Dell, 1971:184, pl. 3, figs. 15, 16; Ramirez-Boehme, 1974:32 [key].

Fissurella latimarginata var. *cumingi,* Pilsbry, 1890:154, pl. 30, fig. 1; Riveros-Zuñiga, 1951:28.

Fissurella stellata Reeve, 1850, pl. 12, fig. 80; Hupé, 1854: 245; Sowerby II, 1862:187, fig. 82; Pilsbry, 1890:148, pl. 32, fig. 32; Dall, 1909:242; Riveros-Zuñiga, 1951:113, fig. 23 [looks like *F. peruviana*]; Dell, 1971:193, pl. 4, figs. 7, 8 [not 5, 6]; Ramirez-Boehme, 1974:30 [key].

Shell. Large (80 to 100 mm mature length); height medium; outline oval, tapered anteriorly; sides slightly raised. Sculpture of fine to medium strength radial ribs, nodulous or beaded in early stages along growth increments; primary ribs only slightly more prominent than secondary ribs. Ground color dark yellowish gray, patterned with dark rays of reddish-purple, anteriormost rays often split. Margin very broad and flat in young shells, showing pattern of rays across the full width. Cut shells not showing zoning of calcitic layer, pigmentation of rays of equal intensity throughout layer. Foramen elongate and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Oval, conical, with straight slopes, earliest area white, reddish rays emerging with edges darkly outlined as if split; lateral white-rayed area prominent. At length of 4 mm scattered brown flecks may be present, forming zigzag pattern in some specimens; by this size ribs have become prominent, secondary ribs nearly the size of primary ribs.

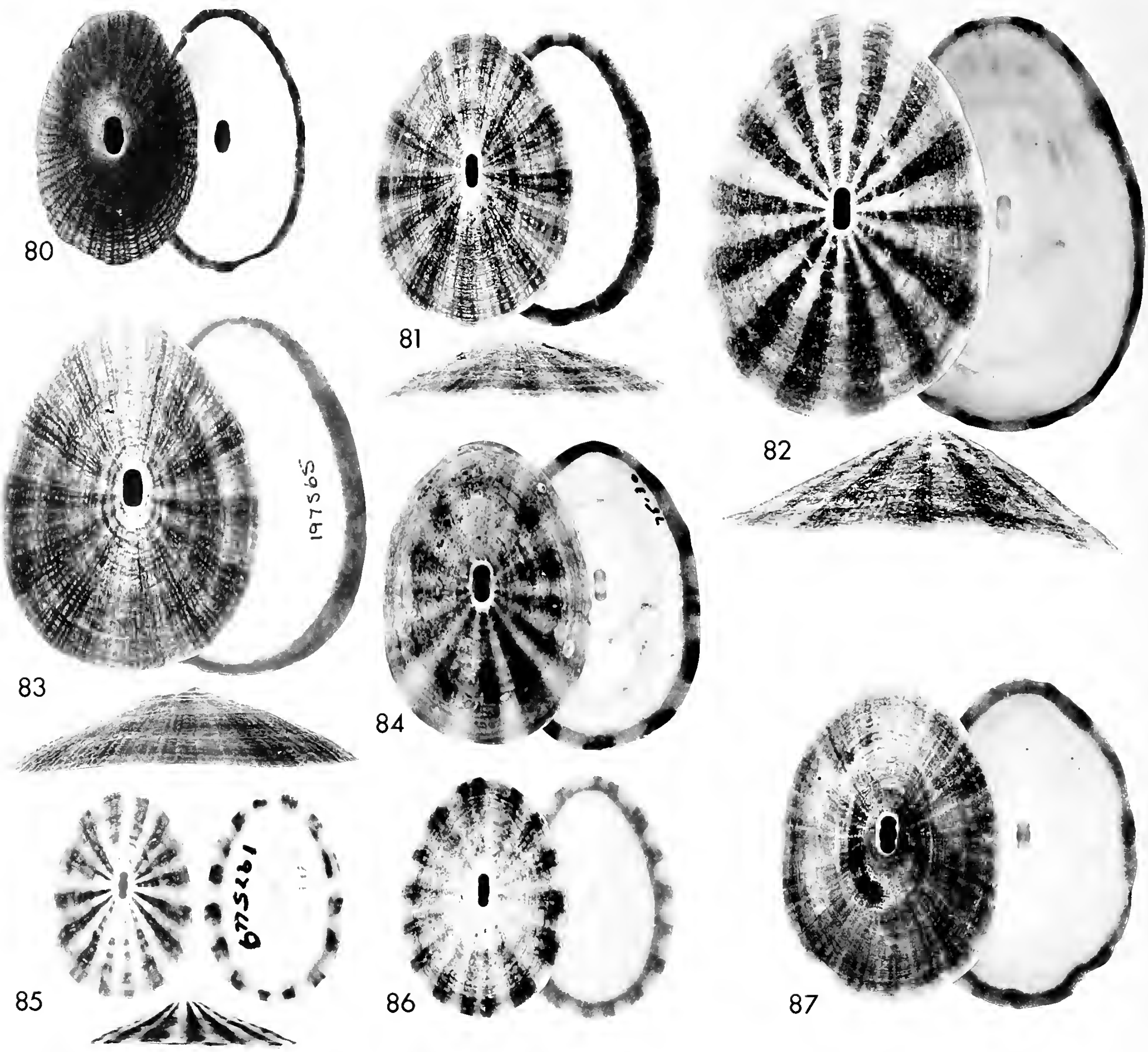
Mantle and Foot. Nearly retractable in shell. Cephalic tentacles yellowish on inner surface. Side of foot with strongly developed tubercles; mantle lobe broad, upper edge with finely branched papillae, lower edge with more prominent papillae, banded in light and dark to correspond to rays on shell. Foot and mantle colored purplish red, lighter or tending toward pink in individuals with lightly pigmented shells. The reddish coloration is characteristic and differs from that of all other species.

Habitat. Lowermost intertidal zone and immediate subtidal zone to 15 m, living on the upper surfaces of rocks. At low tide chiefly in deep tide pools that occur in surf exposed areas. I obtained living specimens from the municipal market at Iquique, evidently taken by divers. Living specimens were collected in lesser numbers along with *F. latimarginata* at 5 m on a rocky bottom at Antofagasta. Large specimens were found in shell piles at Los Molles (32°14′ S). Intertidally occurring specimens were common at Montemar and Mehuin.

Distribution. Matarani, Peru (17°00′ S) (AMNH 150892, B. Marco), to Mehuin, Valdivia Province, Chile (39°23′ S) (LACM 75-36, McLean). The distribution probably extends farther to the north and south. Its distribution is more southern than that of *F. latimarginata* and *F. maxima,* both of which extend much farther to the north in Peru, but seem not to be represented at Mehuin, where *F. cumingi* is common.

Number of Lots Examined. 41 (LACM 16, AMNH 6, ANSP 1, MACN 3, NMHN 10, USNM 5).

Taxonomic History. *Fissurella cumingi* has not hitherto been understood and recognized as a separate species. Previous authors have repeated the early published descriptions



Figures 80 through 87. *Fissurella cumingi* Reeve, 1849. Mature shells. (**80**) 17 m, Huayquique, Tarapaca Province, Chile. LACM 90799, 32.5 × 20.5 × 11.2 mm. (**81**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 50.3 × 34.2 × 10.5 mm. (**82**) Same locality (shell pile). LACM 75-29, 96.3 × 61.1 × 22.8 mm. (**83**) Lectotype, *F. cumingi* Reeve. Valparaíso, Chile. BMNH 197565, 67.2 × 49.1 × 15.2 mm. (**84**) Montemar, Valparaíso Province, Chile. LACM 75-30, 49.9 × 34.4 × 12.8 mm. (**85**) Lectotype, *F. stellata* Reeve, 1850. 11–22 m, Valparaíso, Chile. BMNH 197549, 16.2 × 10.8 × 3.8 mm. (**86**) Montemar, Valparaíso Province, Chile. LACM 75-30, 30.0 × 20.4 × 7.9 mm. (**87**) 75-36, Mehuin, Valdivia Province, Chile. LACM 75-36, 61.2 × 42.2 × 17.7 mm.

and have considered it to be a color form or "variety" of *F. latimarginata*. Confusion over the identity of *F. biradiata* Reeve (a synonym of *F. latimarginata*) and *F. bridgesii* Reeve (a good species) has also contributed to the difficulty. Cleaned specimens found in old collections have usually been misidentified as *F. maxima;* specimens covered with the algal mat are easily mistaken for *F. latimarginata.*

Abundance and Use. *Fissurella cumingi* is not as common as *F. maxima* and *F. latimarginata,* but large specimens can be found by divers, and the species is exploited for food in central and northern Chile. I have seen it in the market at Iquique, and it is a major component in the shell piles in central Chile. The common name is "lapa frutilla," meaning strawberry, which aptly describes the color of the mantle and foot sides.

Characteristics and Variability. The most characteristic features of *F. cumingi* are its tapered front, consistent color pattern of dark ribs on a relatively dark ground, beaded ribs,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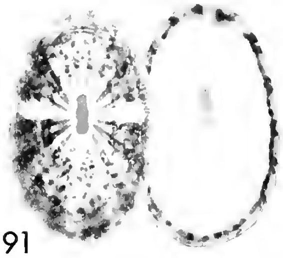
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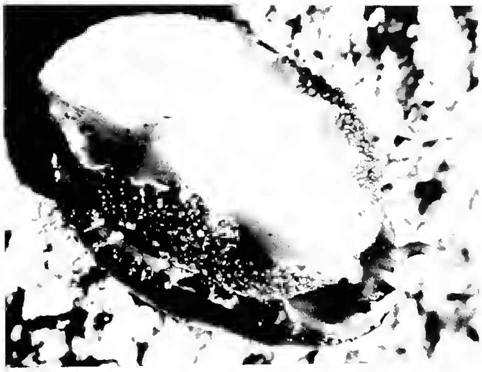
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Figures 88 through 94. *Fissurella cumingi* Reeve, 1849. Radula, cut shell, juvenile shells, living and preserved bodies, mantle lobe. **(88)** Radular ribbon, air-dried. 2–5 m, Antofagasta, Chile. LACM 75-20, width of ribbon 2.8 mm. **(89)** Cut shell. Los Molles, Aconcagua Province, Chile. LACM 75-29, length of cut edge 38.0 mm. **(90)** Juvenile shell. Los Molles, Aconcagua Province, Chile. LACM 75-28, 12.8 × 7.8 × 3.4 mm. **(91)** Juvenile shell. Same locality. LACM 75-28, 9.4 × 5.5 × 2.5 mm. **(92)** Ventral view of living specimen, head at right. Montemar, Valparaíso Province, Chile. LACM 75-30. **(93)** Preserved specimen. 2–5 m, Antofagasta, Chile. LACM 75-20, shell length 73.9 mm. **(94)** Mantle lobe. Same locality. LACM 75-20, length 14 mm.

and the unique reddish color of the mantle and foot. Variation in the species is minimal. The chief variable feature seems to be the intensity of ground color, which may be pale to dark yellow. The rayed pattern is consistent; none have been seen that lack it. Specimens received from M. Bretos from the subtidal mussel beds at Iquique (Fig. 80) are small, elevated, and have narrow margins. Those from the southernmost locality collected (Mehuin, Chile) appeared stunted, and many had narrow shells. However, there seem to be no geographic differences of sufficient importance to recognize subspecies.

Affinity and Comparisons. *Fissurella cumingi* has certain features in common with both *F. maxima* and *F. latimarginata,* suggesting that it is related to both. Its color pattern combines the rayed pattern of *F. maxima,* with the addition of some of the darker ground color of *F. latimarginata.* Its margin shows the pattern of rays across the full, flat width, unlike the solid margin of *F. latimarginata* and the rounded, crenulate and zoned margin of *F. maxima.* It has the same size and proportions as *F. latimarginata,* but specimens with the algal mat may be recognized by the rayed pattern of the margin. The normal, rayed form of *F. cumingi* may be distinguished from the unusual rayed form of *F. latimarginata* by the strength of the ribs; they are fine and sharp in *F. latimarginata,* coarser and beaded in *F. cumingi.* Its outline is more tapered and its ribbing finer than that of either *F. picta lata* or *F. costata;* it does not have the more distinct primary ribbing of either of these species. Juvenile shells of *F. cumingi* have a characteristic color pattern of split rays; they do not have the rounded margin of *F. maxima* nor the primary rays of *F. costata* or *F. picta lata.* The reddish color of the animal is so different from that of any other species that it may be recognized by this feature.

Synonymy and Types. There are 6 syntypes of *F. cumingi* Reeve, 1849, from Quintero, Chile, BMNH 197565, lengths 77.0, 67.2, 62.5, 57.1, 32.7, and 22.5 mm. Reeve (1849) and Dell (1971) figured the 67.2 mm shell; Dell's interior view is of the 77 mm specimen. The 67.3 mm specimen is here figured and designated the lectotype (Fig. 83).

Fissurella stellata Reeve, 1850, was based on small specimens from "Valparaíso, attached to dead shells at a depth of from six to twelve fathoms." There are four syntypes, BMNH 197549, lengths 16.9, 16.2, 15.0, and 14.5 mm. The 16.2 mm specimen is illustrated and designated the lectotype (Fig. 85). These specimens are clearly the juveniles of *F. cumingi;* they are red-rayed, the ribbing of medium strength and nodular, the primary and secondary ribs nearly equivalent. The original specified depth is probably accurate; the species is known from the shallow sublittoral. Other authors have guessed incorrectly with respect to this name; Riveros-Zuñiga (1951) figured the brown and white rayed form of *F. peruviana* as *F. stellata.* Dell (1971) mixed the figure numbers on his plate 4: his figure of a syntype of *F. stellata* should be figs. 7, 8, rather than 5, 6.

Fissurella costata Lesson, 1831

Figures 95–108

Fissurella rudis Deshayes, 1830:134; Deshayes *in* Lamarck, 1836:61; Orbigny, 1841:474 [under *F. costata*]. Not *Patella rudis* Roeding, 1798 [= *F. nodosa* Born, 1778].

Fissurella costata Lesson, 1831:41; Sowerby, 1835b:4, fig. 28; Orbigny, 1841:474; Reeve, 1849, pl. 2, fig. 14; Hupé, 1854:243; Philippi, 1860:181; Sowerby II, 1862:187, figs. 15, 205; Pilsbry, 1890:148, pl. 30, fig. 10, pl. 35, fig. 11; Dall, 1909:177, 241; Ziegenhorn and Thiem, 1925:14, pl. 2, fig. 12; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:108, fig. 21; Dell, 1971:183, pl. 4, figs. 7, 8; Marincovich, 1973:16, fig. 28; Ramirez-Boehme, 1974:31 [key].

Fissurella chilensis Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 36; Orbigny, 1841:474 [under *F. costata*].

Fissurella costata var. *rubra* Ziegenhorn and Thiem, 1925: 14, pl. 2, figs. 13a, b.

Shell. Medium sized (50 to 80 mm mature length), low to medium; outline elongate in young shells, broadly oval in mature shells; base of shell resting flat in one plane. Sculpture of distinctly raised narrow ribs that crenulate margin; interspaces narrower than ribs. Primary ribs more prominent in young shells, but in large shells not differing from secondary ribs. Ground color light yellowish gray; rays gray, often becoming faint in later growth stages. Margin broad, flat, showing gray rays across full width but more distinctly at outer edge. Calcitic layer of cut shells not zoned; rays showing through full width. Foramen exceptionally small, elongate and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Conical at earliest stage, becoming flattened and elongate; primary ribs light yellow, strongly elevated, becoming nodular after shell reaches length of 5 mm; earliest rays reddish, changing to black by shell length of 4 mm; black rays fill interpsaces between primary ribs. With growth, secondary ribs appear between primary ribs and black rays become gray or disappear altogether.

Mantle and Foot. Fully retractable in shell; shell margin not raised and mantle not projecting in living specimens. Cephalic tentacles dark on outer side, yellowish on inside and at tips. Mantle lobe very narrow, papillae of both edges small and width little branching. Side of foot light pinkish brown, surface marbled. Projecting tubercles are not readily apparent in living specimens but visible in preserved specimens. Elaboration of the mantle lobes is the least pronounced in this species.

Habitat. In northern Chile at Iquique and Antofagasta *Fissurella costata* occurs on vertical surfaces of surf-exposed rock walls at the low tide line, near the holdfasts of the large brown alga *Lessonia,* where its habitat is not shared by other species of *Fissurella.* In central Chile I found it more abundantly. At Los Molles and Montemar it also occurs on horizontal surfaces in less exposed areas; here it shares the habitat with other species. The shell margin fits the contours of a habitual site of attachment; when exposed at low tide the shell margin is in tight contact with the substrate. Unlike the other species, individuals do not move when touched by *Heliaster;* the small foramen may protect them from access by this seastar. The shell also seems suited to resist removal by the clingfish *Sicyases* because the margin is less raised that that of other species, which are more subject to predation by *Sicyases.* Specimens are rarely seen with attached *Scurria parasitica.*

Distribution. Punta Pichalo, Tarapaca Province (19°36′ S) (AMNH 137232, J. Bird), to Guabun, Isla de Chiloe, Chile (41°50′ S) (LACM 75-40, McLean). Dall's (1909) record from Mollendo, Peru, was based on a specimen of *F. maxima* (USNM 27743). However, the distribution of this species may extend farther to the north into Peru. In my collecting only the northwestern tip of Isla de Chiloe was sampled at Guabun; the southern limit of the species is therefore not certain. It is apparent, however, that this species has a more southern center of distribution than most species of the Peruvian Faunal Province.

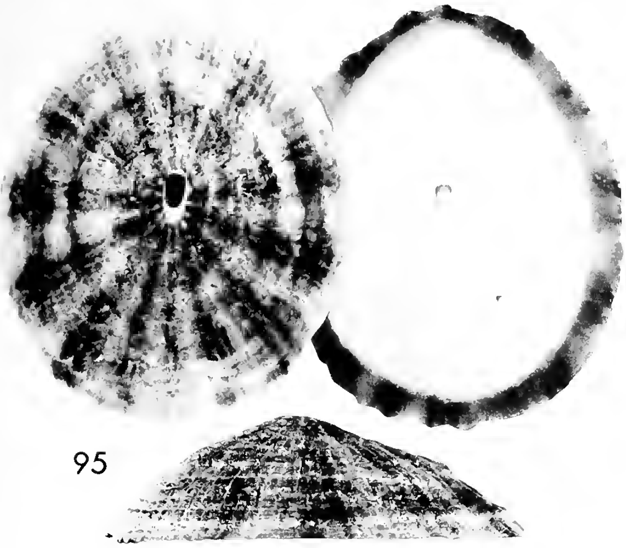
Number of Lots Examined. 70 (LACM 23, AMNH 15, ANSP 3, MACM 9, MNHN 12, USNM 8).

Taxonomic History. *Fissurella costata* has been reasonably well understood by recent authors.

Abundance and Use. *Fissurella costata* is moderately common throughout its range. In northern Chile it is little used for food because its habitat is so exposed to surf that it is usually inaccessible to shore collectors. Beach-worn shells are common along the shore but fresh shells are seldom seen in the shell piles. The common name is "lapa senorita," because of its resemblance to *Scurria viridula,* which is known as the "senorita."

Characteristics and Variability. *Fissurella costata* is characterized by its relatively small foramen, which is broadly oval when mature and narrow in young stages, its relatively low height, and its consistent color pattern of gray rays on a yellow ground. Its mantle lobe is very narrow, and the foot color is light pinkish brown. Variations in height and outline are minor; color variation results from rays that either persist or fade in later stages. There are no geographic differences worthy of note. The low variability of this species is correlated with its rather restricted habitat on surf-exposed rocks in the lower intertidal zone.

Affinity and Comparisons. *Fissurella costata* seems to be most closely related to, and difficult to distinguish from, *F. picta lata.* Both have similar color patterns, a similar, broadly oval outline, strong ribs, and primary ribs that remain strong. Differences are that mantle and foot colors are lighter in *F.*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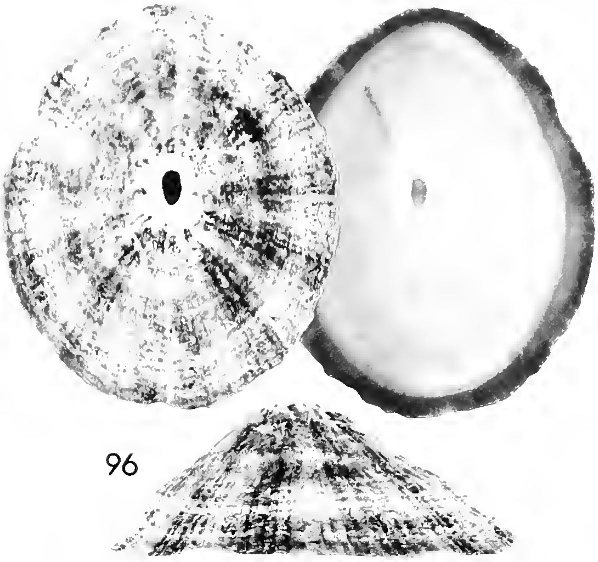
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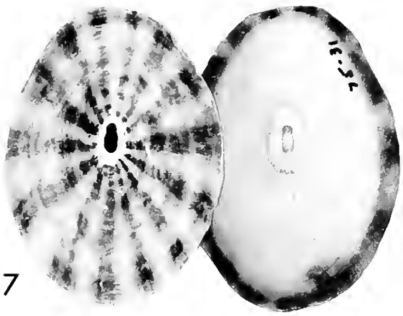
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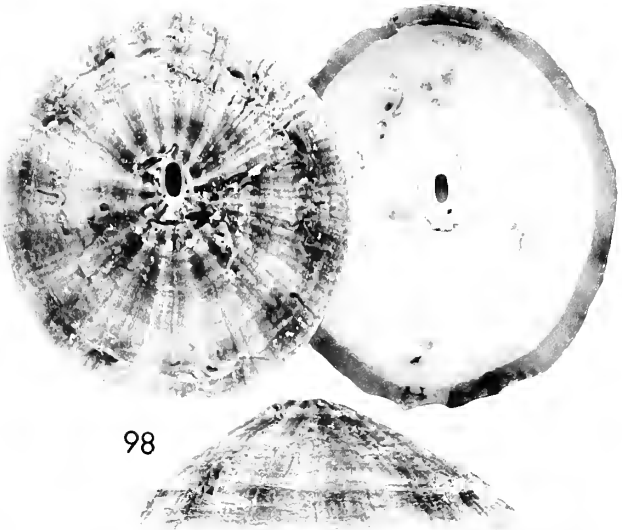
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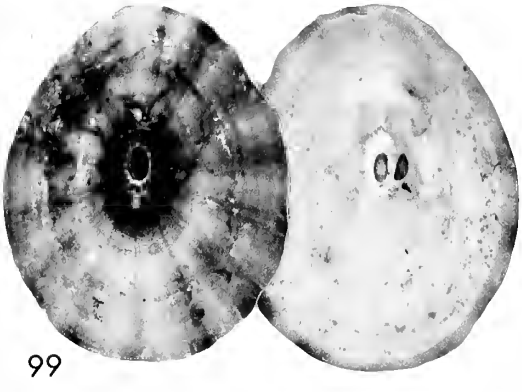
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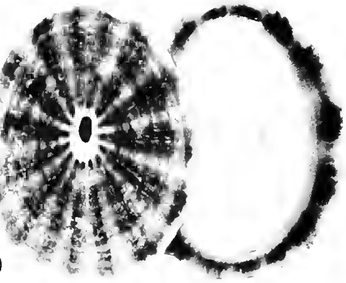
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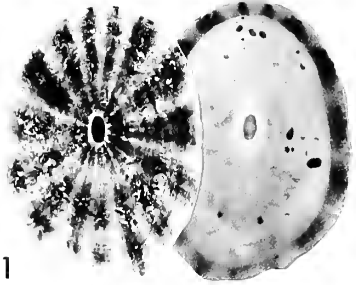
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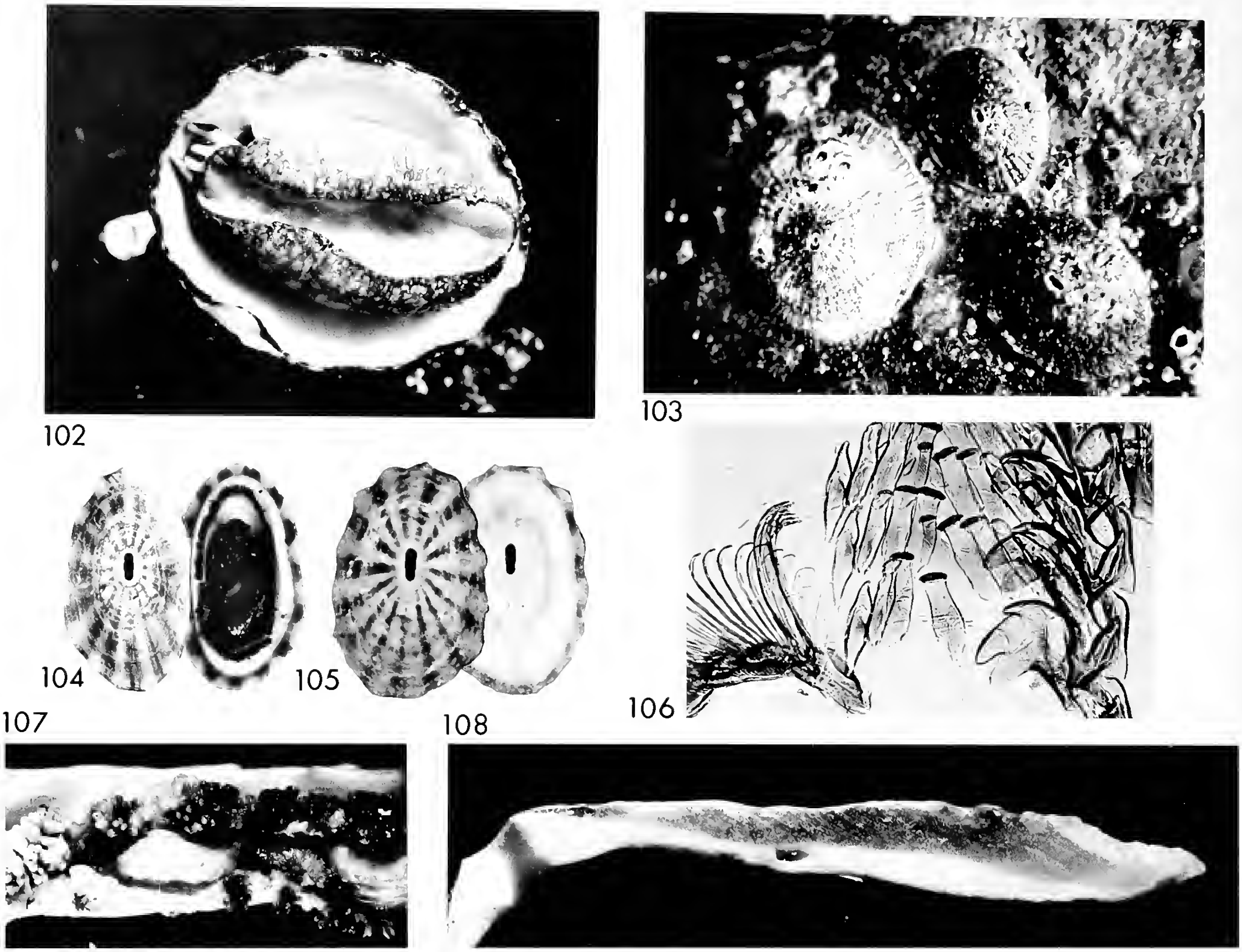
Figures 95 through 101. *Fissurella costata* Lesson, 1831. Mature shells. **(95)** Punta Jara, Antofagasta Province, Chile. LACM 75-18, 72.3 × 59.0 × 20.4 mm. **(96)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 66.8 × 54.5 × 23.3 mm. **(97)** Islota Concon, Valparaíso Province, Chile. LACM 75-31, 43.3 × 31.8 × 9.9 mm. **(98)** Lectotype, *F. rudis* Deshayes. Paita, Peru (probable error). MNHNP, 69.1 × 61.1 × 24.7 mm. **(99)** Río Bio-bio, Concepción Province, Chile. LACM 75-35, 57.7 × 56.4 × 15.3 mm (beach shell). **(100)** Mehuin, Valdivia Province, Chile. LACM 33-2, 33.2 × 25.7 × 9.4 mm. **(101)** Ancud, Chiloe Province, Chile. LACM 62-62, 35.5 × 25.5 × 7.9 mm.



Figures 102 through 108. *Fissurella costata* Lesson, 1931. Living specimens, juvenile shells, radula, and cut shell. (**102**) Ventral view, living specimen. Punta Jara, Antofagasta Province, Chile. LACM 75-18. (**103**) Living specimens in place. Los Molles, Aconcagua Province, Chile. LACM 75-28. (**104**) Juvenile specimen. Same locality. LACM 75-28, 14.2 × 7.9 × 3.1 mm. (**105**) Juvenile specimen (dead shell). Bahía Herradura, Coquimbo Province, Chile. LACM 75-25, 10.9 × 7.3 × 2.4 mm. (**106**) Radula of small specimen. Montemar, Valparaíso Province, Chile. LACM 75-30, width of field 0.8 mm, shell length 24.5 mm. (**107**) Mantle lobe. Punta Jara, Antofagasta Province, Chile. LACM 75-18, length 10 mm. (**108**) Cut shell. Los Molles, Aconcagua Province, Chile. LACM 75-28, length of cut edge 31 mm.

costata; F. costata is somewhat lower than *F. picta lata,* although the extremes of variation seem to overlap; *F. costata* does not have the tendency to reddish rays nor the penciled pattern of the rays of *F. picta lata.* Juveniles of *F. costata* are more elongate, flatter, and have more nodulous primary ribs than those of *F. picta lata.* In northern Chile where *F. picta lata* does not occur, there is no difficulty in recognizing *F. costata* as the species that is the most broadly oval and has the smallest foramen.

Synonymy and Types. Four syntypes of *F. rudis* Deshayes, 1830, have been examined, received on loan from the Paris Museum. The lot is accompanied by a cardboard mount; the shells are 75.8, 69.1, 53.6, and 51.9 mm in length. The largest of these shells is the polished specimen mentioned in the original description. The original dimensions were given as 55 mm length and 43 mm width; one of the specimens is 53.6 mm long and 42.8 mm wide. The 69.1 mm shell is designated the lectotype (Fig. 98). All four specimens are typical and agree with the thorough and accurate original description. The original locality was Paita, Peru: "This shell was first given to us by our friend Lesson, who found it at Paita, Peru; then later we have found it commercially, likewise from Peru." [Translation.] Later, Deshayes *in* Lamarck (1836) changed the locality to "Habite le Chile." The actual occurrence of the species in Peru is uncertain, and Paita is north of the known occurrence of any of the Peruvian species of *Fissurella.* This name is preoccupied by *Patella rudis* Roeding, 1798, a synonym of the Caribbean *F. nodosa* (Born, 1778).

Type material of *Fissurella costata* Lesson, 1831, has never been illustrated, and specimens are not in the collection of the Paris Museum, where some of Lesson's types are known (Bouchet, personal communication). Lesson's description is insufficient to distinguish the species from *F. picta lata,* which is closely related and also abundant in the vicinity of Talcahuano, Chile, the type locality. Lesson described the animal as blackish and the shell margin as bluish with stains of red, features that would more appropriately apply to *F. picta lata.* However, the species is well known under the name *F. costata* and no purpose would be served in rejecting this name, even though there is doubt as to its identity.

Type material for *F. chilensis* Sowerby, 1835, has not been located. It came from "Valparaíso, found on rocks in exposed situations at low water." The habitat is accurately described; *F. costata* is much more common than *F. picta lata* at Valparaíso, and the original illustration shows a densely ribbed shell with a very small foramen. Its identity is certain, in agreement with treatment by previous authors.

Type material of *Fissurella costata* var. *rubra* Ziegenhorn and Thiem, 1925, has not been located. The specimen came from Coquimbo, Chile, and measured 60 × 48 × 15 mm, distinguished from the typical form in having reddish rays. Judging from the illustration, it could be either *F. costata* or *F. picta lata,* although I have not seen reddish rayed specimens of *F. costata.* Lateral profile of the figure is about right for *F. costata;* for *F. picta lata* it would be at the low extreme of variation; the locality is reasonable for *F. costata;* to my knowledge *F. picta lata* does not occur north of Valparaíso, where it is uncommon. I therefore favor retaining this taxon in the synonymy of *F. costata,* admitting that the other alternative is a possibility.

Fissurella picta (Gmelin, 1791)

Figures 109–146

Fissurella picta is here considered to have two geographic subspecies: *F. picta picta* in the Magellanic region of Chile and *F. picta lata* in south-central Chile.

Synonymy for *F. picta picta:*

Patella picta Gmelin, 1791:3729.

Fissurella picta, Lamarck, 1822:10; Deshayes, 1830:131; Sowerby, 1835b:1, figs. 4, 26; Lamarck, 1836:559; Orbigny, 1841:472; Reeve, 1849, pl. 1, fig. 6; Hupé, 1854:237; Sowerby II, 1862:186, figs. 10, 11, 35; Watson, 1886:33; Rochebrune and Mabille, 1889:70; Pilsbry, 1890:144, pl. 45, figs. 9–11; Melvill and Standen, 1898:102; Strebel, 1907:83, pl. 2, fig. 22; Melvill and Standen, 1907:98; Strebel, 1908:79; Dall, 1909:242; Melvill and Standen, 1914: 115; Ziegenhorn and Thiem, 1925:6, pl. 1, figs. 1–4; Carcelles, 1950:51; Powell, 1951:85; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:96, fig. 15; Dell, 1971: 191; Ramirez-Boehme, 1974:31 [key].

Fissurella atrata Reeve, 1850, pl. 11, fig. 73; Sowerby II, 1862:186, fig. 71; Pilsbry, 1890:147, pl. 34, fig. 59 [under *F. philippiana*]; Dell, 1971:190, pl. 3, fig. 7 [under *F. philippiana*].

Fissurella muricata Reeve, 1850, pl. 14, fig. 103; Sowerby II, 1862:106, pl. 4, fig. 68; Pilsbry, 1890:156, pl. 39, fig. 5.

Synonymy for *F. picta lata:*

Fissurella lata Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 63; Reeve, 1849, pl. 1, fig. 5; Hupé, 1854:243; Sowerby II, 1862:187, fig. 13; Pilsbry, 1890:147, pl. 31, figs. 18, 19; Dall, 1909:241; Ziegenhorn and Thiem, 1925:13, pl. 1, fig. 11; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:107; Dell, 1971:187, pl. 4, figs. 12–14; Ramirez-Boehme, 1974:31 [key].

Fissurella navidensis Ramirez-Boehme, 1974:17, 31 [key].

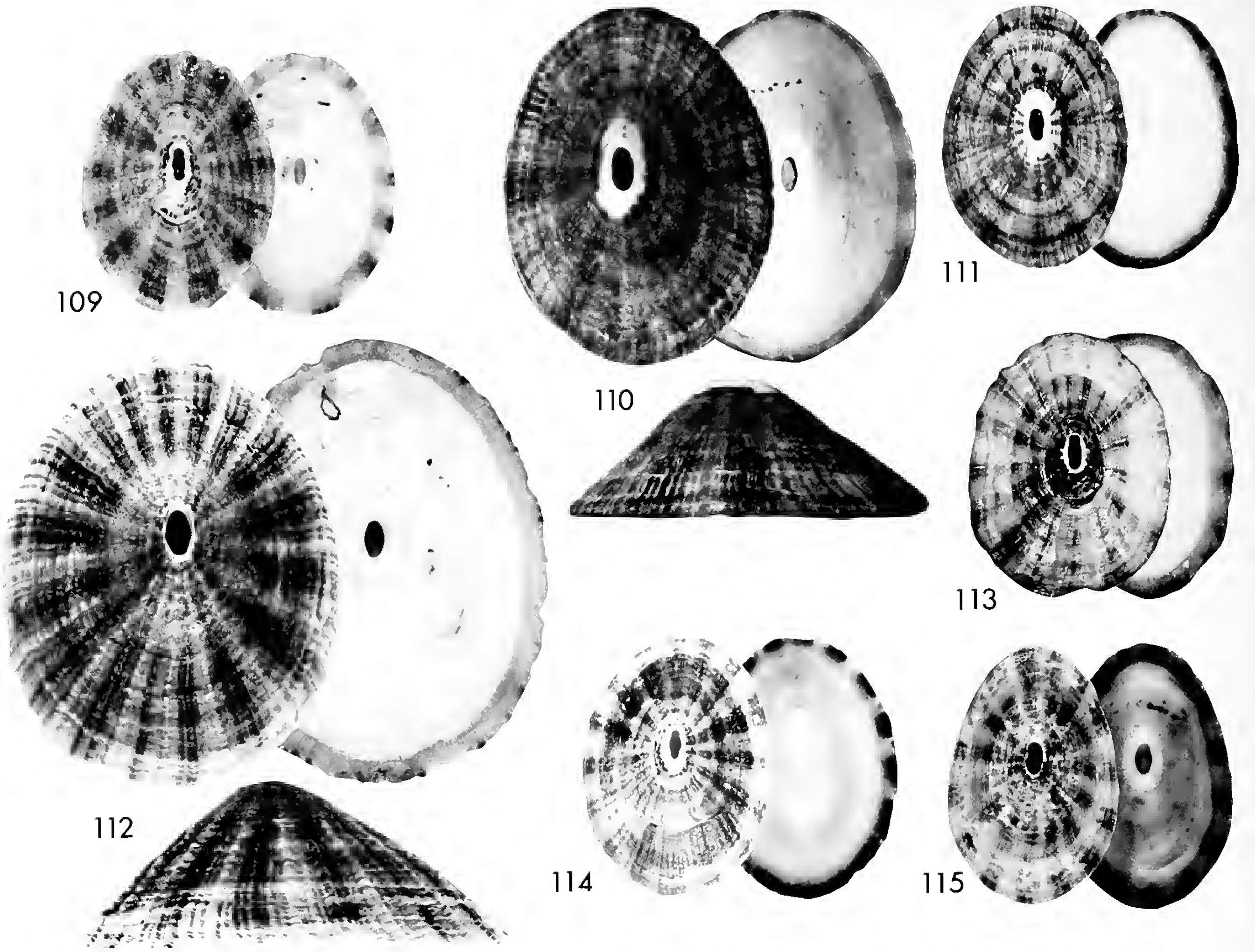
Shell (*F. picta picta*). Medium large (65–95 mm mature length), moderately elevated; outline elongate oval, sides of shell slightly raised. Sculpture of sharp, narrow radial ribs; primary ribs remaining stronger than secondary and tertiary ribs; occasional specimens with weak ribs. Ground color white, sometimes gray, rayed with black and white; strongest ribs centered on both light and dark rays; dark rays usually split into number of fine lines of black, a result of lack of pigment in grooves between fine ribs. Rays faint on light ground in some, or black on gray ground and with rays interrupted to produce concentric patterns of banding. Margin broad and flat, showing penciled pattern of rays. Cut shells show that pigment of rays extends through calcitic layer. Foramen elongate in juvenile shells, elongate to oval in mature shells.

Shell (*F. picta lata*). Medium large (50–80 mm mature length), height moderately to strongly elevated; outline elongate-oval to oval, sides of shell slightly raised. Sculpture of strong radial ribs; primary ribs remaining strong at all growth stages. Ground color yellowish white, rayed with yellowish purple; strongest ribs centered on both light and dark rays; dark rays usually split into number of fine lines coinciding with secondary and tertiary ribs; pigment tending to be absent in grooves between ribs. Color pattern fairly uniform, with dark rays on lighter ground. Margin broad and flat in young shells, sharply defined, gray, showing pattern of rays and penciled pattern. Cut shells showing pigment of rays throughout calcitic layer. Foramen elongate in young shells, oval in mature shells.

Juvenile Shell. Juveniles of both subspecies are oval and high, margin broad; strong primary ribs coincide with light rays, becoming stronger and slightly nodulous in specimens longer than 5 mm. Secondary ribs develop in interspaces between primary ribs; dark rays develop in rib interspaces and show some concentric interruptions in intensity.

Mantle and Foot. Body nearly retractable within shell; cephalic tentacles dark on outer side, reddish on inner side, and yellowish at tips. Mantle lobe relatively narrow, banded to correspond to pattern of rays; papillae of both edges of mantle lobe moderately developed. Side of foot marbled with light and dark, tubercles lighter tipped; southernmost specimens often lighter overall.

Habitat. Mid-tidal to lower intertidal zone on vertical to horizontal surfaces and on the sides of loose boulders; wedged in crevices under more exposed conditions; not extending into the sublittoral zone. At the north end of the range in the



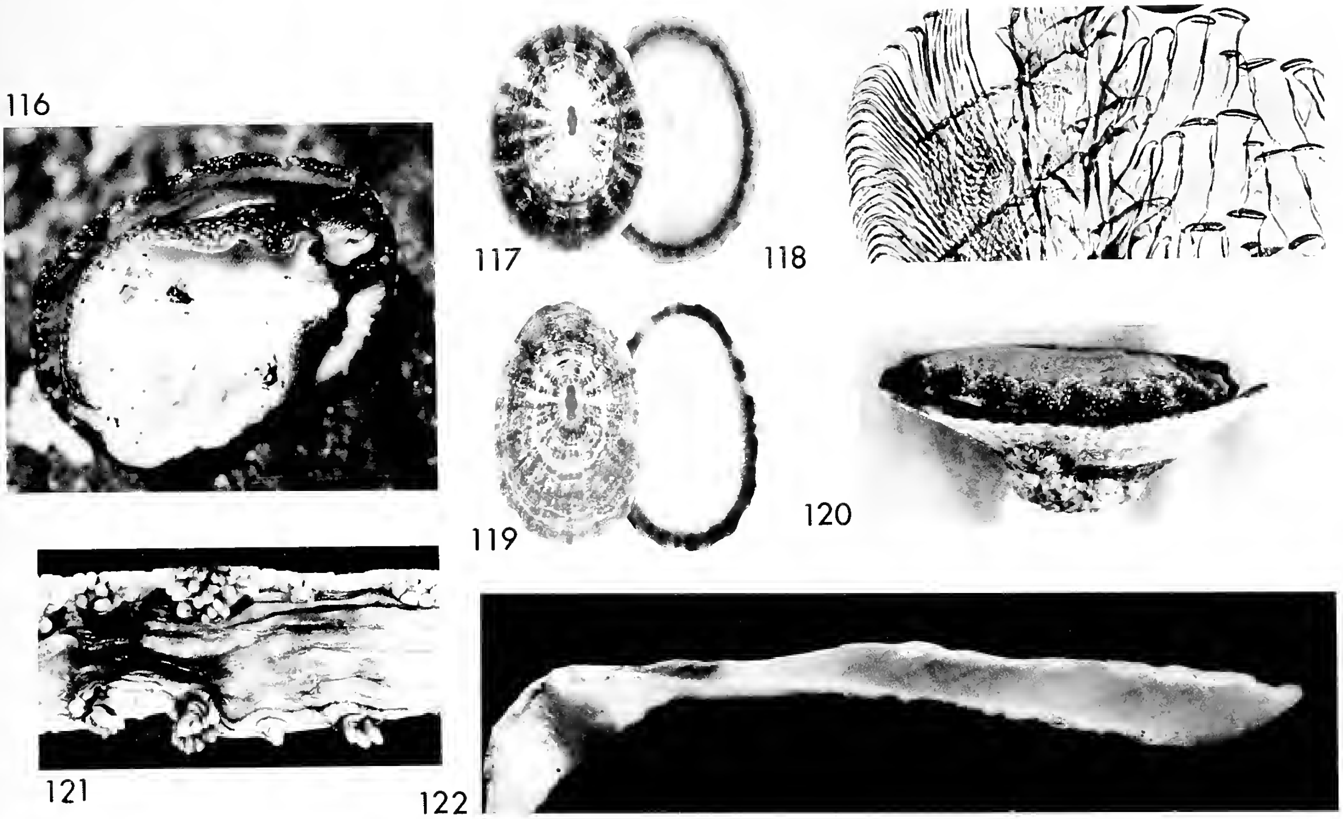
Figures 109 through 115. *Fissurella picta lata* Sowerby, 1835. Mature shells. (**109**) Montemar, Valparaíso Province, Chile. LACM 75-30, 37.9 × 27.8 × 13.4 mm. (**110**) Holotype, *F. navidensis* Ramirez-Boehme. Bahía Navidad, Santiago Province, Chile. MNHN 200376, 66 × 51 × 22 mm. (**111**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 24.8 × 17.6 × 8.2 mm. (**112**) Lectotype, *F. lata* Sowerby. Isla Santa Maria, Bahía Concepción, Chile. BMNH 197571, 83.4 × 64.3 × 31.6 mm. (**113**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 37.9 × 28.7 × 8.8 mm. (**114**) Mehuin, Valdivia Province, Chile. LACM 75-36, 40.4 × 29.2 × 11.7 mm. (**115**) Same locality. LACM 75-36, 40.4 × 26.5 × 12.5 mm.

vicinity of Valparaíso, *F. picta lata* is uncommon; the only two living specimens that I found occurred on horizontal surfaces adjacent to *F. limbata.* At Concepción and Mehuin and in the Strait of Magellan where *F. picta picta* occurs, specimens were common under all conditions of exposure. At these localities, such characteristic northern species as *F. latimarginata* and *F. maxima* were scarce or missing, suggesting a correlation between the dominance of *F. picta lata* and absence of competition from the other species.

Distribution. Islote Concon, Valparaíso Province, Chile (32°52′ S) (LACM 75-31, McLean), to Tierra del Fuego and Isla de los Estados, Argentina, probably south to Cape Horn and east to the Falkland Islands. Fossil specimens are known from shoreline terraces at Comodora Rivadavia, Chubut Province, Argentina (45°52′ S) (MCZ 28329), but living specimens are unknown on the mainland Patagonian coast north of Tierra del Fuego. The subspecies *F. picta picta* occurs in the Magellanic region of Chile, extending north to the vicinity of Isla de Chiloe. Populations that occur in the area of overlap, chiefly in the vicinity of Isla de Chiloe, are consistent but may have features that make assignment to either subspecies arbitrary (see further discussion below).

Number of Lots Examined. *F. picta picta:* 95 (LACM 19, AMNH 15, ANSP 5, MACN 33, MNHN 10, USNM 13). *F. picta lata:* 64 (LACM 11, AMNH 7, ANSP 2, MACN 5, MNHN 35, USNM 4).

Taxonomic History. The typical form of *Fissurella picta* from the Strait of Magellan has been well known and understood by all authors. Juvenile specimens have been given the name *F. atrata* Reeve, but it has otherwise not been burdened



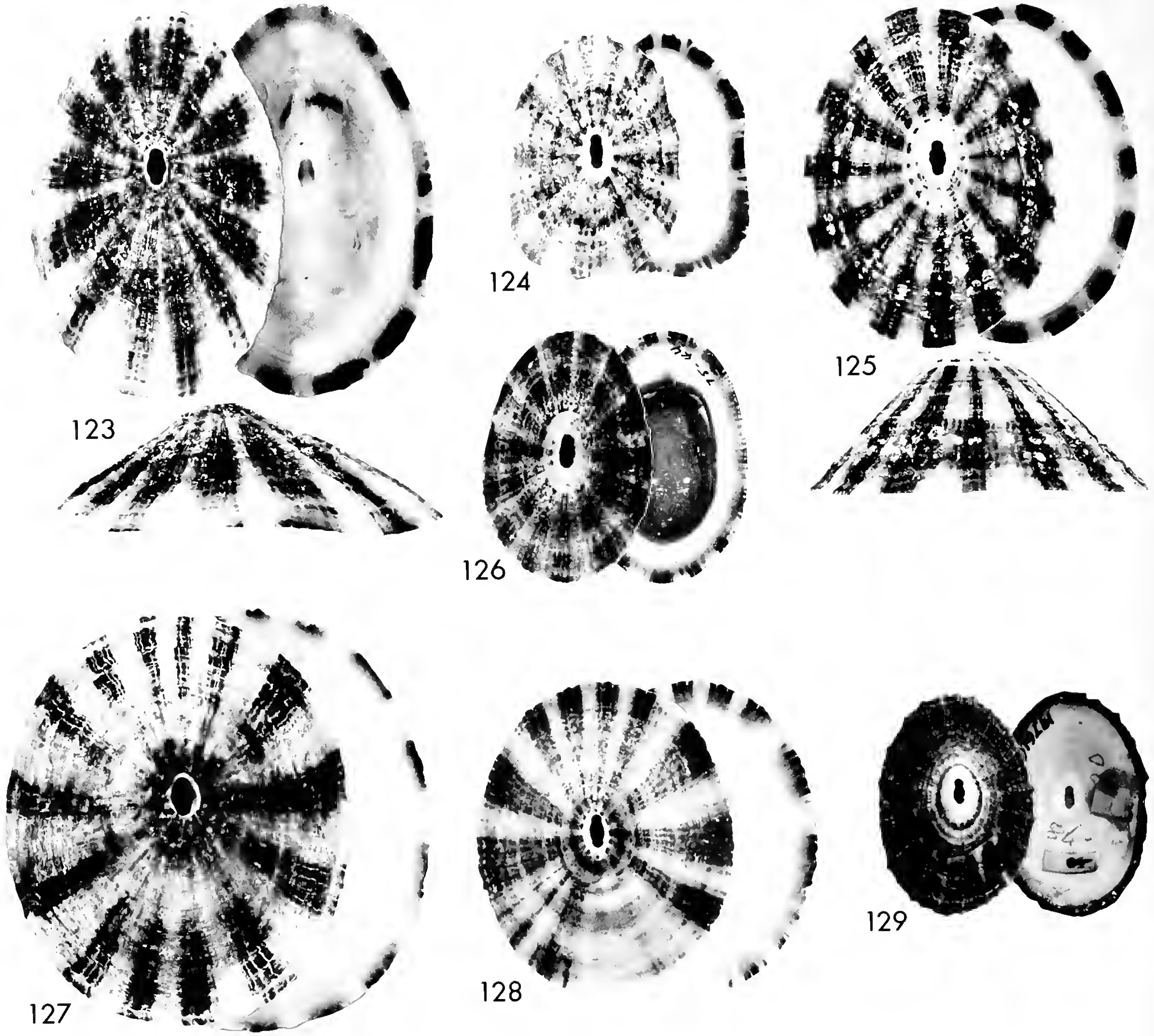
Figures 116 through 122. *Fissurella picta lata* Sowerby, 1835. Bodies of living and preserved specimens, juvenile shells, radula, mantle lobe, and cut shell. (**116**) Living specimen, ventral view, head at right. Río Bio-bio, Concepción Province, Chile. LACM 75-35. (**117**) Juvenile shell. Guabun, Chiloe Province, Chile. LACM 75-40, 12.6 × 8.6 × 3.3 mm. (**118**) Radula of small specimen. Río Bio-bio, Concepción Province, Chile. LACM 75-35, width of field 0.9 mm, shell length 27.3 mm. (**119**) Juvenile shell. Same locality. LACM 75-35, 13.5 × 8.3 × 4.3 mm. (**120**) Preserved specimen. Same locality. LACM 75-35, shell length 59.5 mm. (**121**) Mantle lobe. Island off Mehuin, Valdivia Province, Chile. LACM 75-37, length 8 mm. (**122**) Cut shell. Same locality. LACM 75-37, length of cut edge 32 mm.

with excessive numbers of synonyms, as have the other two common southern species, *F. radiosa* and *F. oriens.* Sowerby's *Fissurella lata* has not previously been a well understood taxon, perhaps because it is rare in the most populated region of central Chile. It is here for the first time regarded as a northern subspecies of the well-known *F. picta.* The original description of *F. lata* included the remark: "This species approaches, in form and colouring, very near to *Fiss. picta,* Lam.," an accurate observation not noticed by subsequent authors. In his discussion of this taxon, Riveros-Zuñiga merely quoted previous authors and figured what is more likely to be a specimen of *F. costata.* However, the Ziegenhorn and Thiem (1925) figure is a good representation of *F. picta lata.*

Abundance and Use. Both subspecies are large enough and common enough, at least at Concepción and to the south, to be important as a food resource. Numerous specimens were seen in shell piles at Mehuin. Moreno et al. (1984) have given an account of the fishery and ecology of this species at Mehuin. I have no information on the utilization of the species at more southern localities.

Characteristics and Variability. The typical *F. picta picta* is large-shelled, with coarse radial ribs and primary ribs that remain strong; the margin is broad; the dark colored rays are split into numerous fine lines by grooves that lack pigment and separate the fine ribs. Variation is extensive, chiefly in strength of ribbing and color pattern. Variations in outline of the base are unusual; some oval shells have been seen (Figs. 127, 128). Sculpture varies from coarse to nearly smooth. Most specimens are colored with gray rays on a white ground; variants with dark ground color are common. There are frequent concentric bands of different color intensity, probably representing seasonal changes in temperature and food availability.

Fissurella picta lata has a broad outline, as the name implies. Like *F. picta picta* it is also characterized as a large-shelled form with coarse ribbing and primary ribs that remain strong; the color rays are also split into thin lines by deep grooves in which the color is lacking. The margin is broad at all growth stages, and the mantle lobe papillae and foot tubercles are developed as in *F. picta picta.* As in the typical subspecies, there is extensive variation in *F. picta lata.* Al-

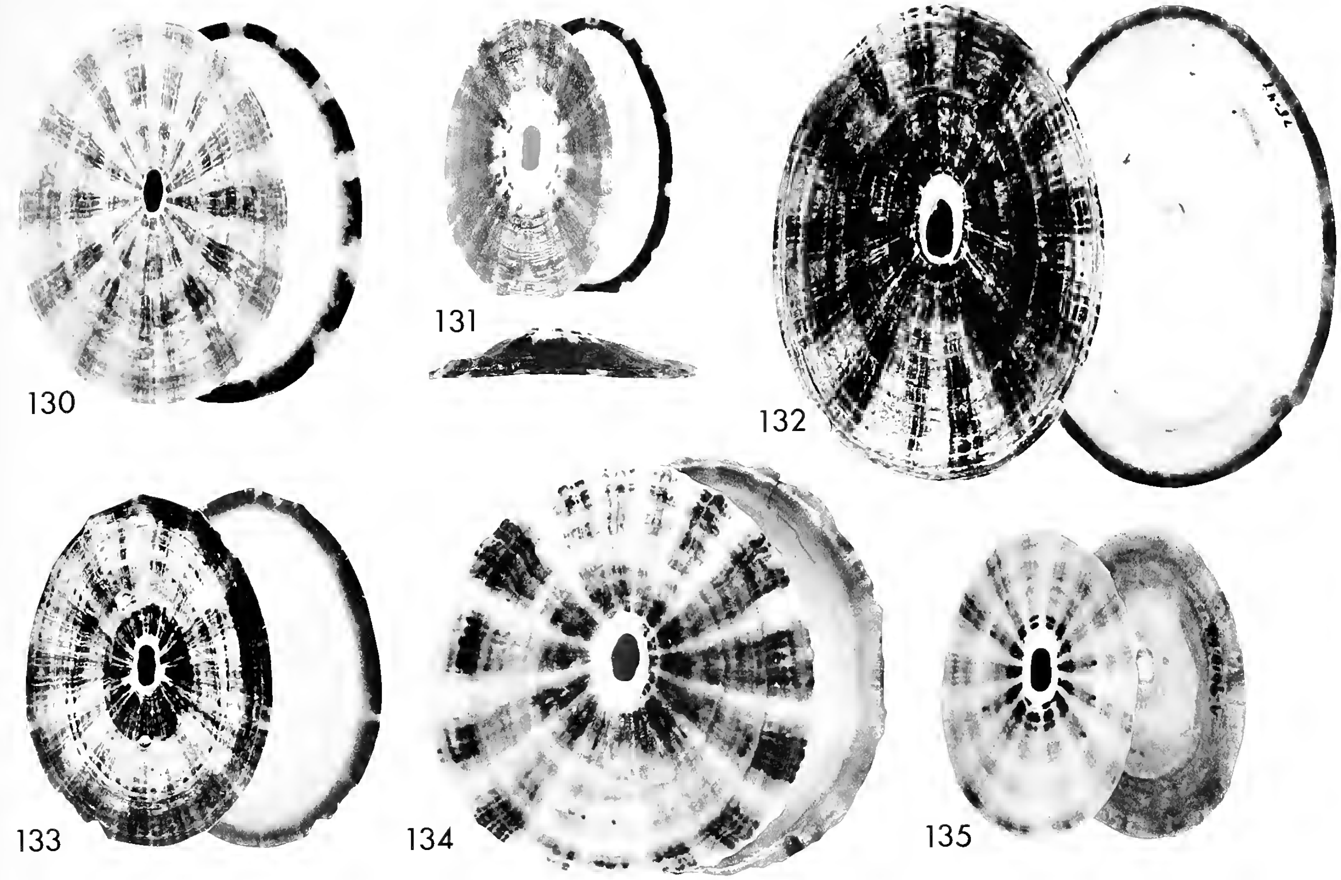


Figures 123 through 129. *Fissurella picta picta* Gmelin, 1791. Mature shells. (**123**) Pargua, Llanquihue Province, Chile. LACM 75-39, 77.2 × 49.3 × 23.1 mm. (**124**) Pumalin, Chiloe Province, Chile. LACM 75-41, 24.5 × 16.9 × 6.5 mm. (**125**) Same locality. LACM 75-41, 59.6 × 43.5 × 24.5 mm. (**126**) Islota Nihuel, Chiloe Province, Chile. LACM 75-44, 39.8 × 26.4 × 16.4 mm. (**127**) Quellón, Chiloe Province, Chile. LACM 75-45, 83.5 × 68.8 × 36.8 mm. (**128**) Pumalin, Chiloe Province, Chile. LACM 75-41, 48.4 × 39.6 × 18.2 mm. (**129**) Holotype, *F. muricata* Reeve. Locality unknown. BMNH 1976144, 25.8 × 18.4 × 13.0 mm.

though most specimens are elevated, the height is variable, and low forms occur in some populations along with more elevated specimens. Ground color ranges from light to dark gray; the rays are usually darker than the ground color but in some cases only slightly darker.

The major difference between the two subspecies is that *F. picta lata* has a more oval outline and usually is more elevated than *F. picta picta*. However, these are variable features within the species as a whole, and specimens occur at either extreme of the distribution having proportions typical of the other extreme. Specimens from the area of overlap, however, are more likely to have the intermediate proportions. Another difference is that of the coloration of the rays: *Fissurella picta picta* has dark purple to gray rays, whereas *F. picta lata* has rays that more clearly show the purple or reddish coloration. In both subspecies, however, the rays change color to reddish if the shells are faded by exposure to the sun. Shells from shell piles along the shore are much redder than those of live-collected or beach-worn specimens.

The extreme differences noted in some populations around Isla de Chiloe seem to be correlated with conditions of exposure to the open coastline on the west, or to a more pro-

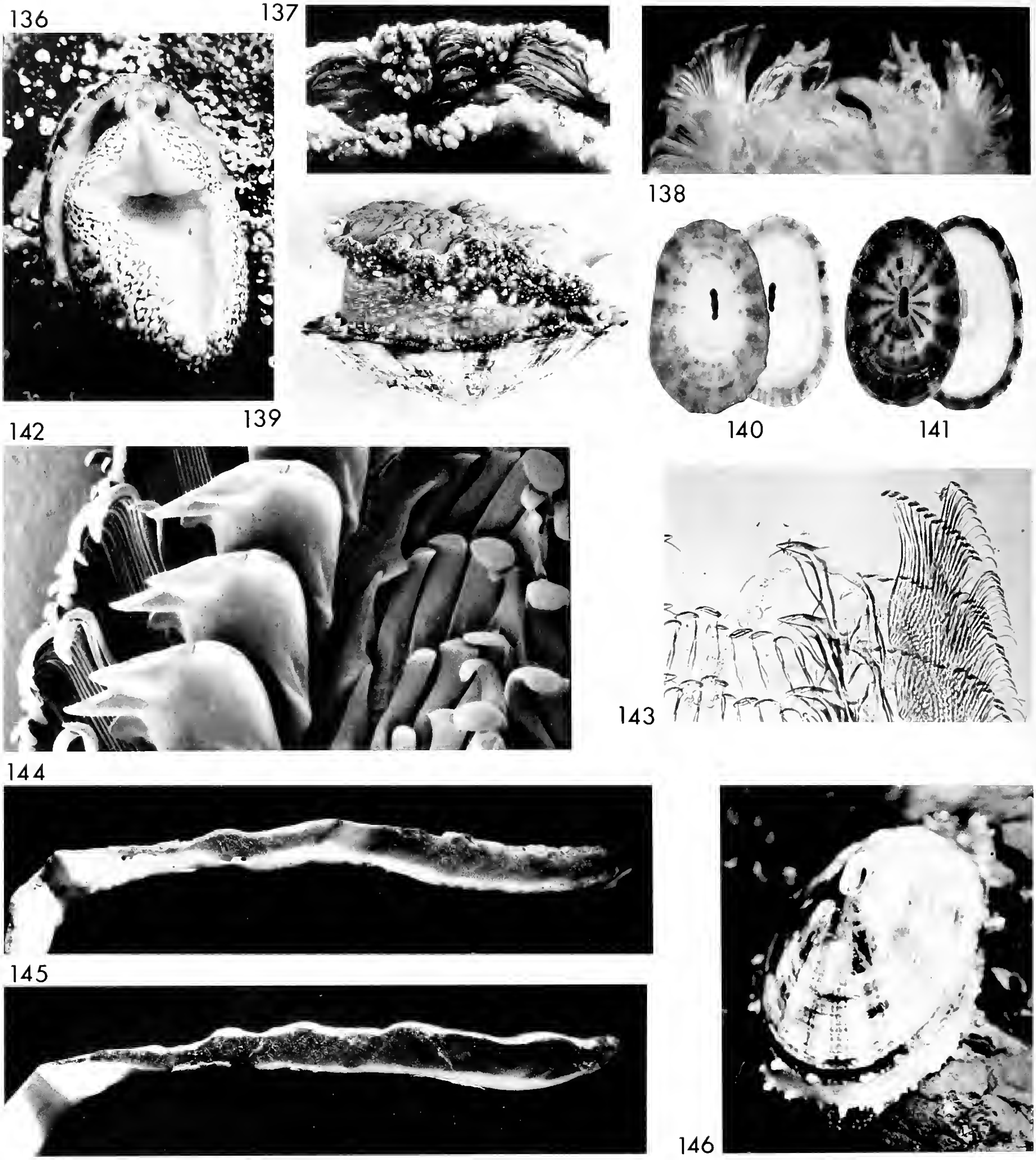


Figures 130 through 135. *Fissurella picta picta* Gmelin, 1791. Mature shells. (**130**) Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 58.2 × 40.4 × 18.3 mm. (**131**) Holotype, *F. atrata* Reeve. Locality unknown. BMNH 197564, 23.8 × 14.0 × 5.0 mm. (**132**) Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 86.3 × 58.3 × 28.3 mm. (**133**) Same locality. LACM 75-49, 49.2 × 34.3 × 13.7 mm. (**134**) Laredo Bay, Magallanes Province, Chile. USNM 118235, 68.6 × 61.7 × 30.0 mm. (**135**) Fox Bay, Falkland Islands. LACM 90800, 43.3 × 27.3 × 11.5 mm.

tected habitat along the channels to the east, where tidal extremes are greater than those of the open coast and water movement is produced by tidal currents. At Guabun, on the northwest, exposed side of the island (41°50′ S, 74°02′ W), the typical purple-rayed, oval, elevated form of *F. picta lata* occurs. Not far away at Pargua, on the mainland side of the Canal de Chacao (41°47′ S, 73°28′ W), I found the gray-rayed, low, elongate form typical of *F. picta picta* (Fig. 123). At Pumalin on the mainland opposite the southern tip of Isla de Chiloe (42°42′ S, 72°52′ W), the population was intermediate between the two extremes, more oval than typical for *F. picta picta,* but having no trace of the reddish rays (Fig. 125). At Isla Laitec off the southeast end of Isla de Chiloe (43°12′ S, 73°36′ W), shells were proportionately more elongate, typical of *F. picta picta.* Based on these four populations, I consider that *F. picta lata* occurs south along the outer coast of Isla de Chiloe and *F. picta picta* occurs to the north along the inner side of Chiloe Island. I do not know, however, whether populations from the exposed sides of islands to the south of Chiloe Island would also agree with *F. picta lata.*

Affinity and Comparisons. *Fissurella picta picta* most resembles *F. radiosa,* a smaller-shelled species that is similar in overall proportion, has sculpture of strong ribbing with persistently strong primary ribs, and has a similar color pattern. However, *F. picta picta* reaches nearly twice the size of *F. radiosa,* has a much broader margin at all growth stages, and has a more centrally placed foramen. The penciled effect of the dark rays of *F. picta picta* is not seen in *F. radiosa. Fissurella picta picta* does not occur sympatrically with any of the large species of northern Chile. It differs from all of them sufficiently to require no comparison.

The subspecies *F. picta lata* does occur sympatrically with many of the other species. The latter subspecies is most closely related to, and difficult to distinguish from, *F. costata. Fissurella picta lata* tends to be higher, more darkly rayed, and to have sculpture with stronger primary ribs and a slightly larger foramen than that of *F. costata.* Separation of the two



Figures 136 through 146. *Fissurella picta picta* Gmelin, 1791. Living and preserved specimens, radulae, juvenile shells, and cut shells. **(136)** Ventral view of living specimen. Pumalin, Chiloe Province, Chile. LACM 75-41. **(137)** Mantle lobe. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, length 12 mm. **(138)** Air-dried radula. Isla Laitec, Chiloe Province, Chile. LACM 75-47, width of ribbon 1.9 mm, shell length 54.3 mm. **(139)** Preserved specimen. Isla de Los Estados, Argentina. LACM 71-284, shell length 71.8 mm. **(140)** Juvenile specimen. Pumalin, Chiloe Province, Chile. LACM 75-41, 10.9 × 6.7 × 3.6 mm. **(141)** Juvenile specimen. Puerto Espanol, Bahía Aguirre, Tierra del Fuego, Argentina. LACM 73-67, 17.4 × 10.6 × 3.6 mm. **(142)** SEM photo of radula. Width of field 1.0 mm. **(143)** Radula of small specimen. Isla Laitec, Chiloe Province, Chile. LACM 75-47, width of field 0.7 mm, shell length 27.9 mm. **(144)** Cut shell. Pumalin, Gulfo Corcovado, Chile. LACM 75-41, length of cut 37 mm. **(145)** Cut shell. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, length of cut 33.2 mm. **(146)** Living specimen attached to substrate. Same locality. LACM 75-49.

species on shell characters may be difficult and sometimes entirely arbitrary, as the range of variation in the two species seems to overlap. It is easy to distinguish the living animals, however. The foot and mantle lobe of *F. picta lata* are gray, those of *F. costata* a pale pinkish brown.

Synonymy and Types. *Fissurella picta* was known to pre-Linnaean authors. It was probably the first of the Chilean species to reach Europe because it is so common in the Strait of Magellan. Gmelin (1791) is credited with the name; his knowledge of it came from figures in several previous nonbinomial works. Lamarck and Deshayes referred to it as the "Fissurelle de Magellan." Deshayes credited the name *picta* to Lamarck, but Sowerby II (1862) and Pilsbry (1890) correctly credited the authorship to Gmelin. Type material is unknown.

The holotype of *Fissurella atrata* Reeve, 1850, is BMNH 197564 (Fig. 131), length 23.8 mm, locality unknown. It is a small, dark-colored specimen of *F. picta,* easily recognized by its relatively broad, dark inner margin.

The holotype of *F. muricata* Reeve is BMNH 1976144, locality unknown (Fig. 129). It is a small dark specimen, the margin sufficiently broad to relate it to *F. picta* rather than *F. radiosa.* Because the interior has not previously been figured, the dark margin has been missed, which explains why no author has related it to any of the Peruvian-Magellanic species.

There are two syntypes of *F. lata* Sowerby, BMNH 197571, from Isla Santa Maria, Bahía Concepción, Chile, dimensions 83.4 mm × 64.3 × 31.6 mm, and 77.0 × 61.3 × 25.5 mm. The larger specimen, figured by Dell (1971), is figured here and designated the lectotype (Fig. 112). Both specimens are reddish rayed and clearly show the strong primary ribs in the light interspaces between the rays.

The holotype of *F. navidensis* Ramirez-Boehme, 1974, from Bahía Navidad, Santiago Province, Chile (33°56′ S, 71°52′ W), MNHN 200376 (Fig. 110), is a worn specimen of *F. picta lata,* with which it was not compared. Its similarity to *F. picta* was noted by its author, however, and the differences described are those that are here used to distinguish the two subspecies of *F. picta.*

Fissurella radiosa Lesson, 1831

Figures 147–175

Fissurella radiosa is here considered to have two geographic subspecies: *F. radiosa radiosa* in the Magellanic region of Chile and Argentina, and *F. radiosa tixierae* in the Golfo San Matias and Peninsula Valdez region of Argentina.

Synonymy for *F. radiosa radiosa:*

Fissurella radiosa Lesson, 1831:411; Orbigny, 1841:473; Pilsbry, 1890:157; Strebel, 1907:85, pl. 1, figs. 4, 5a–d, pl. 9, fig. 6; Melvill and Standen, 1914:115; Carcelles, 1950: 51; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:111; Dell, 1971:192; Ramirez-Boehme, 1974:32 [key]; Scarabino, 1977:178, pl. 1, fig. 5.

Fissurella picta var. *radiosa,* Ziegenhorn and Thiem, 1925: 8, 11, pl. 1, fig. 6.

Fissurella nigra Philippi, 1845:60; Philippi, 1846, pl. 2, fig. 22; Reeve, 1849, pl. 6, fig. 37. Not *F. nigra* Lesson, 1831.

Fissurella darwinii Reeve, 1849, pl. 1. fig. 7; Hupé, 1854: 247; Rochebrune and Mabille, 1889:74; Pilsbry, 1890:144, pl. 30, fig. 7, pl. 46, figs. 15–17; Melvill and Standen, 1898: 102; Strebel, 1907:93; Carcelles, 1950:51; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:98, fig. 16; Dell, 1971:185, pl. 4, fig. 4; Ramirez-Boehme, 1974:30 [key].

Fissurella picta var. *darwinii,* Ziegenhorn and Thiem, 1925: 8, 11, pl. 1, fig. 5.

Fissurella grisea Reeve, 1849, pl. 6, fig. 6; Sowerby II, 1862: 184, pl. 239, fig. 85; Pilsbry, 1890:152, pl. 39, fig. 9.

Fissurella exquisita Reeve, 1850, pl. 11, fig. 74; Hupé, 1854: 246; Sowerby II, 1862:186, figs. 32, 128; Rochebrune and Mabille, 1889:74; Strebel, 1908:78, pl. 5, figs. 74a–c; Carcelles and Williamson, 1951:256; Riveros-Zuñiga, 1951: 112, fig. 22; Métivier, 1969:115, fig. 1B [radula]; Dell, 1971:185, pl. 5, figs. 1, 3; Ramirez-Boehme, 1974:30.

Fissurella philippiana Reeve, 1850, errata page; Sowerby II, 1862:186, fig. 30; Pilsbry, 1890:146, pl. 33, fig. 40, pl. 58, figs. 24–26; Dall, 1909:242; Ziegenhorn and Thiem, 1925: 13, pl. 1, figs. 10a, 10b; Carcelles and Williamson, 1951: 253; Riveros-Zuñiga, 1951:106, fig. 19; Dell, 1971:190.

Fissurella philippii Hupé, 1854:245 (new name for *F. nigra* Philippi, not Lesson).

Fissurella polygona Sowerby II, 1862, fig. 177 (not fig. 137); Pilsbry, 1890:148, pl. 60, fig. 84; Melvill and Standen, 1898:102; Melvill and Standen, 1914:115; Carcelles and Williamson, 1951:254; Dell, 1971:192, pl. 4, figs. 9–11.

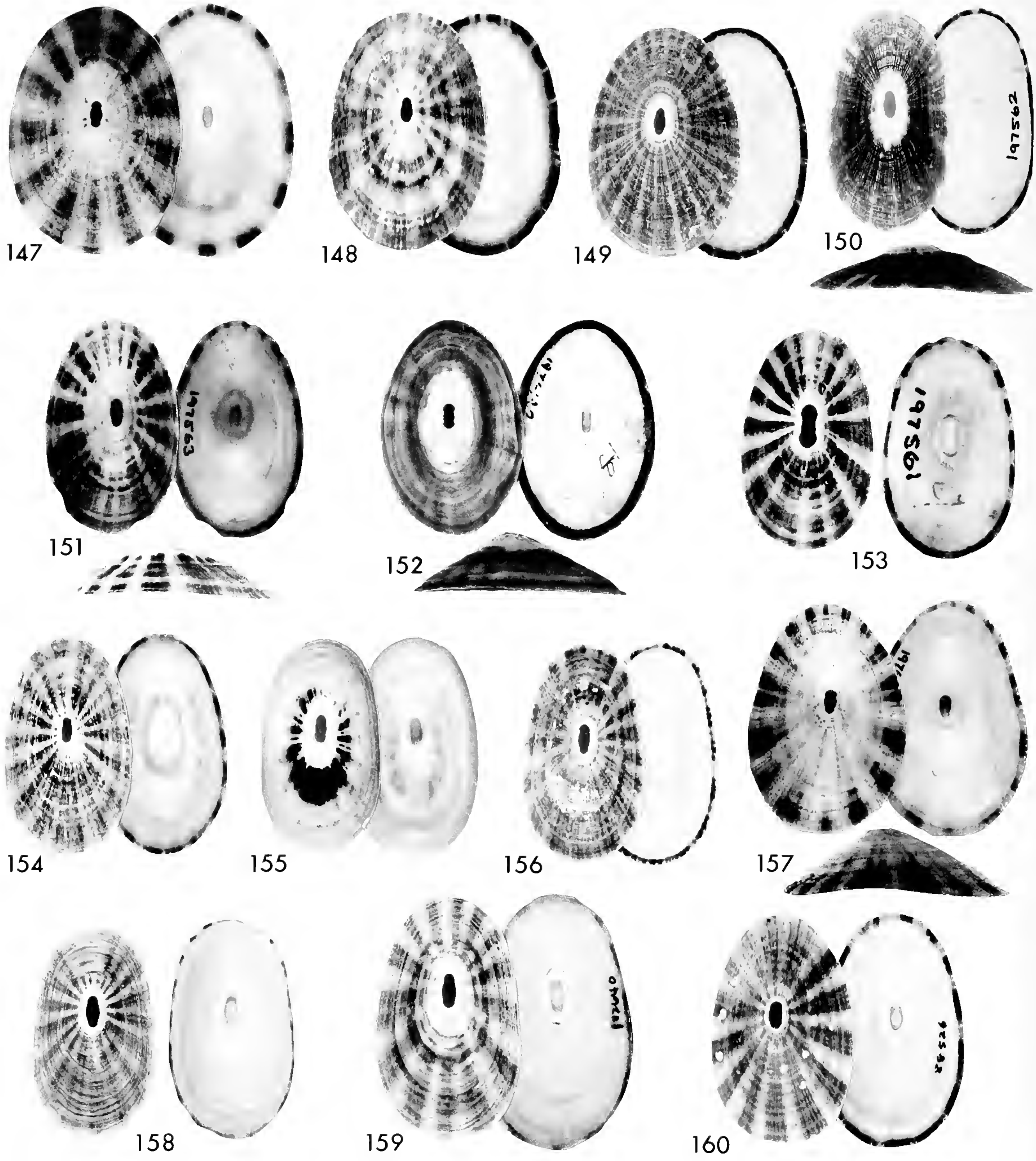
Fissurella dozei Rochebrune and Mabille, 1885:108; Rochebrune and Mabille, 1889:72, pl. 5, fig. 4; Carcelles, 1950: 51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:101, fig. 17; Dell, 1971:185.

Synonymy for *F. radiosa tixierae:*

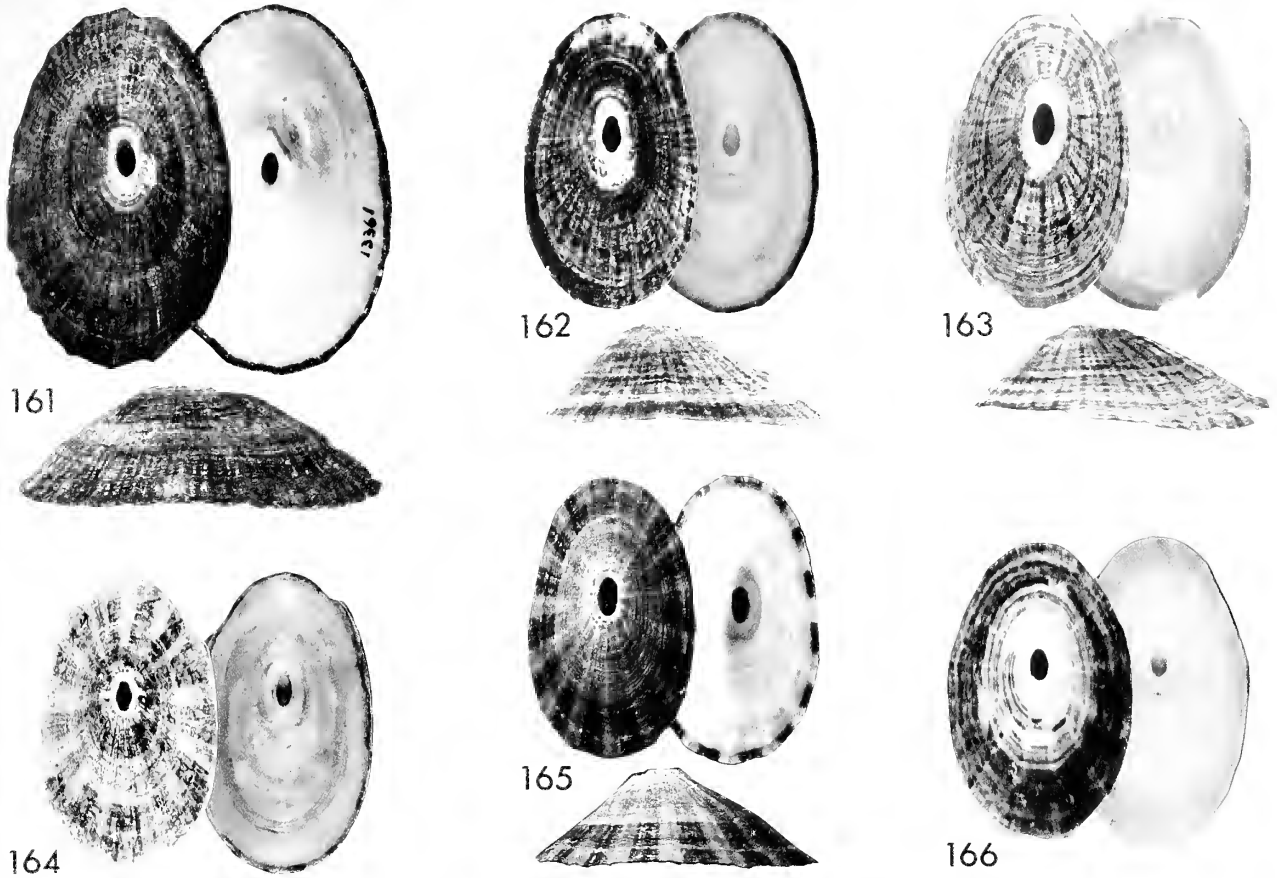
Fissurella tixierae Métivier, 1969:116, fig. 1A [radula], pl. 1, figs. 1–3, 9.

Shell (*F. radiosa radiosa*). Small to medium sized (40 to 55 mm mature length), low to moderately elevated; outline elongate oval, somewhat tapered anteriorly; sides of shell raised. Sculpture of sharply raised, narrow ribs that crenulate margin; primary ribs remaining stronger and more prominent at all growth stages. Ground color varying from white to gray or black with gray or reddish gray rays; the pattern of rays frequently interrupted by concentric changes in color intensity. Primary ribs coinciding with light rays; in uniformly dark shells primary ribs slightly lighter in color. Margin relatively narrow at all growth stages, not zoned; cut shells showing ground color or pattern of rays of uniform intensity throughout calcitic layer. Foramen just anterior of center, elongate and tripartite at all growth stages.

Shell (*F. radiosa tixierae*). Small (20 to 45 mm mature length), moderately to strongly elevated; outline elongate oblong, tapered anteriorly; margin more or less in same plane. Sculpture of narrow ribs that finely crenulate margin. Ground color white to dark gray or black with gray or reddish gray rays, often interrupted by concentric changes in intensity. Primary ribs coinciding with light rays. Margin narrow at all growth stages, showing pattern of rays. Foramen slightly anterior of center, elongate and tripartite at all growth stages.



Figures 147 through 160. *Fissurella radiosa radiosa* Lesson, 1831. Mature shells. **(147)** Pumalin, Chiloe Province, Chile. LACM 75-41, 47.0 × 32.0 × 13.1 mm. **(148)** Same locality. LACM 75-41, 41.9 × 27.4 × 11.8 mm. **(149)** Same locality. LACM 75-41, 43.5 × 28.4 × 13.7 mm. **(150)** "Syntype" [no standing as type] *F. philippiana* Reeve. "Chile." BMNH 197562, 42.0 × 22.8 × 8.6. **(151)** Lectotype, *F. darwinii* Reeve. Strait of Magellan, Chile. BMNH 197563, 36.9 × 22.8 × 11.0 mm. **(152)** Lectotype, *F. grisea* Reeve. Locality unknown. BMNH 1975140, 30.3 × 19.9 × 9.9 mm. **(153)** Lectotype, *F. exquisita* Reeve. Locality uncertain. BMNH 197561, 23.4 × 14.2 × 5.2 mm. **(154)** Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 40.2 × 23.0 × 10.6 mm. **(155)** Same locality. LACM 75-49, 38.2 × 21.4 × 8.2 mm. **(156)** Falkland Islands. USNM 368377, 46.7 × 20.1 × 9.4 mm. **(157)** Lectotype, *F. polygona* Sowerby II. Falkland Islands. BMNH 1976151,



Figures 161 through 166. *Fissurella radiosa tixierae* Métivier, 1969. Mature shells. **(161)** San Antonio Oeste, Rio Negro Province, Argentina. MACN 13361, 48.3 × 31.3 × 14.3 mm. **(162)** Puerto Lobos, Chubut Province, Argentina. MCZ 288334, 24.6 × 14.3 × 8.3 mm. **(163)** Holotype, *F. tixierae* Métivier. Golfo Nuevo, Chubut Province, Argentina. MNHNP, 22.5 × 13.7 × 8.0 mm (beach shell). **(164)** Puerto Madryn, Golfo Nuevo, Chubut Province Argentina. LACM 34858, 24.9 × 14.9 × 8.5 mm (beach shell). **(165)** Punta Cracker, Golfo Nuevo, Chubut Province, Argentina. LACM 78-90, 27.0 × 18.8 × 8.8 mm. **(166)** Puerto Madryn, Golfo Nuevo, Chubut Province, Argentina. USNM 152895, 25.5 × 15.6 × 10.6 mm (beach shell).

Juvenile Shell. Elongate, margin narrow, ribs fine and sharp, primary ribs lighter in color, secondary and tertiary ribs arising after shell reaches 5 mm in length.

Mantle and Foot. Nearly retractable within shell. Mantle lobe relatively narrow, banded to correspond to pattern of rays; black-shelled individuals also banded. Papillae moderately developed, finely branched; side of foot dark, tubercles with lighter tips.

Habitat. Lowermost intertidal zone and offshore to at least 20 m. In 1975 I found it common at Pumalin in the Golfo Corcovado on the undersides of rocks in an area where the exposure is limited chiefly to swiftly moving tidal currents; I also observed it in the sublittoral at Isla Talcon. In the Strait of Magellan it was common at low tide under rocks at Puerto Hambre. Paul Dayton collected it by diving at Isla de los Estados in 1973. In 1978 I found *F. radiosa tixierae* to be common in the Golfo Nuevo and Golfo San Jose, Argentina, on undersides of rocks at low tide and dredged offshore to 20 m.

Distribution. Golfo Corcovado on the east side of Isla Chiloe, Chile (northernmost specimens examined from Pumalin, Chiloe Province, Chile, 42°42′ S, 72°52′ W, LACM 75-41) to Tierra del Fuego, probably south to Cape Horn, east to the Falkland Islands, and north in Argentina to the Golfo San Matias (northernmost specimens from San Antonio Oeste, Rio Negro Province, 40°45′ S, 64°58′ W, MACN 13361, A.

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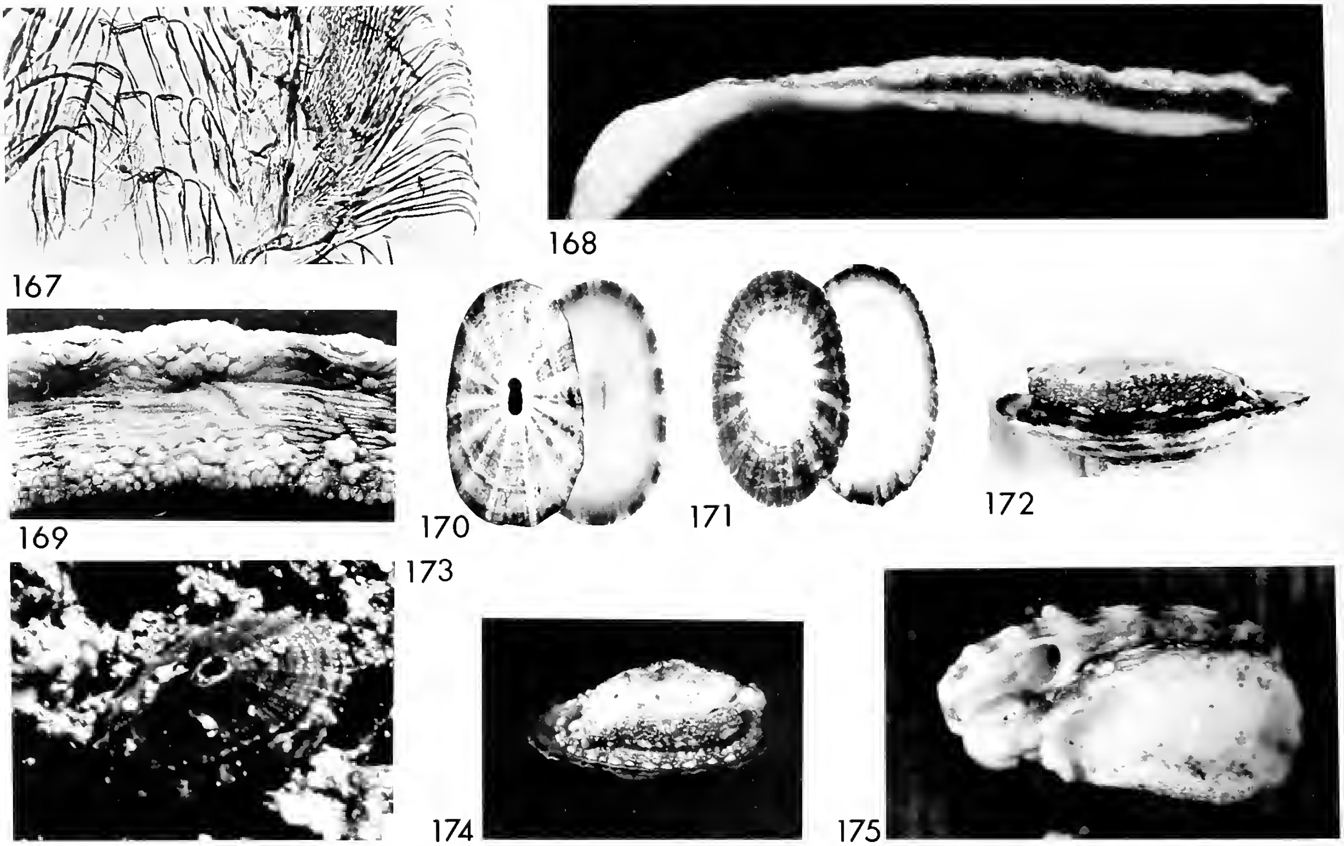
42.4 × 28.9 × 12.3 mm. **(158)** Puerto Deseado, Santa Cruz Province, Argentina. LACM 34851, 27.5 × 15.7 × 5.8 mm. **(159)** Puerto San Julian, Santa Cruz Province, Argentina. AMNH 182640, 45.0 × 26.4 × 12.4 mm. **(160)** Santa Cruz River, Santa Cruz Province, Argentina. ANSP 88526, 41.4 × 25.4 × 13.5 mm.



Figures 167 through 175. *Fissurella radiosa radiosa* Lesson, 1831, and *F. radiosa tixierae* Métivier, 1969. Radula, cut shell, mantle lobe, juvenile shell, living and preserved specimens. **Figures 167 through 172.** *F. radiosa radiosa.* (**167**) Radula. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, width of field 0.8 mm, shell length 20.8 mm. (**168**) Cut shell. Pumalin, Chiloe Province, Chile. LACM 75-41, length of cut edge 18.5 mm. (**169**) Mantle lobe. Fuerte Bulnes, Magallanes Province, Chile. LACM 75-48, length 11 mm. (**170**) Juvenile shell. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 13.8 × 7.8 × 3.3 mm. (**171**) Juvenile shell. Pumalin, Chiloe Province, Chile. LACM 75-41, 10.0 × 6.0 × 2.7 mm. (**172**) Preserved specimen. Fuerte Bulnes, Magallanes Province, Chile. LACM 75-48, shell length 56.5 mm. **Figures 173 through 175.** *Fissurella radiosa tixierae.* (**173**) Living specimen attached to substrate. Punta Cracker, Golfo Nuevo, Chubut Province, Argentina. (**174**) Preserved specimen. Punta Ninfas, Golfo Nuevo, Chubut Province, Argentina. LACM 78-88, shell length 19.3 mm. (**175**) Ventral-lateral view of living specimen. Same locality. LACM 78-88.

Carcelles). The subspecies *F. radiosa tixierae* is characteristic only of the Golfo San Matias and the Golfo Nuevo and Golfo San Jose; specimens from such localities as Puerto Deseado and Puerto San Julian, Santa Cruz Province, Argentina, are consistently larger and lower in profile, identified as *F. radiosa radiosa.* This is the only species of *Fissurella* that ranges throughout the Magellanic Faunal Province in both Chile and Argentina, and the only one that does not extend into the region of overlap with the Peruvian Faunal Province in south-central Chile.

Number of Lots Examined. *F. radiosa radiosa:* 55 (LACM 14, AMNH 5, ANSP 1, MACN 27, MNHN 1, USNM 7); *F. radiosa tixierae:* 28 (LACM 7, AMNH 1, MACN 19, USNM 1).

Taxonomic History. *Fissurella radiosa* Lesson, 1831, was not originally illustrated. Most of the accounts dealing with this species have consisted of copies and translations of original descriptions of its numerous synonyms. Accounts with additional observations are those of Strebel (1907), who was the first to recognize the species, Ziegenhorn and Thiem (1925), and Riveros-Zuñiga (1951), who recognized a specimen under the name of *F. dozei* Rochebrune and Mabille. The species has been misidentified as *Lucapinella henseli* (Martens, 1900), from Puerto Deseado, Santa Cruz Province, Argentina, by Ringuelet et al. (1962).

The Argentinian subspecies *F. radiosa tixierae* was described as a distinct species by Métivier (1969), based on a single specimen. He also identified *F. exquisita* Reeve from the Golfo Nuevo (here considered a synonym of *F. radiosa*), apparently not having sufficient specimens to realize that a single species is represented in the Golfo Nuevo.

Abundance and Use. *Fissurella radiosa* is common throughout its range. It is a rather small form occurring to the south of the populated regions of Chile; I have no information as to whether it has been exploited for food.

Characteristics and Variability. The shell of *Fissurella ra-*

diosa radiosa is relatively small and elongate, with a narrow dark margin, the ribbing fine and sharp, and the primary ribs evident at all growth stages. Shell height varies from low to moderately high. Color variation includes rayed forms and some that are uniformly dark. Changes in color often occur with growth. Some shells are nearly colorless in early stages and later acquire rays; others are strongly rayed at first and then lose the rays entirely. Normally rayed specimens may have growth increments that are uniformly dark. The ribs can be very evident or so weak that one can barely distinguish primary ribs from secondary ribs. In the eollections at hand there seem to be more of the weakly sculptured examples from the vicinity of the Strait of Magellan, whereas the strongly sculptured specimens are known from more northern localities in Chile and Santa Cruz Province, Argentina. The uniformly dark specimens have been seen only at Pumalin, in the Golfo Corcovado, where they occur with rayed forms. The largest observed specimen of the typical subspecies is 65 mm in length (LACM 75-42, Isla Talcon, Chile).

The large series of specimens of *F. radiosa tixierae* that I collected in the Golfo Nuevo and Golfo San Jose in 1978 are as variable in color as those of the typical subspecies, including many that are uniformly dark (Figs. 161, 162). There is such a preponderance of elevated specimens that the separation of a geographic subspecies based on this feature is justified. However, some specimens are as low as the typical subspecies. The largest specimen observed measures 48.3 mm in length (Fig. 161).

Affinity and Comparisons. *Fissurella radiosa* most resembles *F. picta. Fissurella radiosa* is smaller, has a narrower margin, a more anterior foramen, and lacks the penciled pattern of the rays. Unlike *F. picta picta,* which has gray rays only, there are some reddish-rayed forms. In shell morphology *F. radiosa* approaches *F. oriens,* which it may resemble in size, shape, and range of color possibilities, but it differs in having a narrower margin, more anterior foramen, and primary ribs that are raised, slightly nodular, and larger than the adjacent ribs, in contrast to the nearly smooth aspect of *F. oriens.* The papillae of the mantle fold are more strongly developed in *F. radiosa* than in *F. oriens. Fissurella radiosa* is more elongate than *F. peruviana* and has an elongate rather than oval foramen.

Synonymy and Types. Type material of *F. radiosa* Lesson, 1831, from the Falkland Islands, has never been illustrated and may not be extant. It is not housed in the Paris Museum where some of Lesson's material is now known (Bouchet, personal communication). Lesson's description stated: "The ribs are separated by profound narrow grooves, and they are arranged with three small ribs between each pair of larger ones, all over." This could also apply to *F. picta,* which was then well known, but the broad margin of *F. picta* was not mentioned; hence, by elimination we are left with *F. radiosa.* Strebel (1907) was the first to use the name *F. radiosa* in the sense adopted here.

Type material of *F. nigra* Philippi, 1845, not Lesson, 1831, has not been located. The locality was given only as "Chile." Philippi's illustration and description indicate that the shell was predominantly black, the young stages with lighter rays, the ribbing strong and unequal, and the margin narrow. Specimens collected at Pumalin, east of Isla de Chiloe, are a good match (Fig. 149), and the synonymy with *F. radiosa* is certain. Both Reeve and Hupé were to offer replacement names for the preoccupied name of Philippi.

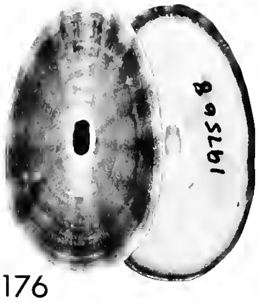
Fissurella darwinii Reeve, 1849, from the "Straits of Magalhaens," is represented by four syntypes, BMNH 197563, lengths, 37.0, 36.9, 33.9, and 21.3 mm. The smallest specimen has a margin broader than any in the three larger ones and is clearly a young *F. picta.* Dell (1971) figured the second largest specimen (36.9 mm in length); this is here figured and designated the lectotype (Fig. 151). The rays are reddish purple. Because the margin, which has not previously been illustrated, is narrow, I identify the type lot as *F. radiosa.* Pilsbry (1890) copied Reeve's illustration but also identified and figured a shell with a broader margin—that figure is here identified as *F. picta.*

Fissurella grisea Reeve, 1849, described without locality, is represented by two syntypes, BMNH 1976140, measuring 30.3 and 21.1 mm in length. The largest (Fig. 152) has been figured by Reeve and Sowerby II (1866) and is here designated the lectotype. Authors have not recognized this taxon. The shell is gray and has faint dark rays. The surface of the shell has evidently been treated with acid and only a trace of radial sculpture remains. I tentatively assign it to the synonymy of *F. radiosa,* suggested particularly by the tripartite foramen.

There are 5 specimens labeled *F. exquisita* Reeve, 1850, BMNH 197561. One small specimen is broken; the other four measure 45.3, 37.8, 34.0, and 23.4 mm in length. The Reeve locality is "Strait of Magalhaens," but the original label reads "Falkland Islands." The smallest intact specimen (Fig. 153) is a good match for the Reeve figure and was figured and designated the lectotype by Dell (1971). The largest specimen was also figured by Dell. All specimens are relatively low, have a narrow margin, are similarly rayed with reddish brown, and clearly show strong primary ribs.

Fissurella philippiana Reeve, 1850, was a name introduced on the errata page of the *Fissurella* monograph: "Sp. 37. For *F. nigra* Philippi, read *F. philippiana* Reeve." Reeve was renaming a homonym, although he did not explicitly state this. The specimens considered syntypes by Dell therefore have no standing as types. There are four specimens, BMNH 197562, the locality "Chile" in ink on the original mounting board, although Reeve gave the locality as "Southern Chile." The specimens measure 42.0, 38.6, 33.6, and 32.3 mm in length. They represent the dark form of *F. radiosa* in which the primary ribs are prominent and the margin narrow. Dell (1971) figured the 38.6 mm specimen; the largest is figured here (Fig. 150). The "syntypes" are very similar to those I found at Pumalin (Fig. 149). Dall (1909) inexplicably gave the locality as "Concepción, Chile," and this has been repeated by subsequent authors. No specimens corresponding to this locality have been found at the USNM. Concepción is well to the north of the known distribution of *F. radiosa.*

Fissurella philippii Hupé, 1854, was proposed as a replacement name for *F. nigra* Philippi, not Lesson. Hupé was unaware of the similar name proposed by Reeve.



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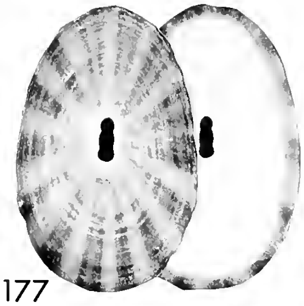

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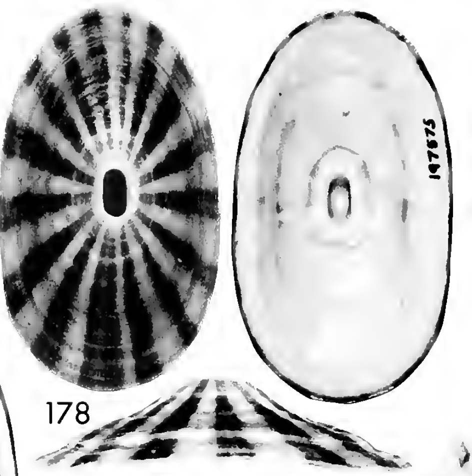

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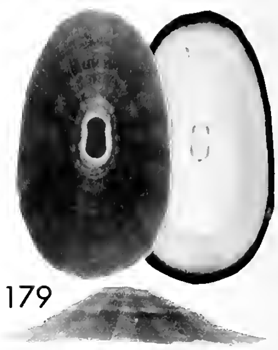

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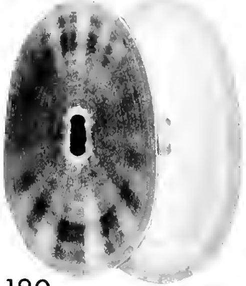

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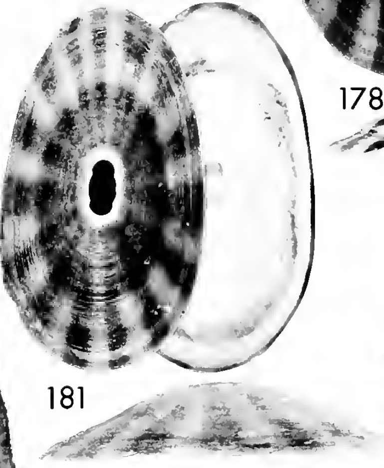

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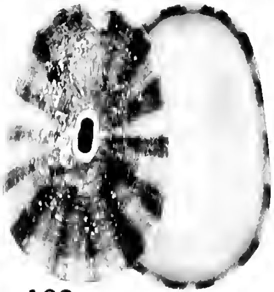

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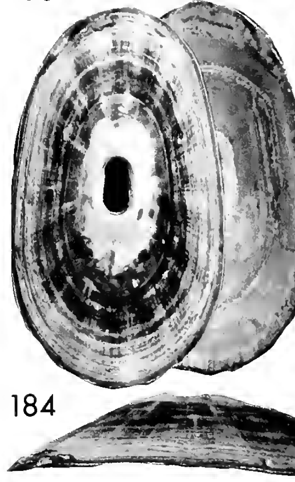

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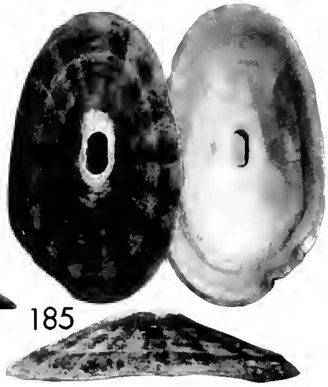

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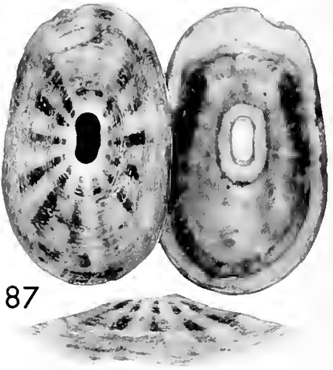

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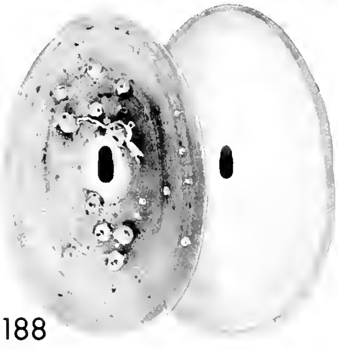

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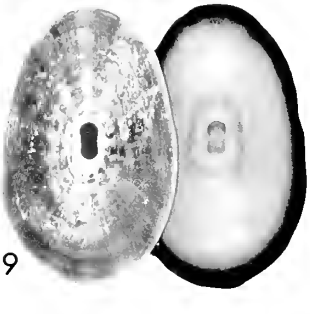

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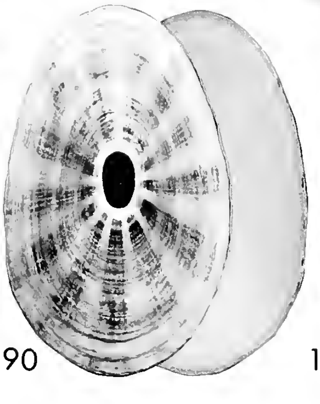

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Figures 176 through 191. *Fissurella oriens fulvescens* Sowerby, 1835, and *F. oriens oriens* Sowerby, 1835. Mature shells. **Figures 176 and 177.** *F. oriens fulvescens.* **(176)** Lectotype, *F. fulvescens* Sowerby. Valparaiso, Chile. BMNH 197568, 39.7 × 23.0 × 6.8 mm. **(177)** Islota Concon, Valparaiso Province, Chile. LACM 75-31, 23.2 × 14.8 × 4.5 mm (beach shell). **Figures 178 through 191.** *F. oriens oriens.* **(178)** Paralectotype, *F. oriens* Sowerby. Locality uncertain. BMNH 197575, 62.4 × 35.7 × 14.8 mm. **(179)** Lectotype, *F. mexicana* Sowerby. Locality unknown. BMNH 1944593, 38.6 × 22.2 × 8.6 mm. **(180)** Pargua, Llanquihue Province, Chile. LACM 75-39, 45.8 × 19.6 × 6.8 mm. **(181)** Pumalin, Chiloe Province, Chile. LACM 75-41, 58.0 × 32.7 × 12.0 mm. **(182)** 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43, 41.5 × 24.3 × 8.5 mm. **(183)** Same locality. LACM 75-42, 49.3 × 33.0 × 18.4 mm. **(184)** Holotype, *F. oblonga* Ramirez-Boehme. Punta

There are two syntypes of *F. polygona* Sowerby II, 1862, BMNH 1976151, from the Falkland Islands. The largest measures 42.4 mm in length and was figured by Dell (1971). It is here designated the lectotype (Fig. 157). The smaller specimen measures 22.2 mm in length and has proportions similar to the larger. Primary ribs are not as pronounced as shown in the original figure (copied by Pilsbry, 1890); the rays are reddish brown. The specimens represent the broad, elevated extreme of *F. radiosa,* which may be the typical form, as it has the same general type locality as that of the senior synonym.

Type material of *Fissurella dozei* Rochebrune and Mabille, 1885, described from Santa Cruz, Patagonia, was not located in the Paris Museum by P. Bouchet, although type material of two other Rochebrune and Mabille taxa is known in the Paris Museum. The drawing given by the authors in 1889 is a fair rendition of *F. radiosa* with well marked ribs, the figure showing that there are primary ribs that are slightly more prominent than the secondary ribs; the width of the margin is not mentioned. Puerto Santa Cruz, Santa Cruz Province, Argentina (50°01′ S) is north of the eastern entrance to the Strait of Magellan. This is a region in which *F. radiosa* is now known to be the only living species of *Fissurella.* The synonymy of *F. dozei* with *F. radiosa* is therefore reasonably certain.

Fissurella tixierae Métivier, 1969, was based on one specimen in poor condition, MNHNP uncataloged, from the intertidal zone in the Golfo Nuevo, Argentina (42°56′ S, 64°24′ W), length 22.5 mm, width 13.7 mm, height 8 mm (Fig. 163).

Fissurella oriens Sowerby, 1835

Figures 176–199

Fissurella oriens is here considered to have two geographic subspecies: *F. oriens oriens* in the Magellanic region of Chile and *F. oriens fulvescens* in south-central Chile.

Synonymy for *F. oriens oriens:*

Fissurella oriens Sowerby, 1835a:124; Sowerby, 1835b:3, figs. 25, 60; Reeve, 1849, pl. 2, fig. 13; Hupé, 1854:237; Sowerby II, 1862:186, figs. 19, 20; Pilsbry, 1890:152, pl. 46, figs. 18, 19, pl. 34, fig. 58; Melvill and Standen, 1907:97; Strebel, 1907:88, pl. 1, figs. 8–14, pl. 2, figs. 15–20; Strebel, 1908:78, pl. 6, figs. 97a, b; Dall, 1909:242; Melvill and Standen, 1914:114; Powell, 1951:85; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:123, fig. 30; Dell, 1971:185, pl. 5, figs. 3, 4; Ramirez-Boehme, 1974:30 [key].

Fissurella mexicana Sowerby, 1835b:8, fig. 61; Reeve, 1849, pl. 6, fig. 40; Sowerby II, 1862:186, figs. 26–28; Pilsbry, 1890:153, pl. 34, fig. 60; Melvill and Standen, 1898:102; Strebel, 1907:88 [under *F. oriens*].

Fissurella australis Philippi, 1845:61; Philippi, 1845:142; Strebel, 1907:88 [under *F. oriens*].

Fissurella alba Philippi, 1845:61; Philippi, 1845:34, pl. 1, fig. 4; Hupé, 1854:247; Rochebrune and Mabille, 1889:71; Pilsbry, 1890:292, pl. 62, figs. 3–5; Strebel, 1907:94, pl. 1, figs. 1–3, pl. 2, fig. 21; Ziegenhorn and Thiem, 1925:14, pl. 2, figs. 14a, 14b, 15; Carcelles, 1950:51, pl. 1, fig. 11; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951: 100; Dell, 1971:181; Ramirez-Boehme, 1974:30 [key].

Fissurella (Corrina) alba Christiaens, 1973:93, pl. 4, figs. 46, 47.

Fissurella flavida Philippi, 1857:165; Pilsbry, 1890:292; Strebel, 1907:97; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951: 121; Dell, 1971:186; Ramirez-Boehme, 1974:30 [key].

Fissurella hedeia Rochebrune and Mabille, 1885:109; Rochebrune and Mabille, 1889:72, pl. 5, fig. 3; Carcelles, 1950:51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951, fig. 32; Dell, 1971:186; Ramirez-Boehme, 1974:30 [key].

Fissurella arenicola Rochebrune and Mabille, 1885:109; Rochebrune and Mabille, 1889:73, pl. 5, fig. 1; Carcelles, 1950:51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:124, fig. 31; Dell, 1971: 182; Ramirez-Boehme, 1974:30 [key].

Fissurella (Carcellesia) doellojuradoi Perez-Farfante, 1952: 32, fig. 1; Christiaens, 1973:92, pl. 4, fig. 45.

Fissurella cheullina Ramirez-Boehme, 1974:17, 30 [key], pl. 1, figs. 2a–c.

Fissurella oblonga Ramirez-Boehme, 1974:18, 30 [key], pl. 2, figs. 4a–c.

Synonymy for *F. oriens fulvescens:*

Fissurella fulvescens Sowerby, 1835a:127; Sowerby, 1835b: 6, fig. 49; Reeve, 1849, pl. 6, fig. 42; Hupé, 1854:245; Sowerby II, 1862:184, fig. 36; Pilsbry, 1890:152, pl. 33, fig. 49; Dall, 1909:241; Riveros-Zuñiga, 1951:122, fig. 29; Dell, 1971:186, pl. 5, fig. 6; Ramirez-Boehme, 1974:30 [key].

Shell (*F. oriens oriens*). Small to medium sized (mature length 40–70 mm), low to moderately elevated; outline elongate oval to very elongate, lateral profile variable, ranging from flat or with either ends or sides raised. Sculpture of fine radial ribs, ribs very broad and flat at margin, ending in extremely fine crenulations; under magnification fine con-

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Chulao, Chiloe Province, Chile. MNHN 200375, 55.5 × 31.0 × 12.2 mm. **(185)** Holotype, *F. cheullina* Ramirez-Boehme. Isla Quellin, Llanquihue Province, Chile. MNHN 200327, 43 × 23 × 9 mm. **(186)** Holotype, *F. hedeia* Rochebrune and Mabille. Punta Arenas, Magallanes Province, Chile. MNHNP, 29 × 24 × 7 mm. **(187)** Orange Harbor, Chile. USNM 17328, 37.4 × 22.9 × 8.2 mm. **(188)** 13–29 m, Strait of Magellan, Chile. LACM 90801, 47.3 × 29.7 × 10.6 mm. **(189)** 18–27 m, Falkland Islands. USNM 368309, 23.2 × 14.7 × 5.0 mm. **(190)** Punta Arenas, Magallanes Province, Chile. LACM 75-50, 54.2 × 33.2 × 16.9 mm. **(191)** Holotype, *F. arenicola* Rochebrune and Mabille. Locality uncertain. MNHNP, 42.2 × 26.5 × 14.2 mm.

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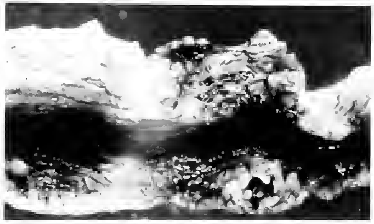

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Figures 192 through 199. *Fissurella oriens oriens* Sowerby, 1835. Living specimens, radula, mantle lobe, juvenile shells, and cut shell. **(192)** Detached living specimens. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43. **(193)** SEM view of radular ribbon. Pargua, Llanqihue Province, Chile. LACM 75-39, width of field 0.7 mm. **(194)** Radula. Pumalin, Chiloe Province, Chile. LACM 75-41, width of field 0.5 mm. **(195)** Mantle lobe. Same locality. LACM 75-41, length 9 mm. **(196)** Juvenile shell. 11–13 m, Isla Carlos III, Magallanes Province, Chile. LACM 73-70, 7.8 × 4.5 × 1.9 mm. **(197)** Juvenile shell. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43, 13.4 × 8.2 × 3.4 mm. **(198)** Air-dried radula. Pumalin, Chiloe Province, Chile. LACM 75-41, width of ribbon 3.0 mm, length of shell 48.8 mm. **(199)** Cut shell. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-42, length of cut edge 17 mm.

centric lamellae visible in early growth stages. Ground color variable, from colorless to yellow or dark red; rays mostly reddish or gray, solid or split into two or more broad bands and frequently with concentric interruptions; gray rays often changing to reddish or black to gray. Some specimens completely colorless. Margin relatively narrow, somewhat broader in rapidly growing specimens, not zoned, showing full pigmentation of rays throughout calcitic layer. Foramen elongate and tripartite in young shells, elongate-oval in mature shells.

Shells of the northern subspecies, *F. oriens fulvescens,* smaller (maximum length 45 mm), relatively low, ends usually elevated relative to sides. Color consistent; ground color yellow orange, rays dark red, rays frequently split into two adjacent bands, young shells speckled with red. This coloration and the speckled pattern of young shells is not matched by that in any specimens of the typical subspecies.

Juvenile Shell. Elongate oval, more conical than at later stages, usually reddish overall, with white apical area and color pattern emerging unevenly; rays arising after shell reaches about 4 mm in length.

Mantle and Foot. Animal usually large, not retractable in flattened shell. Cephalic tentacles reddish brown, yellowish at tips. Mantle lobe rather thin in preserved specimens, edges with finely branched papillae, banded to correspond to rayed pattern; side of foot mottled brown to pinkish brown, light in specimens with colorless shells. Epipodial tentacles especially prominent.

Habitat. Chiefly sublittoral throughout the range, but extending up to the lower intertidal zone in places exposed to currents but not heavy surf. The northern subspecies *F. oriens fulvescens* is probably limited to the sublittoral zone, for I was unable to find living specimens at low tide. I observed the typical subspecies at Mehuin in deep tide pools. I found it at Pumalin in the Golfo Corcovado, occurring at low tide in rocky areas free of sand where tidal currents were strong; at Islote Nihuel in the Golfo Corcovado I found it at a depth of 10 m on rocks near the sand–rock interface. At Puerto Hambre in the Strait of Magellan I found it at low water in sheltered rocky areas. Specimens have been dredged to depths of 30 m by the R/V HERO near Isla de los Estados, Argentina.

Distribution. Islote Concon, Valparaíso Province, Chile (32°52′ S) (LACM 75-31, McLean), south to Tierra del Fuego and probably Cape Horn, east to Isla de los Estados, Argentina, and the Falkland Islands. Not known living from mainland Argentina. Pleistocene specimens are known from Comodoro Rivadavia, Chubut Province, Argentina (MCZ 288329), as is also true for *F. picta.* Scarabino's (1977) record of the species from the Golfo San Matias, Argentina, is probably based upon specimens of *F. radiosa tixierae.* Populations from the northern end of the range in the vicinity of Valparaíso and south at least to Concepción are of the subspecies *F. oriens fulvescens.* Those at Mehuin and to the south are the typical subspecies *F. oriens oriens.*

Number of Lots Examined. *F. oriens oriens:* 97(LACM 34, AMNH 10, ANSP 6, MACN 28, MNHN 6, USNM 13); *F. oriens fulvescens:* 4 (LACM).

Taxonomic History. *Fissurella oriens* Sowerby has been reasonably well understood by most authors, although the extent of its variability and the extreme number of synonyms has not generally been recognized. Most of the synonyms have not come into general use, with one exception, that of *F. alba* Philippi, which was based on white-shelled forms. The northern subspecies, *F. oriens fulvescens* Sowerby, is here recognized for the first time.

Abundance and Use. *Fissurella oriens* is primarily a species of the Magellanic Faunal Province, where it is common at low water and much more abundant in the sublittoral. Although many shells are small, it reaches sizes large enough to be used for food. I have no information on the extent of its use.

Characteristics and Variability. The most characteristic features of *F. oriens* are the relatively small size and lack of strong ribbing, the radial sculpture being better described as consisting of striae or grooves. It is one of the most variable species in proportions, size of the foramen, and color pattern. Local populations tend to be consistent, with many similarly appearing individuals. The ground color of the typical subspecies ranges from colorless to dark red, but most commonly has strong rays that may change with growth from gray to reddish and increase or diminish in intensity. White shelled specimens have been noticed in scattered populations throughout the range of the species. Some populations have shells that are relatively flat, while in others the shells are more elevated. This is one of the few species in which the variation includes specimens with either elevated sides or elevated ends. The margin is usually narrow, though not as narrow as that of *F. radiosa.* However, some specimens that are growing rapidly may have a relatively broad margin. In some gerontic specimens, the foramen may become very large and broadly oval; in others it remains narrow and elongate.

Affinity and Comparisons. *Fissurella oriens* most resembles *F. radiosa,* a species of similar size in which there is similar variation in proportions and color. *Fissurella oriens* differs chiefly in lacking the strong ribbing of *F. radiosa* and in having a more centrally placed foramen. However, some conspicuously ribbed specimens of *F. oriens* may so resemble weakly ribbed specimens of *F. radiosa* that the only reliable character to separate them is the presence of primary ribs larger than the adjacent ribs on *F. radiosa,* and the absence of such primary ribs on *F. oriens.* Strongly rayed specimens of *F. oriens* may have a superficial resemblance to uneroded specimens of *F. limbata,* but *F. oriens* lacks the broad two-zoned margin that is the hallmark of *F. limbata.*

Synonymy and Types. Eleven names seem to be referable to *F. oriens,* the large number of synonyms correlated with the high variability of the species and the tendency for local populations to have uniform features.

There are five syntypes of *F. oriens* Sowerby, 1835, BMNH 197575, lengths 69.3, 62.4, 59.6, 53.7, and 16.7 mm. The largest specimen, that figured by Reeve (1849) and Dell (1971) is designated the lectotype; the second largest specimen, a paralectotype, is figured here (Fig. 178). Although Reeve gave the locality as Valparaíso, Sowerby's original locality is "Insulam Chiloe," with a "variety" mentioned from Valparaíso. The specimens are relatively large, rayed in reddish brown, and represent the normal, elongate, moderately elevated form, similar to what I have observed from the vicinity of Isla de Chiloe. The type locality should therefore be limited to Isla de Chiloe. Sowerby's original figure in the "Conchological Illustrations" was of a smaller specimen, probably the 59.6 mm specimen.

Sowerby did not clearly document the above-mentioned "variety" of *F. oriens* from Valparaíso. However, in the same publication (Sowerby, 1835a) he described *F. fulvescens* from Valparaíso, which may have been intended as the "variety." In 1975 I found beach-worn specimens matching the type lot on cobble beaches in that vicinity of Chile (Fig. 177). The type lot consists of four specimens, BMNH 197568, lengths 39.7, 37.0, 33.0, and 27.9 mm. The largest specimen (Fig. 176) was figured originally by Sowerby (1835b), later by Reeve (1849), and more recently by Dell (1971), who designated it the lectotype. All the specimens are low and elongate, yellow-orange in ground color, the rays reddish, and the margin narrow. The specimens are in good condition and were evidently collected alive; according to Sowerby, they were taken under rocks on the shore.

Fissurella mexicana Sowerby, 1835, was said to come from "Real Llejos, Mexico," obviously in error. There are four specimens in the type lot, BMNH 1966493, lengths 40.6, 40.4, 38.6, and 29.6, the smallest specimen broken and repaired. They are elongate, moderately elevated, and rather thin-shelled, well within the range of variation of *F. oriens.* The 38.6 mm specimen is designated the lectotype (Fig. 179).

Fissurella australis Philippi, 1845, from "Fretum Magellanicum," was never illustrated and I have not been able to locate type material. Philippi described its color and sculpture as similar to that of a young *F. oriens,* but thinner-shelled and with extremities raised, the shell resting on the sides. Inasmuch as specimens of *F. oriens* with raised ends and thin shells are well known, the synonymy is reasonably certain.

Fissurella alba Philippi, also from "Fretum Magellanicum," was illustrated subsequently by Philippi, but again, type material has not been located. A white, finely sculptured shell was figured, and Philippi himself indicated that it could be a variant of *F. oriens.* This note was, surprisingly, overlooked by Pilsbry (1890) and the taxon has been accepted without question by subsequent authors and even made the type species of a subgenus based upon the character of weak ribbing. Nevertheless, it is clearly a white-shelled variant of *F. oriens.* I have seen white shells from numerous stations at which rayed forms also occur (see Fig. 188, from a lot of six specimens, four of which are white and two are rayed).

Fissurella flavida Philippi, 1857, from the "Magellenstrasse," has not been figured and I have not located type material. The description indicates a shell that is solid, elliptical, moderately convex, with obscure sculpture, and a moderately broad margin. The coarse sculpture that characterizes *F. picta* and *F. radiosa* were not mentioned. Inasmuch as only three species occur in the region, this name can be relegated to the synonymy of *F. oriens* by eliminating the other possibilities.

The holotype of *F. hedeia* Rochebrune and Mabille, 1885, from Punta Arenas in the Strait of Magellan, was received on loan from the Paris Museum (Fig. 186). Although not compared by its authors to other species, it is an elongate, finely sculptured specimen of *F. oriens.*

Fissurella arenicola Rochebrune and Mabille, 1885, also was not compared to other species. Two specimens in the Paris Museum labeled "type et paratype," were studied. The locality inked on the mounting board is "Baie Orange"; the published locality is "Punta-Arenas Patagoniae, Baie Orange." The holotype (Fig. 191) is a white-shelled *F. oriens,* 42.2 mm in length, very worn except at the margin, where no traces of primary ribs are evident. The paratype is 38.2 mm in length, also white-shelled, but primary ribs are apparent throughout. I therefore identify the paratype as *F. radiosa.* Based on the holotype, the name *F. arenicola* is placed in the synonymy of *F. oriens.*

Fissurella (*Carcellesia*) *doellojuradoi* Pérez-Farfante, 1952, was based on a single specimen from "Tierra del Fuego." The specimen, 35 mm in length, was borrowed by its author from the Museo Argentino de Ciencias Naturales in Buenos Aires. A new subgenus was based on the single feature of the raised ends of the specimen, but as discussed above, such variants are frequently seen in *F. oriens,* with which it was not originally compared. The synonymy of this taxon therefore seems certain.

Fissurella cheullina Ramirez-Boehme, 1974, was based on eight specimens from Isla Queullin, Llanquihue Province, Chile (41°53′ S, 72°55′ W), holotype MNHN 200377 (Fig. 185). *Fissurella oblonga* Ramirez-Boehme, 1974, was based on a single specimen from Punta Chulao, Chiloe Province, Chile (42°17′ S, 72°50′ W), holotype MNHN 200375 (Fig. 184). Neither taxon was compared by its author to any other species. Both were described as moderately elevated, elongate, weakly sculptured, and with narrow margins. These specimens are well within the range of variation known for *F. oriens.*

Fissurella nigra Lesson, 1831

Figures 200–211

Fissurella nigra Lesson, 1831:412; Orbigny, 1841:473; Philippi, 1846:65, fig. 2; Reeve, 1849, pl. 2, fig. 11; Hupé, 1854:241; Sowerby II, 1862:184, fig. 14; Pilsbry, 1890: 149, pl. 35, figs. 1, 2; Dall, 1909:177, 242; Ziegenhorn and Thiem, 1925:15, pl. 2, figs. 16a, b; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:116, fig. 25; Dell, 1971:188, pl. 3, figs. 17–19; Ramirez-Boehme, 1974:31 [key].

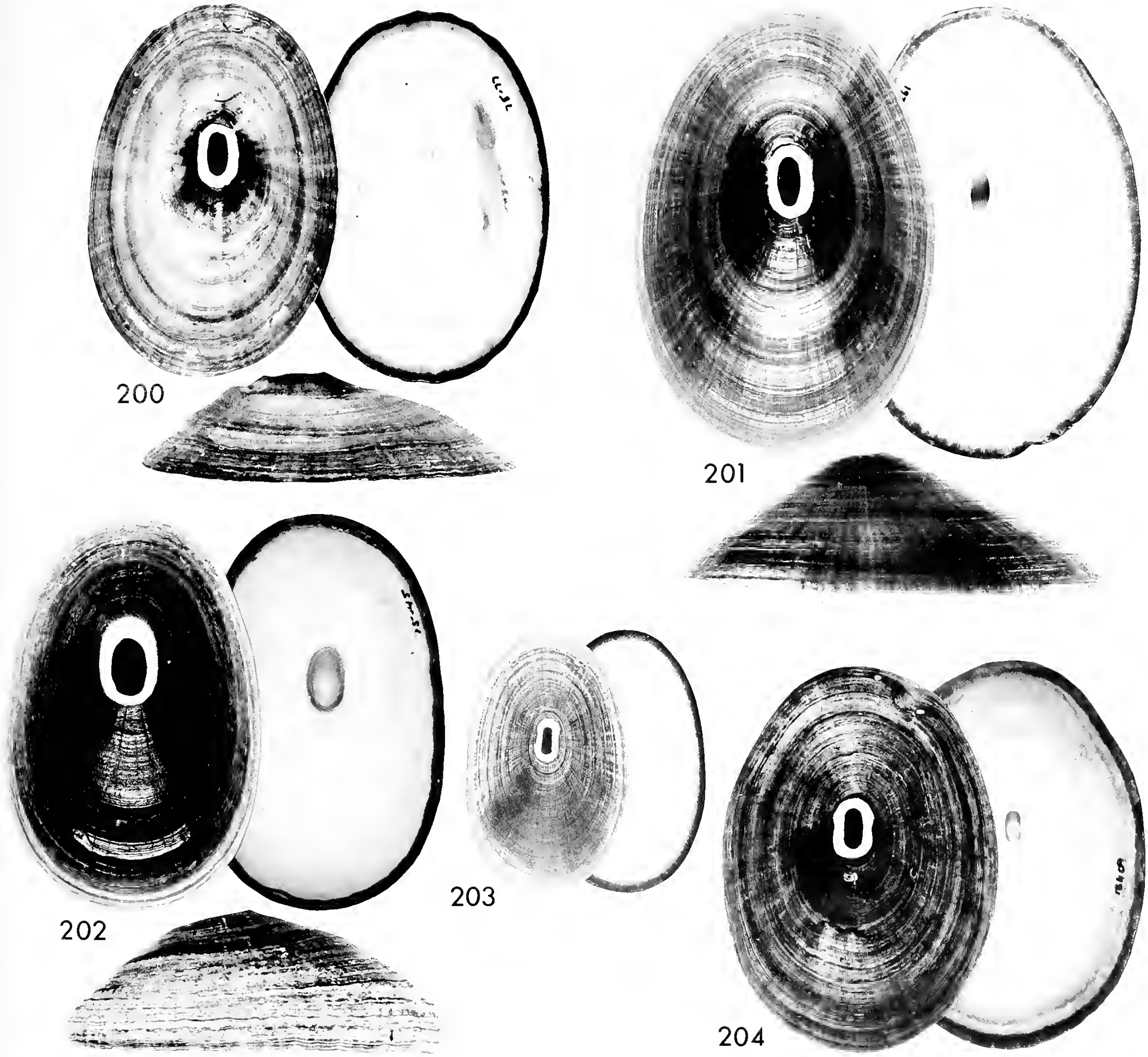
Fissurella violacea Rathke, 1833 [*ex* Eschscholtz manuscript]:21, pl. 23, fig. 6; Orbigny, 1841:473 [under *F. nigra*]; Philippi, 1846:66, pl. 2, fig. 3.

Fissurella grandis Sowerby, 1835a:123; 1835b:3, fig. 48; Orbigny, 1841:473 [under *F. nigra*]; Philippi, 1846:65, pl. 2, fig. 1.

Shell. Relatively large (70 to 110 mm mature length), moderately elevated; outline elongate oval, base resting flat or with ends slightly raised, rarely with raised sides. Overall appearance smooth, sculptured with fine radial ribs that persist to margin. Color black or gray, sometimes pale and showing concentric variation in shading; rays lacking or faint, consisting of narrow lines slightly darker than adjacent ground. Margin broad and flat in growing shells, narrow in mature shells; two-zoned, outer zone black, inner zone translucent gray; cut shells showing that two zones are nearly equal in thickness. Foramen anterior to center, elongate and tripartite in young shells, elongate-oval in mature shells, worn or beveled at apex to reveal aragonitic layer, so that it always appears white-bordered. Old shells that continue to grow by increasing height without expanding at base may contract basal area, forming thick edge and losing distinct zoning of margin.

Juvenile Shell. Radial ribs fine and sharp; primary and secondary ribs appearing early. Whitish in earliest stage, changing abruptly or gradually to black, some showing two lateral white rays that quickly fade.

Mantle and Foot. Nearly containable in shell. Entire animal gray; yellow coloration lacking in cephalic tentacles. Mantle lobe greatly expandable, faintly banded, narrow when preserved; papillae of upper edge moderately developed, finely branched; those of lower edge nearly equal in size. Side of

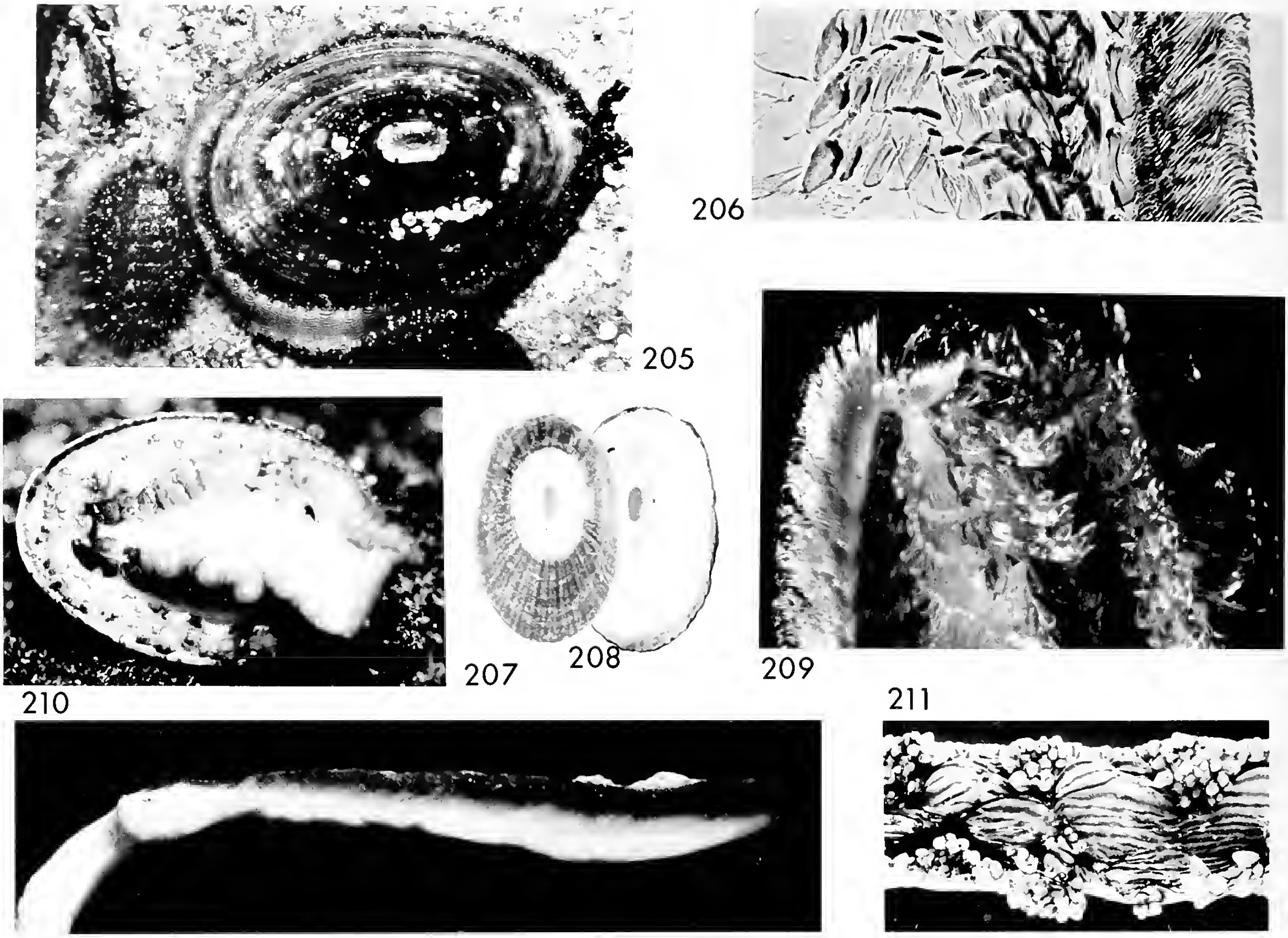


Figures 200 through 204. *Fissurella nigra* Lesson, 1831. Mature shells. **(200)** Island off Mehuin, Valdivia Province, Chile. LACM 75-37, 74.7 × 50.2 × 19.5 mm. **(201)** Lectotype, *F. grandis* Sowerby, 1835. Locality uncertain. BMNH 1976143, 101.0 × 67.9 × 30.9 mm. **(202)** Quellón, Chiloe Province, Chile. LACM 75-45, 79.5 × 51.1 × 30.1 mm. **(203)** Pumalin, Chiloe Province, Chile. LACM 75-41, 43.8 × 27.5 × 12.4 mm. **(204)** Isla Bertrand, off Isla Navarino, Magallanes Province, Chile. NMNZ 18409, 78.9 × 56.5 × 25.4 mm.

foot darker than mantle lobe; tubercles small and widely scattered. This is the only species with a completely gray animal.

Habitat. Intertidal zone only, on the undersides of rocks in the mid-tidal to lower intertidal zone. Several large specimens may occur close together on the undersides of large rocks. Shells are mostly clean, except for scattered incrustations of barnacles, bryozoa, or spirorbid worms. None have been found with attached *Scurria parasitica,* as would be expected if the habitat were more exposed. This is the only species occurring under rocks in the mid-littoral of south central and southern Chile; only juveniles of other species of *Fissurella* occur in this habitat in northern Chile.

Distribution. Valparaíso, Santiago Province, Chile (33°02′ S) (USNM 48218, Bridges), to Puerto Grandi, Isla Bertrand, off south side Isla Navarino, Chile (55°12′ S, 67°02′ W) (Dell,



Figures 205 through 211. *Fissurella nigra* Lesson, 1831. Living specimens, radulae, juvenile shell, cut shell, and mantle lobe. **(205)** Living specimen on underside of overturned boulder. Island off Mehuin, Valdivia Province, Chile. LACM 75-37. **(206)** Radula. Same locality. LACM 75-37, width of field 0.8 mm, shell length 26.4 mm. **(207)** Ventral view of living specimen. Río Bio-bio, Concepción Province, Chile. LACM 75-35. **(208)** Juvenile shell. Island off Mehuin, Valdivia Province, Chile. LACM 75-37, 5.5 × 3.5 × 1.5 mm. **(209)** Air-dried radula. Same locality. LACM 75-37, width of ribbon 2.6 mm. **(210)** Cut shell. Same locality. LACM 75-37, length of cut edge 39 mm. **(211)** Mantle lobe. Same locality. LACM 75-37, length 10 mm.

1971). The northernmost specimen personally collected is a single beach-worn juvenile from Punta el Lacho, Santiago Province, Chile (33°30′ S). The species is rare in the vicinity of Valparaíso, if it now occurs there at all. Dall's (1909) record from Callao, Peru, is not represented by USNM specimens and should be discounted. I found this species commonly at Concepción and Mehuin, and at all stations in the vicinity of Isla de Chiloe, both on the exposed outer coast and on the eastern side where water motion is primarily that of tidal currents. It is evidently uncommon and sporadic in the southernmost region, for I found no trace of it at Punta Arenas or Puerto Hambre in the Strait of Magellan. It is unknown from the Falkland Islands. In addition to the above record of Dell (1971), the following southern records are known to me: USNM 170205, Port Otway, Chile (46°49′ S); MACN 12491, Canal Smyth (at western end of Strait of Magellan); AMNH 173403, Beagle Canal (south side Tierra del Fuego).

Number of Lots Examined. 67 (LACM 11, AMNH 8, ANSP 3, MACN 8, MNHN 33, USNM 4).

Taxonomic History. *Fissurella nigra* is an easily recognized species that has been understood by most authors.

Abundance and Use. Common, at least in the northernmost portion of the range. Its intertidal habitat is accessible, and it is exploited for food.

Characteristics and Variability. The most characteristic features of *F. nigra* are the gray to black surface, the rays, if present, being faint and split into lines, and the prominent zoning of the calcitic layer at the margin, the outer zone dark and the inner zone a light translucent gray. Variation is chiefly in color pattern. Some specimens change from black to gray or light brown; such specimens being more likely to show the fine brown radial pattern. There may be changes in color intensity with growth, but never as pronounced as that which occurs in *F. picta, F. radiosa,* or *F. oriens.* The size record for the species, perhaps for the genus as well, is length 135 mm, width 100 mm, height 62 mm (Isla de Chiloe, collected in 1892, MNHN).

Affinity and Comparisons. *Fissurella nigra* does not closely resemble any other species. Although its overall appearance is smooth, juvenile shells are sharply ribbed, and there are definite primary and secondary ribs. The presence of these ribs in the juvenile dissociates it from the smooth-shelled species in the "group of *F. limbata*" in which early sculpture consists only of broad primary ribs. Its closest affinity is probably with *F. radiosa,* with which it shares similar proportions, an anteriorly positioned foramen, and the three series of ribs, although the total number of ribs is greater in *F. nigra.* The dark outer zone of *F. nigra* is unique. There is only a superficial resemblance of *F. nigra* to dark gray specimens of *F. latimarginata.* Compared to the latter, *F. nigra* has fine radial ribs, a dark rather than lighter outer zone to the margin, and a more anterior and more inwardly beveled foramen.

Synonymy and Types. Type material of *F. nigra* Lesson, 1831, is unknown. It is not represented in the Paris Museum where some of the Lesson collection is now housed. Although there were no original illustrations, the species is easily recognized from the description. It is common in the vicinity of its type locality "Saint-Vincent," now San Vicente (36°43′ S), near Concepción, Chile.

Fissurella violacea Rathke, 1833, was described before the Lesson work was known. The original figure is clear; the type locality is Concepción. Type material may be in Leningrad, where some of the Eschscholtz and Rathke types are extant.

Fissurella grandis Sowerby, 1835, is another early name evidently introduced before Lesson's work was known. There are two specimens in the type lot, BMNH 1976143, lengths, 110.1 and 77.2 mm. The larger specimen was figured by Sowerby (1835b), Reeve (1849), and Dell (1971). It is here designated the lectotype (Fig. 201). The original locality was given as "Valparaíso and Chiloe," so it is not certain whether both specimens are from the same place. The correct locality may be Isla de Chiloe, because the species is rare in the vicinity of Valparaíso.

Group of *Fissurella limbata*

Relatively large-shelled species in which the thickness of the calcitic layer greatly exceeds that of the interior aragonitic layer. Radial sculpture in the early stage is either absent or consists of broad, low primary ribs; there are no secondary ribs. Mature shells may retain the broad primary ribs as low undulations or be entirely smooth.

Although shells of this group have the thick calcitic layer of the *F. maxima* group, they differ from the latter in not having secondary ribs. Whether this difference in sculpture has taxonomic significance should be tested at the biochemical level. It is premature to justify a separation at the subgeneric level.

There are four species in this group: *F. limbata, F. crassa, F. bridgesii,* and *F. pulchra.* The latter three have elongate shells with low profiles, the animals too large to be retracted within the shell. These species tend to be more stenotopic than those of the *F. maxima* group. Variation in each species is less extreme, which is correlated with the relatively few synonyms in the group.

The four species in the group are limited to the Peruvian Faunal Province, unlike the *F. maxima* group, in which there are both Peruvian and Magellanic members.

Fissurella limbata Sowerby, 1835

Figures 212–224

Fissurella limbata Sowerby, 1835a:123; Sowerby, 1835b:3, figs. 42, 66, 74; Orbigny, 1841:474; Reeve, 1849, pl. 2, figs. 10, 12; Hupé, 1854:239; Sowerby II, 1862:184, figs. 23, 24; Pilsbry, 1890:149, pl. 32, figs. 26–39; Dall, 1909: 242; Ziegenhorn and Thiem, 1925; 15, pl. 2, figs. 17–19, 20a, 20b; Riveros-Zuñiga, 1951:114, fig. 24; Peña, 1970: 156; Dell, 1971:188, pl. 5, fig. 5; Marincovich, 1973:18, fig. 30; Ramirez-Boehme, 1974:32 [key].

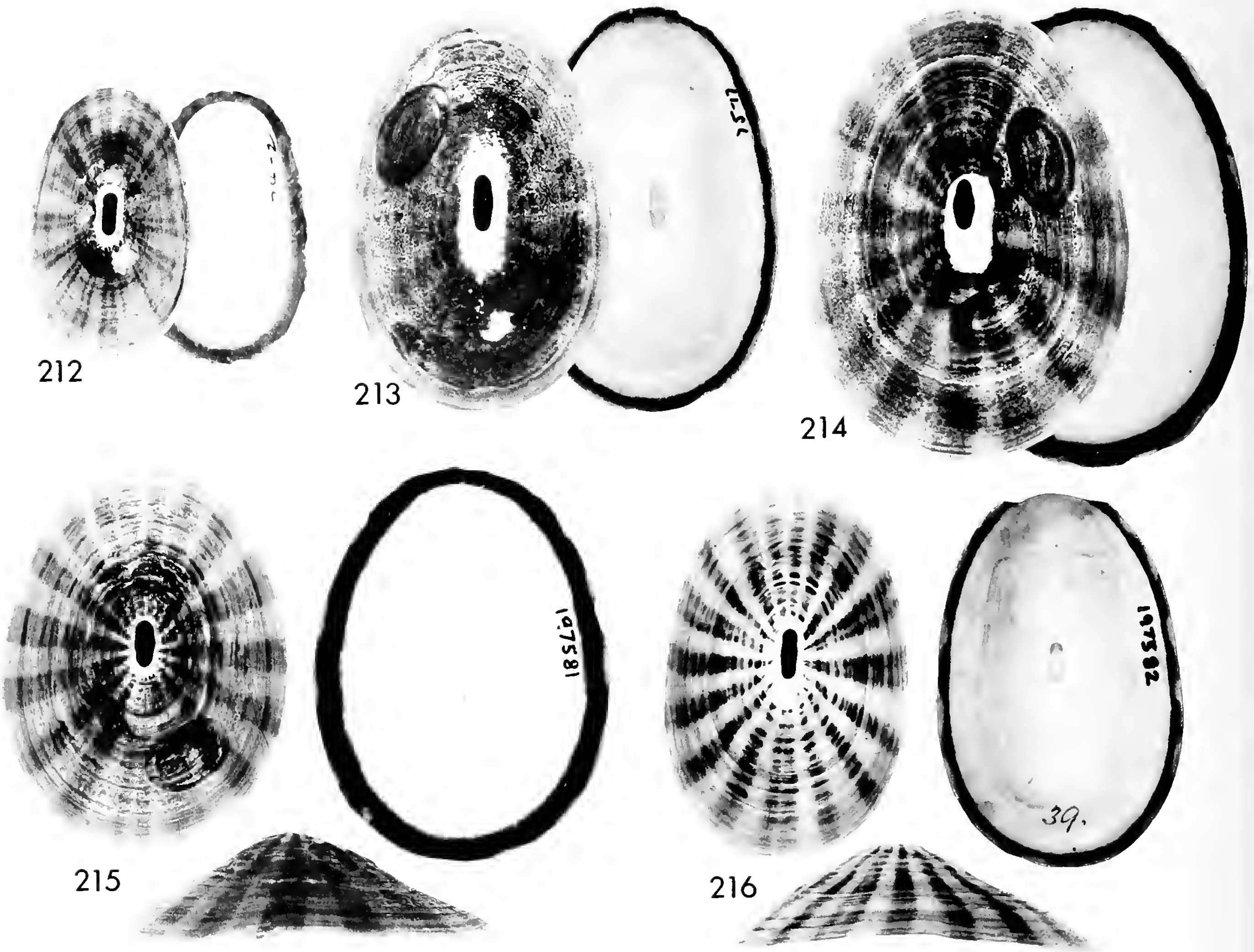
Fissurella limbata var. *multilineata* Ziegenhorn and Thiem, 1925:16, pl. 2, fig. 21.

Shell. Medium large (60–90 mm mature length), moderately elevated; outline elongate oval; base usually resting flat, with ends or sides slightly raised. Sculpture of wavy, irregular radial ribs; overall aspect mostly smooth. Color of uneroded shells (lacking epibiotic *Scurria*) consisting of yellowish ground and purple rays, rays often split. Calcitic layer zoned, consisting of inner layer of solid dark purple and translucent outer layer. Eroded shells (those with *Scurria*) worn to white aragonitic layer near foramen; area farther away from foramen consisting of deep purple portion of calcitic layer, with pattern of rays evident only near margin. Margin broad in growing shells, dark purple next to aragonitic interior, outer edge lighter and revealing pattern of rays. Cut shells showing outer zone about one-fourth thickness of solid purple zone. Foramen elongate at all stages, tripartite in young shells, constricted in middle in mature shells.

Juvenile Shell. Elongate-oval, elevated; primary ribs broad, weak. Color generally white, marked with concentric zigzag purple lines coalescing into purple rays; inner purple zone of calcitic layer apparently lacking in juvenile shells.

Mantle and Foot. Shell edge enveloped by mantle on attached specimens exposed at low tide, body retractable within shell. Mantle lobe light gray, appearing narrow in preserved specimens, marked with concentric lines of black, and only faintly banded to correspond to rays of shell. Papillae at edges very small, finely branched. Side of foot gray; tubercles small, scattered. Preserved specimens retaining broad dark ring with lighter edge where the smooth innermost edge of mantle lobe is in contact with shell. This is the only species in which a dark zone on the inner lobe shows in preserved specimens.

Habitat. Mid-intertidal to low-intertidal zones in surf-exposed areas, primarily on horizontal and sloping surfaces, rather than vertical surfaces. This is the predominant species on flat areas of exposed reefs. I saw no specimens in the sublittoral zone at localities where I dived. Most shells have a single *Scurria parasitica,* which produces a deeply etched attachment scar.



Figures 212 through 216. *Fissurella limbata* Sowerby, 1835. Mature shells. (**212**) Isla Guanape, Peru. LACM 74-2, 37.0 × 22.9 × 12.1 mm. (**213**) Shore opposite Isla Santa Maria, Antofagasta Province, Chile. LACM 75-17, 65.8 × 41.0 × 20.0 mm. (**214**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 82.4 × 57.7 × 25.0 mm. (**215**) Paralectotype, *F. limbata* Sowerby. Valparaíso, Chile. BMNH 197581, 65.0 × 48.5 × 117.8 mm. (**216**) Lectotype, *F. limbata* Sowerby. Valparaíso, Chile. BMNH 197582, 60.5 × 40.0 × 17.4 mm.

Distribution. Isla Guanape, Peru (8°30′ S) (LACM 74-2, McLean), to Isla de Chiloe, Chile (AMNH 155914, O. Ruiz). The exact locality for the southern record is not known, but it was probably the accessible northwestern tip at approximately 41°50′ S. However, I was unable to find specimens in that vicinity at Guabun, Isla de Chiloe. The species does not occur in the sheltered waters of the Golfo Corcovado on the eastern side of Isla de Chiloe. I discount the record of Riveros-Zuñiga (1951) from Fuerte Bulnes in the Magellan Strait.

Number of Lots Examined. 100 (LACM 35, AMNH 20, ANSP 8, MACN 8, MNHN 10, USNM 19).

Taxonomic History. *Fissurella limbata* has been correctly interpreted by most authors.

Abundance and Use. This species is common throughout its range and is exploited for food. Large specimens are seldom seen, because of the accessibility of the habitat at low tide. It is called the "lapa gaviota" at Iquique. Gaviota is the name for seagull, a predator on this species.

Characteristics and Variability. The most characteristic and unusual feature of *F. limbata* is the zonation of the calcitic layer, in which the pattern of rays is confined to the thin, lighter colored surface layer. The greater thickness of the calcitic layer consists of the dark purple inner zone, which is much darker than the rays. There is little variation; differences in appearance are a result of patterns of wear in which the outermost rayed layer is lost, leaving a uniform purple layer. Further wear results in complete loss of the calcitic layer near the foramen, which exposes the white aragonitic layer. Erosion of the shells is greatly accelerated when *Scurria parasitica* is present.

Affinity and Comparisons. *Fissurella limbata* seems not

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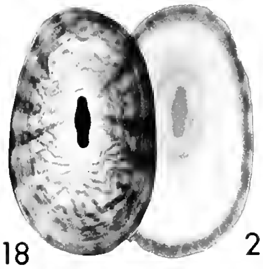

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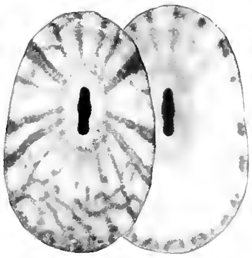

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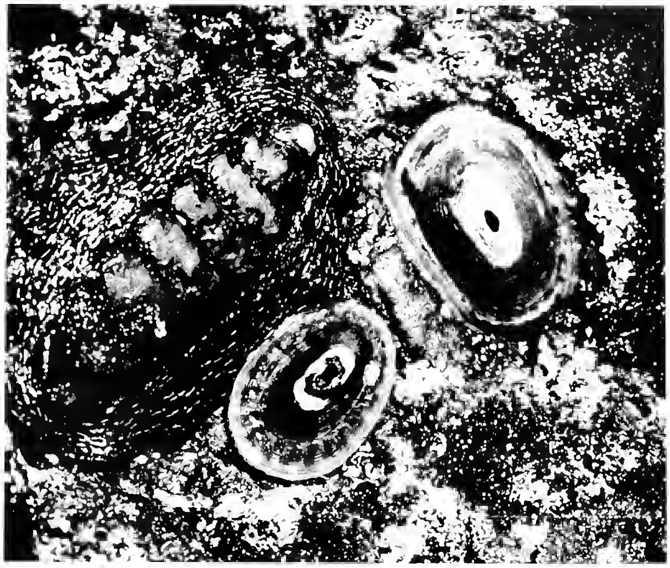

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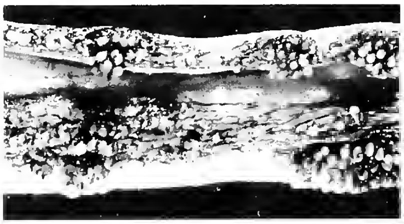

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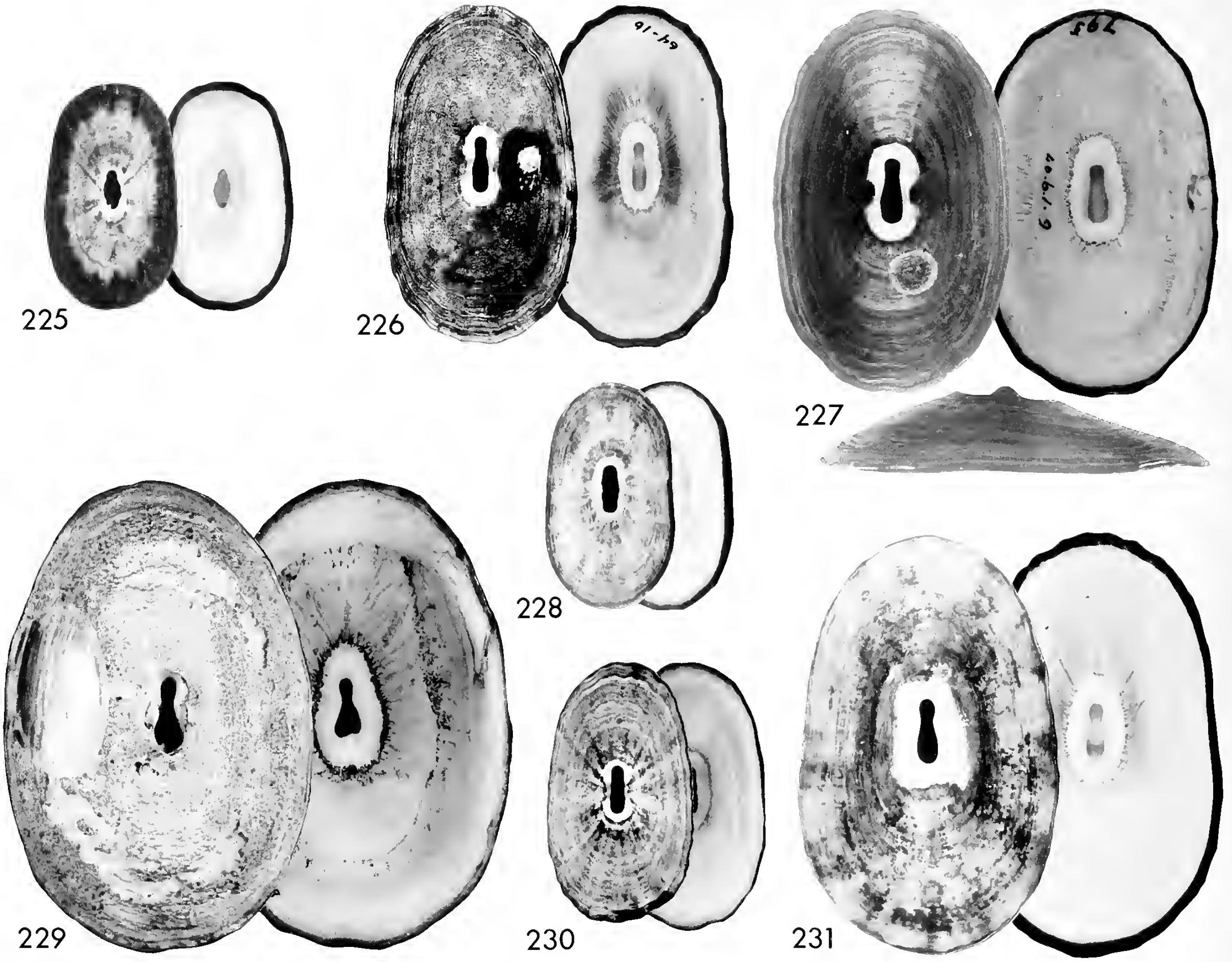
Figures 217 through 224. *Fissurella limbata* Sowerby, 1835. Living specimens, juvenile shells, radula, cut shell, and mantle lobe. **(217)** Ventral view of living specimen. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14. **(218)** Juvenile shell. Iquique, Chile. LACM 64-14, 11.8 × 6.8 × 3.0 mm. **(219)** Air-dried radula. Montemar, Valparaíso Province, Chile. LACM 75-30, width of ribbon 2.4 mm. **(220)** Radula of small specimen. Ancon, Lima Province, Peru. LACM 74-21, width of field 0.5 mm, shell length 18.8 mm. **(221)** Juvenile shell. Iquique, Chile. LACM 64-16, 5.4 × 3.3 × 1.6 mm. **(222)** Living specimens with mantle extended next to chiton *Enoplochiton niger*. Iquique, Chile. LACM 75-12. **(223)** Cut shell. Mehuin, Valdivia Province, Chile. LACM 75-36, length 24 mm. **(224)** Mantle lobe, Islota Concon, Valparaíso Province, Chile. LACM 75-31, length 12 mm.

closely related to any other species. It has some features in common with *F. crassa*—sculpture essentially lacking and a very elongate foramen. Both are limited to the intertidal zone, although *F. limbata* is found at lower levels than is *F. crassa.* The margin is broad and flat, unlike the upturned margin of *F. crassa.* Also, *F. limbata* has relatively weak development of mantle papillae and foot tubercles, whereas both of these features are strongly developed in *F. crassa.* It probably has more in common with *F. nigra,* with which it shares a relatively smooth shell, similar weak development of mantle papillae, and foot tubercles. However, the zoning of the calcitic layer is reversed; the darkest layer is at the surface in *F. nigra. Fissurella oriens* has a rayed pattern similar to that of *F. limbata,* but has some radial sculpture and an unzoned calcitic layer.

Synonymy and Types. Two lots of *F. limbata* from the Cuming Collection in the British Museum have been examined. For each lot the locality "Valparaíso" is written in ink on the boards. Single specimens from each lot were illustrated by Reeve, 1849, although neither of the two spec-



Figures 225 through 231. *Fissurella crassa* Lamarck, 1822. Mature shells. **(225)** Bahía Independencia, Ica Province, Peru. AHF 375-35, 15.6 × 9.3 × 3.5 mm. **(226)** Iquique, Chile. LACM 64-16, 56.9 × 32.3 × 14.0 mm. **(227)** Holotype, *F. clypeiformis* Sowerby. Locality unknown. BMNH 40.6.1.9, 71.4 × 43.4 × 15.6 mm. **(228)** Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14, 19.8 × 11.4 × 4.6 mm. **(229)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 92.0 × 61.0 × 27.4 mm. **(230)** Viña del Mar, Valparaíso Province, Chile. LACM 66-46, 45.5 × 19.8 × 7.0 mm. **(231)** Mehuin, Valdivia Province, Chile. LACM 75-36, 80.3 × 49.0 × 22.1 mm.

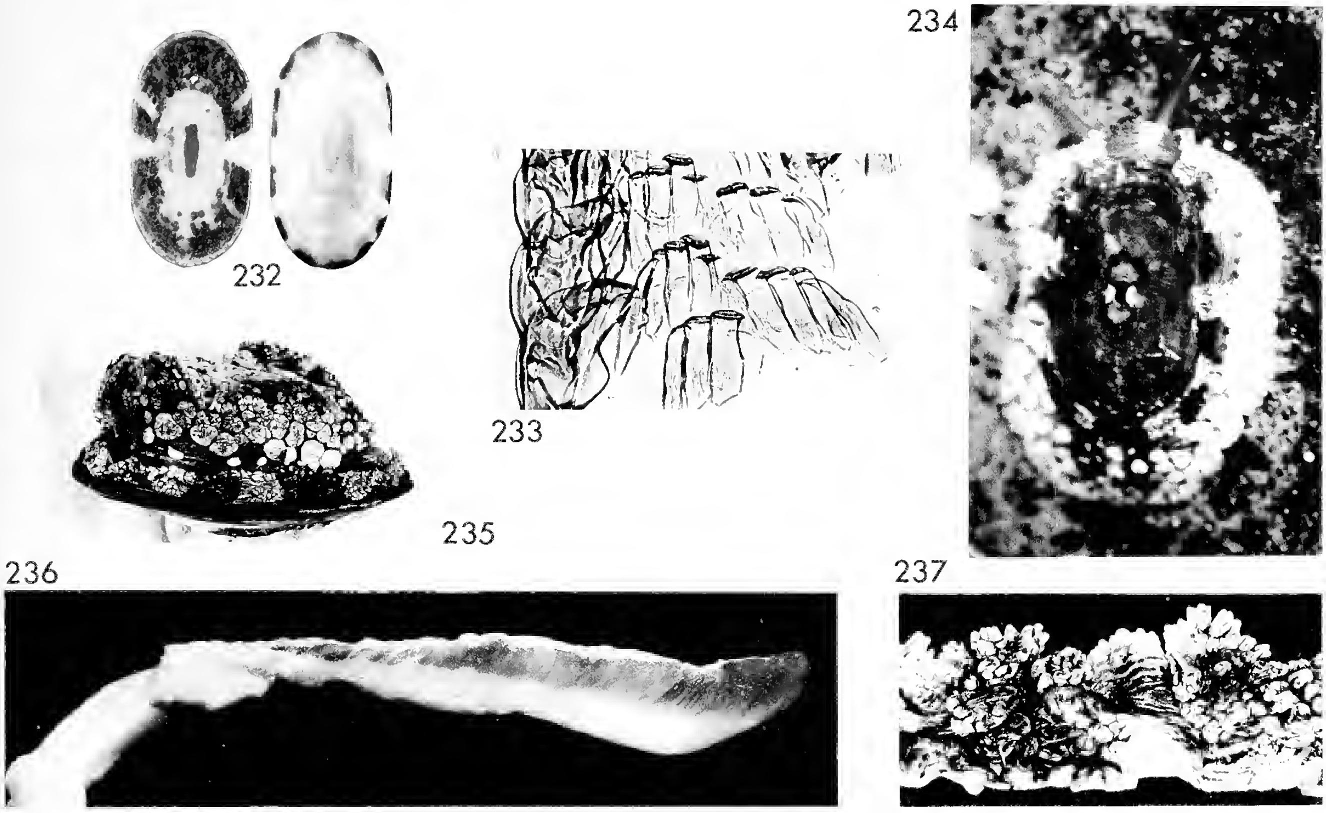
imens illustrated by Sowerby in the "Conchological Illustrations" are included in these lots. However, there is no mistaking the type figure of Sowerby (1835b, figs. 66, 74, internal and external view) as this species. Of the lots figured by Reeve, BMNH 197582 has six specimens, length, 60.5 (anterior end chipped), 59.2, 49.2, 48.4, 33.6, and 28.2. The largest was figured by Reeve (1849) and Dell (1971) and is here refigured and designated the lectotype (Fig. 216). All specimens in this lot lack *Scurria*-made scars and show the complete normal color pattern of the outer zone of the calcitic layer. BMNH 197581 has four specimens, length 67.3, 65.0, 63.1, and 61.1 mm. The largest was figured by Reeve, although the scar of a *Scurria* was omitted; most of the rayed outer zone of the calcitic layer was removed by the *Scurria*, leaving the shell dark purple except for later growth stages. The 65.0 mm shell is figured here (Fig. 215); it has a *Scurria*-made scar but is less eroded.

Fissurella limbata var. *multilineata* Ziegenhorn and Thiem, 1925, was based on two shells from Coquimbo, Chile, the largest 16.5 mm in length. The figure shows the normal zigzag pattern of purple lines found in all juveniles (Figs. 218, 221); the name, therefore, has no systematic value.

Fissurella crassa Lamarck, 1822

Figures 225–237

Fissurella crassa Lamarck, 1822, 6(2):11; Deshayes, 1830: 134; Sowerby, 1835b:1, figs. 9, 11; Deshayes *in* Lamarck, 1836, 7:592; Gray, 1839:148, pl. 39, fig. 9; Orbigny, 1841: 472; Reeve, 1849, pl. 1, fig. 4; Hupé, 1854:240; Philippi,



Figures 232 through 237. *Fissurella crassa* Lamarck, 1822. Juvenile shell, radula, preserved and living specimens, cut shell, and mantle lobe. **(232)** Juvenile shell. Miraflores, Lima Province, Peru. LACM 71-187, 6.9 × 3.5 × 11.6 mm. **(233)** Radula of small specimen. Cartagena, Santiago Province, Chile. LACM 75-34, width of field 1.5 mm, shell length 22.1 mm. **(234)** Living animal submerged in tidepool. Iquique, Chile. LACM 75-12. **(235)** Preserved specimen. Mehuin, Valdivia Province, Chile. LACM 75-36, shell length 46.9 mm. **(236)** Cut shell. Bahía Moreno, Antofagasta Province, Chile. LACM 75-16, length 35 mm. **(237)** Mantle edge, Iquique, Chile. LACM 75-12, length 11 mm.

1860:181; Sowerby II, 1862:184, figs. 16, 17; Watson, 1886: 32; Pilsbry, 1890:154, pl. 34, figs. 51–53; Dall, 1909:177, 241, pl. 24, figs. 5, 6 [fig. looks like *F. limbata*]; Ziegenhorn and Thiem, 1925:18, pl. 2, fig. 24; Carcelles and Williamson, 1951:255; Mermod, 1950:702; Riveros-Zuñiga, 1951: 93, fig. 14; Peña, 1970:156; Dell, 1971:184; Marincovich, 1973:17, fig. 27; Ramirez-Boehme, 1974:30 [key].

Fissurella depressa Lamarck, 1822, 6(2):15; Sowerby, 1835b: 1 (under *F. crassa*); Mermod, 1950:713 [type lost].

Fissurella clypeiformis Sowerby, 1825, app., p. vi; Sowerby, 1835b:1 [under *F. crassa*].

Shell. Medium large (60–90 mm mature length), height low to moderately elevated, elongate oval to very elongate, some with elevated sides, others with elevated ends or with both (so that shells rests on four corners). Sculpture smooth except for early primary ribs that become broad and low, forming wide marginal crenulations. Color caramel brown, occasionally with faint rays of darker brown, surface eroded if epibiotic *Scurria* is present, clean and uneroded if not. Margin upwardly rounded at all growth stages. Shell margin showing light inner zone and darker outer zone. Cut shells also showing very thin lighter-colored layer, layer not evident at edge. Foramen elongate and tripartite in young shells, very elongate and constricted in middle in mature shells, posterior portion much wider and longer than anterior; foramen in mature shells beveled inward at ends. Aragonitic layer of interior between callus and muscle scar pinkish gray throughout and radially ridged.

Juvenile Shell. Sculpture of strong light-colored primary ribs that become wide and low, interspaces wide and dark-colored, two lateral white rays prominent. Shell becomes dark overall on reaching length of 7 mm. Upwardly rounded margin begins in earliest stages.

Mantle and Foot. Shell too low to accommodate large animal within it. Cephalic tentacles brown; mantle lobe broad, banded in light and dark, bands not matched by shell rays but no doubt corresponding to rayed pattern of early juveniles. Papillae of upper edge very large, those of lower edge much less developed. Side of foot with large, bulbous,white-tipped tubercles. Papillae project at both ends of foramen.

Habitat. Mid-intertidal zone, in crevices on rocky reefs, in surf-exposed or partially protected areas, occurring at higher levels than the other species, tightly wedged in narrow crevices during low tide. The upturned margin may be an adaptation to the rather cramped position of the animal when exposed at low tide. Most specimens have a single *Scurria parasitica* on the shell. Bretos (1978, 1980) has studied growth in this species.

Distribution. Huarmey, Peru (10°06′ S) (AMNH 134571), to Punta Pulga, Isla de Chiloe, Chile (42°06′ S) (Dell, 1971). Dall (1909) cited the Galápagos Islands, Ecuador, and USNM 59260 is so labeled, but this record is discounted. The southern limit is uncertain. The species is known from the northwestern tip of Isla de Chiloe but may extend farther south. I did not find it on the eastern side Isla de Chiloe, where there is little exposure to surf. The record of Riveros-Zuñiga (1951) from Fuerte Bulnes in the Magellan Strait is rejected.

Number of Lots Examined. 88 (LACM 31, AMNH 23, ANSP 7, MACN 7, MNHN 10, USNM 10).

Taxonomic History. *Fissurella crassa* has been correctly interpreted by authors. It differs sufficiently from all other species that it can not be confused with any of them.

Abundance and Use. Common throughout its range and widely exploited for food. The upper intertidal habitat is so accessible that large specimens are seldom seen. It is known as the "lapa de sol," because it occurs relatively high, where it is exposed to the sun.

Characteristics and Variability. The most characteristic features of *F. crassa* are the uniformly brown color of the shell, the lack of radial ribs other than the broad undulations, the lavender staining of the interior, the great enlargement of the posterior end of the foramen, and of most importance, the upturned margin. The foot also has the strongest development of tubercles in any of the species. Variation is not extensive and is limited to rather minor differences in height and amount of elevation of the sides or ends.

Affinity and Comparisons. The closest affinity of *F. crassa* seems to be with *F. limbata*. In both species the foramen remains elongate, the sculpture is undulating, and strong ribs are lacking. As in *F. limbata* there is a thin outermost zone to the calcitic layer that is lighter in color. The upturned margin of *F. crassa* is unique. Although the margin of *F. maxima* is also unusual, in that species only the junction between the margin and the internal aragonitic layer is rounded.

Synonymy and Types. The original description of *F. crassa* Lamarck mentioned no locality. Mermod (1950:702), in his report on types of Lamarck in the Geneva collection, gave notes on a specimen 73 mm in length, which he considered to be Lamarck's original.

The locality for the very briefly described *F. depressa* Lamarck, 1822, was given as the "Indian Ocean." Sowerby (1835b:1) stated under *F. crassa:* "Lamarck's *F. depressa* is only a worn fragment of this species, as Mr. Gray informs me." Presumably, Gray had examined the Lamarck collection. Mermod (1950:713) reported that the type specimen now is lost.

The holotype of *F. clypeiformis* Sowerby, 1825, is an unworn specimen of *F. crassa,* BMNH 40.6.1.9, 70.4 mm in length (Fig. 227). It was described without locality and was placed in synonymy shortly after publication by Sowerby (1835b) himself.

Fissurella bridgesii Reeve, 1849

Figures 238–253

Fissurella bridgesii Reeve, 1849, pl. 3, fig. 15; Hupé, 1854: 238; Philippi, 1860:180; Sowerby II, 1862:184, figs. 21, 22, 34; Pilsbry, 1890:151, pl. 30, fig. 3; Dall, 1909:241; Riveros-Zuñiga, 1951:121, fig. 28; Dell, 1971:183, pl. 3, figs. 8, 9; Ramirez-Boehme, 1974:31 [key].

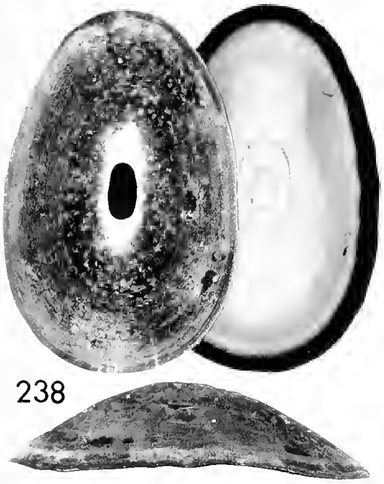
Shell. Medium large (65–90 mm mature length), low; outline elongate-oblong, lateral profile mostly straight, but some specimens with slightly raised sides or ends. Sculpture of fine low ribs in young shells; mature shell nearly smooth, with traces of very broad, irregular radial ribs and irregular radial striae. Color grayish or reddish brown, with faint lighter and darker rays, two lateral rays often more prominent; ground color changing gradually to light gray in large shells. Margin broad in growing shells, flat and often beveled out and up (except at front end) so that its edge is not in contact on a flat surface; margin narrower and rounded in mature shells. Calcitic layer zoned, inner zone dark reddish brown, changing to translucent gray at outer surface, outer zone usually lighter. Foramen unusually large and oval at all growth stages, broadly tripartite in some and showing two projections at sides, others lacking these projections.

Juvenile Shell. None seen under 20 mm in length; primary and secondary ribs weak, nearly equal in size at shell length of 20 mm; foramen large and oval at this shell length. Young shells have two lateral white rays.

Mantle and Foot. Body too large to retract beneath low shell; the mantle lobe broad and thin, enveloping shell edge. Papillae of upper edge tongue-shaped, finely branched, those of lower lobe similarly shaped but smaller and more numerous. Mantle lobe vertically banded with light and dark to correspond to weak pattern of rays on shell. Side of foot marbled; in preserved specimens, dark tubercles are surrounded by lighter areas.

Habitat. *Fissurella bridgesii* occurs on surf exposed rocks surrounded by sandy areas in the intertidal zone and the shallow sublittoral zones, a habitat entirely unlike that of the others. I missed seeing this species because I did not examine this habitat in Chile in 1975. However, the occurrence of *F. bridgesii* has been detailed by Bretos (1979). Shells are usually overgrown with an algal mat. Only rarely do shells have attachment scars of *Scurria,* indicating that they usually live deeper than the mid- to upper intertidal zone preferred by *Scurria.* The Californian acmaeid limpet *Notoacmea fenestrata* (Reeve, 1855) has a comparable habitat on rocks surrounded by sand.

Distribution. Isla Guanape, Peru (8°32′ S) (LACM 74-3, McLean), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). There is but a single record from



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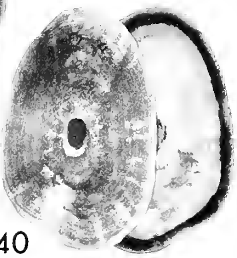

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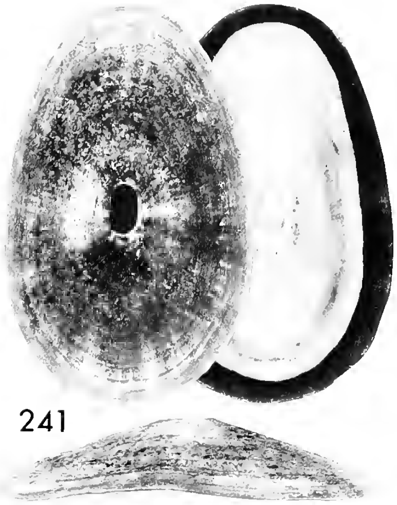

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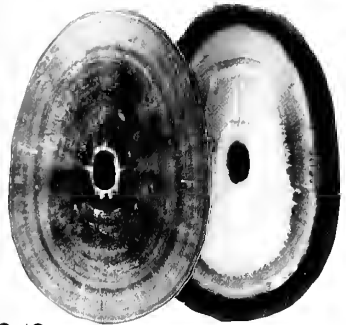

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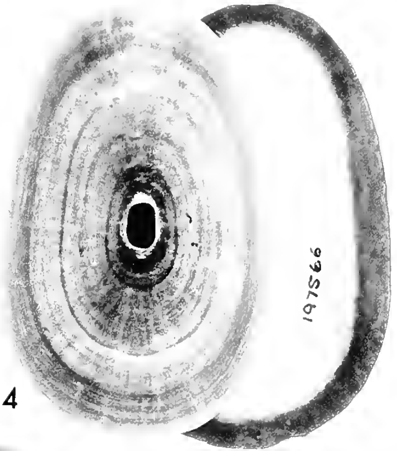

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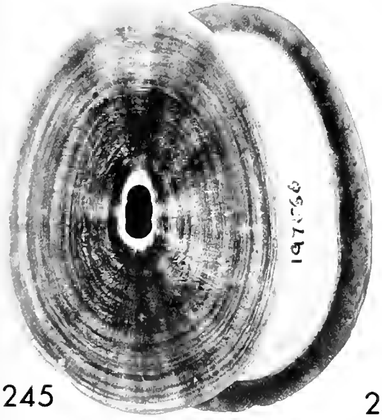

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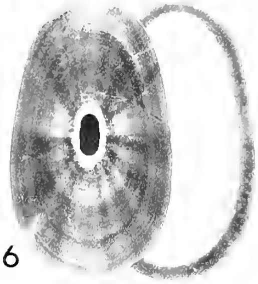

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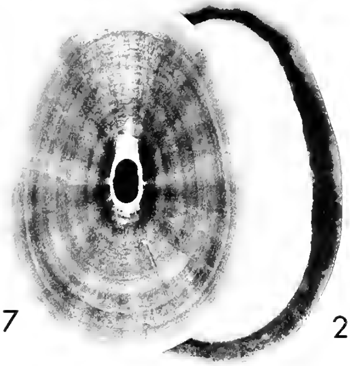

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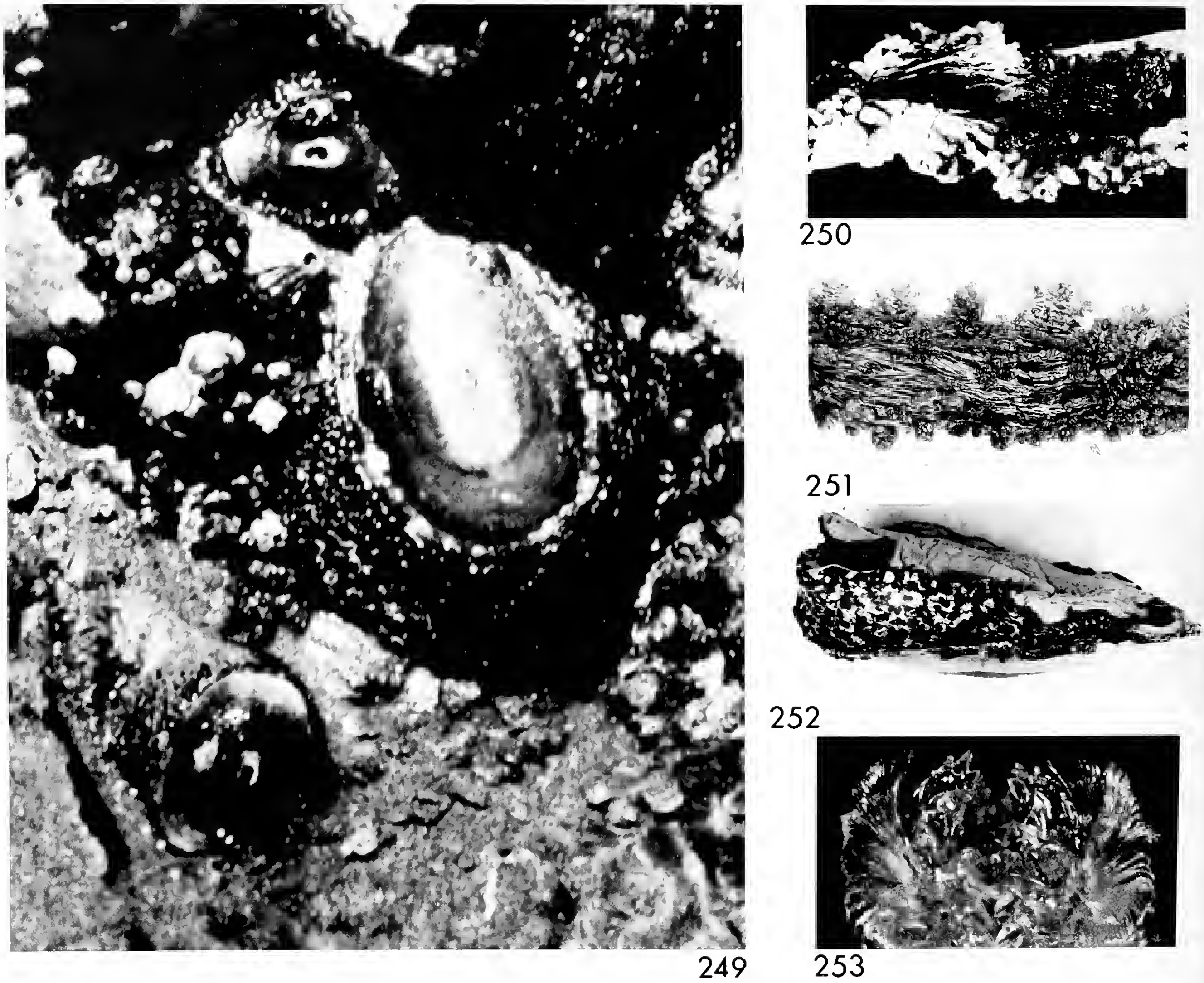
Figures 238 through 248. *Fissurella bridgesii* Reeve, 1849. Mature shells. **(238)** 3–5 m, Isla Guanape, Peru. LACM 74-3, 66.0 × 46.0 × 15.0 mm. **(239)** Iquique, Chile. LACM 90802, 22.4 × 15.7 × 5.3 mm. **(240)** Same locality. LACM 90802, 20.0 × 12.8 × 5.9 mm. **(241)** Iquique, Chile. LACM 90803, 65.5 × 41.3 × 14.5 mm. **(242)** Paposo, Antofagasta Province, Chile. LACM 54764, 44.4 × 28.6 × 9.3 mm. **(243)** Quintero, Valparaíso Province, Chile. USNM 48221, 89.3 × 57.0 × 23.5 mm. **(244)** Paralectotype, *F. bridgesii* Reeve. Quintero, Valparaíso Province, Chile. BMNH 197566, 77.6 × 49.1 × 114.3 mm. **(245)** Lectotype, *F. bridgesii* Reeve. Quintero, Valparaíso Province, Chile. BMNH 197566, 68.0 × 47.5 × 13.7 mm. **(246)** Valparaíso, Chile. USNM 56255, 33.0 × 19.5 × 10.2 mm. **(247)** Valparaíso, Chile. AMNH 20055, 52.8 × 36.0 × 10.4 mm. **(248)** Río Bio-bio, Concepción Province, Chile. LACM 75-35, 42.4 × 26.5 × 9.0 mm.



Figures 249 through 253. *Fissurella bridgesii* Reeve, 1849. Living and preserved specimens, mantle lobe and radula. (**249**) Three living specimens in place. Tocopilla, Antofagasta Province, Chile, photo courtesy A. Viviani. (**250**) Mantle lobe. Iquique, Chile. LACM 90803, length 15 mm. (**251**) Mantle lobe. 3–5 m, Isla Guanape, Peru. LACM 74-3, length 20 mm. (**252**) Preserved specimen. Iquique, Chile. LACM 90803, shell length 65.5 mm. (**253**) Air-dried radula. Iquique, Chile. LACM 90804, width 3.5 mm, shell length 74.4 mm.

Peru, the living specimen I collected in 1974 at Isla Guanape (Fig. 238). I have examined specimens from the following localities in Chile: Iquique, Paposa, Quintero, Valparaíso, and Río Bio-bio, near Concepción.

Number of Lots Examined. 15 (LACM 8, AMNH 1, MACN 1, MNHN 3, USNM 2). This species is uncommon in the collections examined.

Taxonomic History. Accounts of *F. bridgesii* in the literature prior to the report of Bretos (1979) were copies of the original description of Reeve (1849). Dell (1971) considered this taxon a synonym of *F. latimarginata*. The validity of the species was confirmed in 1977, when I compared a preserved specimen sent to me for identification by M. Bretos with the syntypes from the British Museum then on loan at the LACM. Although I was unable to find living examples of this species during my fieldwork in Chile, puzzling beach-worn shells were collected at several localities, and I later discovered that I had purchased live specimens at the market in Iquique. The specimen I had earlier collected in Peru at Isla Guanape was then recognized as *F. bridgesii*. The specialized habitat of this species accounts for its scarcity in collections. It may be, however, that Ramirez-Boehme (1974) had recognized the species, because his key mentions the characteristic upwardly beveled margin ("bordes laterales reflejados hacia arriba"), a feature not discussed elsewhere in the literature.

Abundance and Use. *Fissurella bridgesii* is used for food at Iquique, and it may have more economic importance than suggested by the paucity of specimens in collections. According to M. Bretos, it is known to the fishermen as the "lapa jerguilla," or the "lapa de arena" (sand). The jerguilla is a fish, *Aplodactylus punctatus,* which has a color pattern resembling that of the body of *F. bridgesii.*

Characteristics and Variability. The most characteristic features of *F. bridgesii* are the lack of regularly defined radial sculpture in mature shells, a relatively large foramen, a faintly rayed pattern on a gray-brown ground, and the broad, flat margin, which is beveled upward in young, growing specimens. Some specimens have an elongate foramen that is bidentate on the sides; others of the same size may have a more oval foramen. Color patterns include faintly rayed specimens and some uniformly gray shells lacking traces of rays. The northernmost specimen from Isla Guanape, Peru, lacks rays (Fig. 238).

Affinity and Comparisons. *Fissurella bridgesii* most resembles *F. latimarginata.* The normal weakly rayed pattern of *F. bridgesii* can be related to the unusual rayed color form of *F. latimarginata.* Both have a broad margin and a lighter outer zone to the calcitic layer, but only *F. bridgesii* has an upwardly beveled margin. Both species have similar elaboration of the tongue-shaped papillae of the mantle edge, more so than do other species. In its light outer shell layer it also resembles *F. limbata,* but may be distinguished from that species in lacking the purple coloration to the shell. *Fissurella bridgesii* also resembles *F. pulchra* in its low profile, weakly contrasting pattern of rays, and the lighter outermost zone to the calcitic layer. It differs in lacking the speckled pattern of *F. pulchra* and in having a larger foramen and a more pronounced upward-beveled margin. Although the size of the foramen varies somewhat in *F. bridgesii,* it is always larger than that of similarly sized specimens of *F. pulchra.* Before I understood *F. bridgesii,* my guess was that young beach-worn specimens, such as the one from Concepción (Fig. 248), were most likely to be variants of *F. pulchra.*

Synonymy and Types. There are four syntype specimens of *F. bridgesii* Reeve, 1849, from Quintero, Valparaíso Province, Chile (32°47′ S), BMNH 197566, lengths 77.7, 68.0, 61.8, and 46.0 mm. The 68.0 mm specimen was figured by Reeve (1849), Sowerby II (1862), and Dell (1971), and is here designated the lectotype (Fig. 245); the larger 77.7 mm specimen has been figured only by Sowerby II (1862). These two large specimens (Figs. 244, 245) illustrate two of the most variable features of the species. They are nearly of the same width, but one is much more elongate. The larger, elongate specimen has an oval foramen; the broader specimen has a bidentate foramen. The two remaining paralectotypes are broad; the 61.8 mm specimen has an oval foramen; the 46.0 mm specimen has an elongate foramen with the bidentate structure nearly imperceptible. Shape of the foramen is therefore not correlated with shell proportions.

Fissurella pulchra Sowerby, 1835

Figures 254–267

Fissurella pulchra Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 24; Reeve, 1849, pl. 2, fig. 9; Hupé, 1854:244; Philippi, 1860:181; Sowerby II, 1862:184, fig. 31; Pilsbry, 1890: 151, pl. 33, fig. 50; Dall, 1909:242; Riveros-Zuñiga, 1951: 120, fig. 27; Dell, 1971:191, pl. 3, fig. 5; Ramirez-Boehme, 1974:30 [key].

Shell. Medium-sized (35–75 mm mature length), consistently low; outline elongate oval, tapered anteriorly, sides slightly raised relative to ends. Radial sculpture in early growth stages consisting of low, rounded primary ribs, becoming obsolete when shell reaches length of 20 mm; mature shell smooth except for faint radial striae. Color grayish lavender to pink, with alternating lighter and darker rays; entire surface with fine reddish speckles or zigzag markings especially pronounced near foramen; concentric interruptions to rays changing color from pink to gray or brown in some. Margin of moderate width, flat, reddish gray, zoned to make edge slightly lighter in color; broken shells showing lighter outer zone of calcitic layer; margin becoming very narrow in large, full grown shells. Foramen elongate and tripartite in young shells, only slightly less elongate in mature shells; interior callus bordered by pink colored ring in attachment region.

Juvenile Shell. Primary ribs rounded, coinciding with lighter rays, speckled pattern conspicuous. Sides of shell raised bordering foramen, indicating that earliest stage is more conical.

Mantle and Foot. Not retractable in flattened shell; mantle lobe normally extending well over shell edge. Cephalic tentacles lavender, yellowish at tips. Mantle lobe pinkish gray or brown, faintly banded to match rayed pattern, lined concentrically with brown. Papillae of upper edge well developed, those of lower edge more numerous and smaller. Side of foot same color, tubercles well developed.

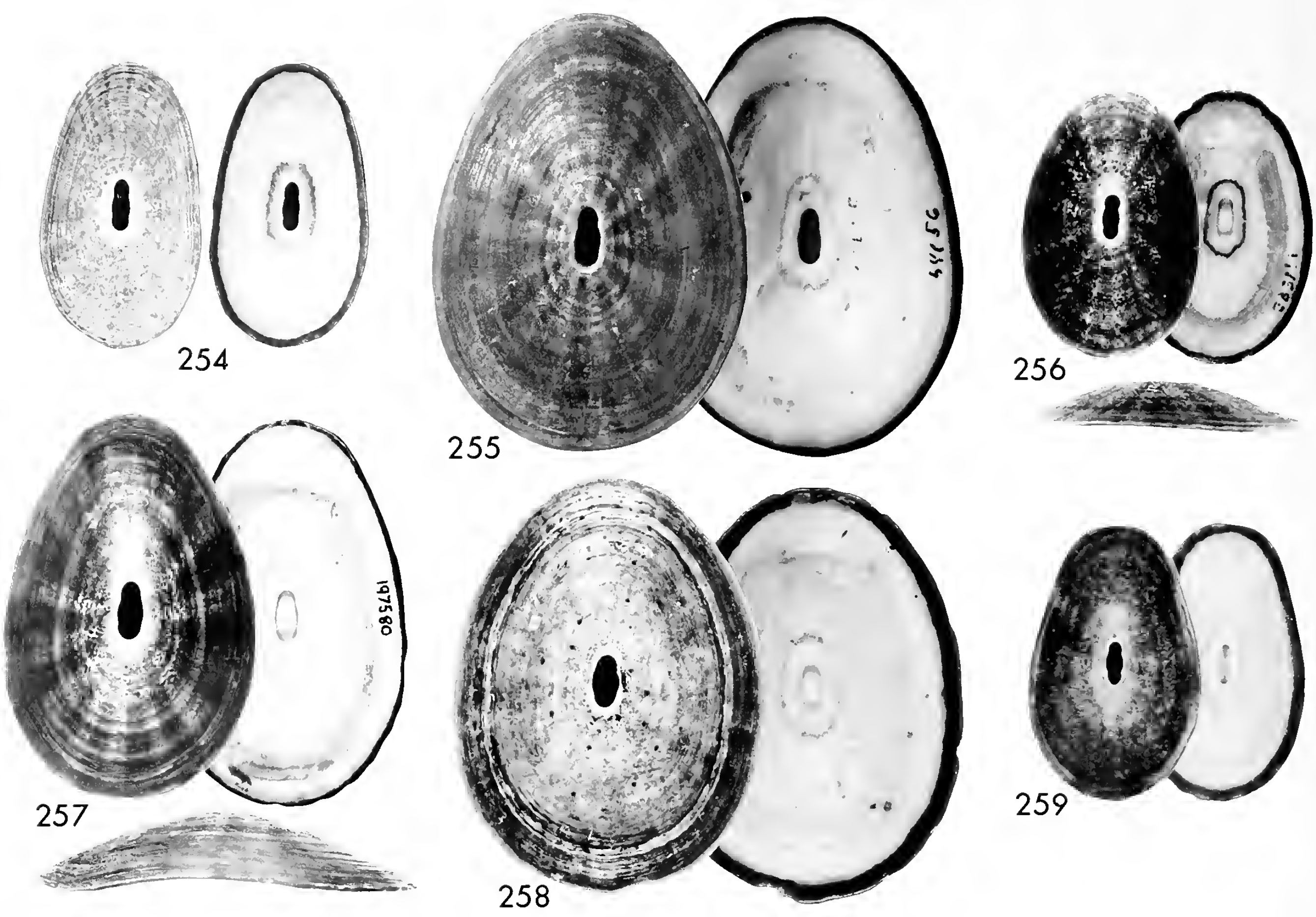
Habitat. Low intertidal and sublittoral zones in crevices or on undersides of large rocks in deep tidepools, protected from direct exposure to surf. Shells are free of algal incrustations; epibiotic organisms on the shell are bryozoans and spirorbid polychaetes.

Distribution. Salaverry, Peru (8°14′ S) (USNM 368490, W. Schmitt), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). Except for *F. bridgesii,* this is the least common species in the Peruvian Faunal Province. I have found small specimens at most localities in central Peru. In northern Chile it was rare at Iquique; at Antofagasta there was no trace of it, even in the beach-worn shell debris. It was more common in central Chile, where I found living specimens on undersides of boulders in tidepools at Los Molles, Aconcagua Province. Beach-worn specimens were found at other localities in central Chile.

Number of Lots Examined. 21 (LACM 13, AMNH 1, ANSP 3, USNM 4, none at MACN or MNHN).

Taxonomic History. Most authors have merely copied the original account of *F. pulchra,* except for Pilsbry (1890), who emphasized the characteristic speckled pattern. The habitat is cryptic, and beach-worn shells are sufficiently scarce that the species has escaped notice in recent years. Riveros-Zuñiga (1951) merely quoted previous authors, and Peña (1970) did not mention it. The collection from Iquique of Marincovich (1973) did not include it. Ramirez-Boehme (1974) included it in his key but did not mention the conspicuous speckles.

Abundance and Use. The species is sufficiently uncommon



Figures 254 through 259. *Fissurella pulchra* Sowerby, 1835. Mature shells. (**254**) Miraflores, Lima Province, Peru. LACM 71-187, 24.2 × 13.5 × 4.1 mm. (**255**) Pupudo, Aconcagua Province, Chile. LACM 54656, 78.5 × 56.0 × 17.0 mm. (**256**) Paralectotype, *F. pulchra* Sowerby. Valparaíso, Chile. BMNH 197580, 39.6 × 25.8 × 6.6 mm. (**257**) Lectotype. *F. pulchra* Sowerby. Valparaíso, Chile. BMNH 197580, 62.2 × 40.2 × 12.8 mm. (**258**) Cartagena, Santiago Province, Chile. LACM 75-34, 68.5 × 50.8 × 14.3 mm. (**259**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 37.5 × 23.3 × 6.6 mm.

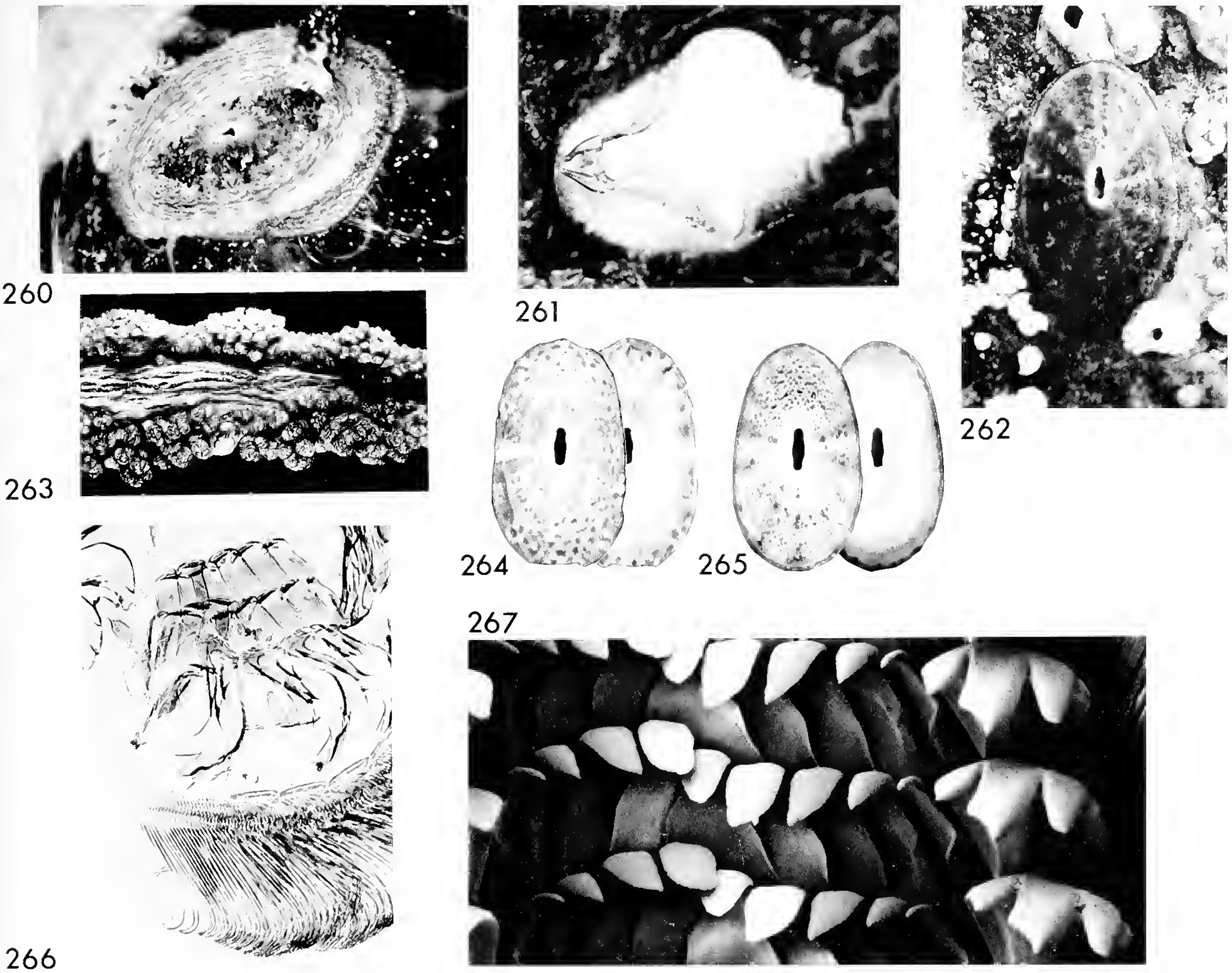
to be negligible as a food resource. Large specimens are particularly uncommon; living specimens that I found were about half the size of shells in the type lot, although I found some beach-worn shells that approached the maximum size. The largest specimen I have examined is 78.5 mm in length, from Papudo, Aconcagua Province, Chile, donated to the LACM by J. Ramirez-Boehme (Fig. 255). The species has no common name in northern Chile, according to M. Bretos.

Characteristics and Variability. *Fissurella pulchra* is aptly named. It is rayed in pinkish brown and gray and is the only species in which a speckled pattern persists through all growth stages. It is one of the least variable species; I have noticed no unusual color forms. Shells are consistently low and tapered anteriorly. Most shells are relatively smooth, although the weak primary ribs may be more pronounced in some specimens.

The radula of *F. pulchra* (Figs. 266, 267) is the most distinctive among the Peruvian-Magellanic species. The inner laterals have longer overhanging cusps than the other species, and the enlarged outer lateral is unique in having a concave edge to the second cusp.

Affinity and Comparisons. On shell characters, *F. pulchra* surely fits within the group having broad primary ribs and no secondary ribs. It is closest to *F. bridgesii,* with which it shares similar proportions, general overall coloration, and faint rays. It differs in its speckled pattern, more consistently narrowed foramen, and pink bordered internal callus. The margin is less broad than that of *F. bridgesii;* it is similarly beveled upward but to a lesser extent than in *F. bridgesii.* The tapered anterior end of *F. pulchra* resembles the condition of the otherwise not closely related *F. latimarginata* and *F. cumingi.*

Synonymy and Types. There are 5 syntypes of *F. pulchra* Sowerby, 1835, from Valparaíso, Chile, BMNH 197580, lengths 70.8 (broken in half), 62.2, 48.7, 39.6, and 24.0 mm. The largest of these has not been figured. The 62.2 mm specimen was figured originally by Sowerby (1835b), then by Reeve (1849) and by Dell (1971); it is here designated the



Figures 260 through 267. *Fissurella pulchra* Sowerby, 1835. Living specimens, mantle lobe, juvenile shells, radulae. **(260)** Living specimen with mantle expanded, in tidepool. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14. **(261)** Same specimen, ventral view. **(262)** Living specimen on underside of overturned boulder. Los Molles, Aconcagua Province, Chile. LACM 75-28. **(263)** Mantle lobe. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14, 8 mm. **(264)** Juvenile specimen. Los Molles, Tarapaca Province, Chile. LACM 75-28, 5.8 × 3.5 × 1.3 mm. **(265)** Juvenile shell. Pucusana, Lima Province, Peru. LACM 72-76, 11.7 × 6.7 × 2.0 mm. **(266)** Radula of small shell. Same locality. LACM 72-76, 1.5 mm, shell length, 22.1 mm. **(267)** SEM view of radula. Los Molles, Aconcagua Province, Chile. LACM 75-28, width of field 0.6 mm.

lectotype. The lectotype and the 39.6 mm paralectotype are figured here (Figs. 256, 257).

LACM LOCALITIES FOR FIGURED SPECIMENS

[All collections from intertidal zone, unless otherwise indicated.]

AHF 375-35. Bahía Independencia, Ica Province, Peru (14°14′ S, 76°12.7′ W), 13 January 1935.

AHF 380-35. Bahía Independencia, Ica Province, Peru (14°14′ S, 76°08.5′ W), 14 January 1935.

AHF 828-38. Bahía San Juan, Ica Province, Peru (15°20.7′ S, 75°09.3′ W), 8 February 1938.

62-26. Ancud, Chiloe Province, Chile (41°52′ S, 73°05′ W), H.C. McMillin, 24 March 1962.

64-16. Iquique (near Ave. Baquedena), Tarapaca Province, Chile (20°13′ S, 70°10′ W), L. Marincovich, June through August, 1964.

66-46. Renaca, Viña del Mar, Valparaíso Province, Chile (33°06′ S, 71°50′ W), R. Seapy, 24 July 1966.

70-68. Iquique (10 km S), Tarapaca Province, Chile (20°15′ S, 70°09′ W), L. Marincovich, July, 1970.

71-187. Miraflores, Lima Province, Peru (12°08′ S, 77°04.5′ W), T. Bratcher, 24 February 1971.

71-277. Bahía York, Isla de los Estados, Argentina (54°47.11′ S, 64°17.9′ W), 5 May 1971.

71-284. Puerto San Juan del Salvamento, Isla de los Estados, Argentina (54°43.9′ S, 63°52′ W), 13 May 1971.

72-76. 0–5 m, Pucusana, Lima Province, Peru (12°30′ S, 76°49′ W), J.H. McLean, 30 March 1972.

72-77. Laguna Granda, lca Province, Peru (14°18′ S, 76°15′ W), J.H. McLean, 31 March 1972 (beach-worn shells).

72-79. Paracas, Ica Province, Peru (13°49′ S, 76°14.5′ W). J.H. McLean, 2 April 1972 (beach-worn shells).

74-2. NE side, lsla Guanape, La Libertad Province, Peru (08°32′ S, 78°58′ W), J.H. McLean, 18 January 1974.

74-3. 3–5 m, NE side, lsla Guanape, La Libertad Province, Peru (08°32′ S, 78°58′ W), J.H. McLean, 18 January 1974.

74-21. 1–2 m, Playa Hermosa, Ancon, Lima Province, Peru (11°47′ S, 77°11.5′ W), J.H. McLean, 26 January 1974.

74-24. 1–4 m, lsla San Lorenzo, Lima Province, Peru (12°06.7′ S, 77°13′ W), J.H. McLean, 29 January 1974.

75-10. Pozo Toyo (S of Iquique), Tarapaca Province, Chile (20°25′ S, 70°10.5′ W), J.H. McLean, 29 September and 1 October 1975.

75-12. Iquique (at Marine Laboratory, Universidad del Norte), Tarapaca Province, Chile (20°15.5′ S, 70°08′ W), J.H. McLean, 2 October 1975.

75-14. Cumbres Borascosas, Tarapaca Province, Chile (20°42′S, 70°11.5′ W), J.H. McLean, 3 October 1975.

75-15. Antofagasta (S end of city), Antofagasta Province, Chile (23°42′ S, 70°27′ W), J.H. McLean, 5 and 6 October 1975.

75-16. Bahía Moreno, Antofagasta Province, Chile (23°28′ N, 70°31′ W), J.H. McLean, 7 October 1975 (beach shells).

75-17. [Shore opposite] lsla Santa Maria, Antofagasta Province, Chile (23°25′ S, 70°36′ W).

75-18. Punta Jara, Antofagasta Province, Chile (23°49′ S, 70°29′ W), J. Tomicic, 8 October 1975.

75-19. Los Colorados, Antofagasta Province, Chile (23°29′ N, 70°22′ W), J.H. McLean, 9 October 1975.

75-20. 2–5 m, Antofagasta (S end of city), Antofagasta Province, Chile (23°42′ S, 70°27′ W), J.H. McLean, 10 October 1975.

75-21. 7–20 m, El Rincon de Mejillones, Antofagasta Province, Chile (23°02′ S, 70°31′ W), J.H. McLean, 11 October 1975

75-23. 2–4 m, El Rincon de Mejillones, Antofagasta Province, Chile (23°05′ S, 70°30′ W), J. Tomicic, 12 October 1975.

75-25. Bahia Herradura, Coquimbo Province, Chile (29°59′ S, 71°22′ W), J.H. McLean, 14 October 1975.

75-27. Bahia El Teniente, Coquimbo Province, Chile (30°58′ S, 71°39′ W), J.H. McLean, 15 October 1975.

75-28. Los Molles, Aconcagua Province, Chile (32°14′ S, 71°32′ W), J.H. McLean, 16 through 18 October 1975.

75-29. Los Molles, Aconcagua Province, Chile (32°14′ S, 71°32′ W), J.H. McLean, 16 October 1975 (shell pile).

75-30. Montemar (at Estacion de Biología Marina), Valparaíso Province, Chile (32°57′ S, 71°32′ W), J.H. McLean, 19 and 20 October 1975.

75-31. lslota Concon, N of Vina del Mar, Valparaíso Province, Chile (32°52′ S, 71°33′ W), J.H. McLean, 21 and 22 October 1975.

75-34. Cartagena, Santiago Province, Chile (33°33′ S, 71°38′ W), J.H. McLean, 23 October 1975.

75-35. Río Bio-bio, Concepción Province, Chile (36°48′ S, 73°11′ W), J.H. McLean, 29 October 1975.

75-36. Mehuin, Valdivia Province, Chile (39°23′ S, 73°14′ W), J.H. McLean, 31 October and 2 November 1975.

75-37. [Island off] Mehuin, Valdivia Province, Chile (39°26′ S, 73°16′ W), J.H. McLean, 1 November 1975.

75-39. Pargua, Canal de Chacao, Llanquihue Province, Chile (41°47′ S, 73°28′ W), J.H. McLean, 3 November 1975.

75-40. Guabun, Isla de Chiloe, Chiloe Province, Chile (41°50′ S, 74°02′ W), J.H. McLean, 4 November 1975.

75-41. Pumalin, Golfo Corcovado, Chiloe Province, Chile (42°42′ S, 72°52′ W), J.H. McLean, 4 through 6 November 1975.

75-42. 2–4 m, Punta Estero, Isla Talcon, Golfo Corcovado, Chiloe Province, Chile (42°46′ S, 72°56′ W), J.H. McLean, 6 November 1975.

75-43. 4–13 m, Islota Nihuel, Golfo Corcovado, Chiloe Province, Chile (42°38′ S, 72°57′ W), J.H. McLean, 7 November 1975.

75-44. Islota Nihuel, Golfo Corcovado, Chiloe Province, Chile (42°38′ S, 72°57′ W), J.H. McLean, 7 November 1975.

75-45. Quellón, Isla de Chiloe, Chiloe Province, Chile (43°09′ S, 73°37′ W), J.H. McLean, 8 November 1975.

75-47. Isla Laitec, off SE side Isla de Chiloe, Chiloe Province, Chile (43°14′ S, 73°36′ W), 9 November 1975.

75-48. Fuerte Bulnes, Peninsula Brunswick, Magellan Strait, Magallanes Province, Chile (53°38′ S, 70°54.5′ W), J.H. McLean, 16 November 1975.

75-49. Puerto el Hambre, Peninsula Brunswick, Magellan Strait, Magallanes Province, Chile (53°37′ S, 70°56′ W), J.H. McLean, 16 and 19 November 1975.

78-88. Punta Ninfas, Golfo Nuevo, Chubut Province, Argentina (42°56.5′ S, 64°19.5′ W), J.H. McLean, 18 July 1978.

78-90. Punta Cracker, Golfo Nuevo, Chubut Province, Argentina (42°56.5′ S, 64°30′ W), J.H. McLean, 19 July 1978.

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LITERATURE CITED

Acuna, E. 1977. Estudio preliminar de edad y crecimiento de *Fissurella latimarginata* (Sowerby, 1834) en Tocopilla, Chile (Mollusca, Gastropoda, Fissurellidae). *Revista Biología Marina, Departamento de Oceanología, Universidad de Chile, Valparaíso* 16(2):117–124.

Bøggild, O.B. 1930. The shell structure of the mollusks. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, Niende Raekke, Naturvidenskabelig og Mathematisk Afdeling* 9, Raekke 2:231–326, pls. 1–15.

Boutan, L. 1885. Recherches sur l'anatomie et le développement de la *Fissurella*. *Archives de Zoologie Expérimentale et Générale,* séries 2, tome 3, mémoire 4:1–173, pls. 31–44.

Bretos, M. 1978. Growth in the keyhole limpet *Fissurella crassa* Lamarck (Mollusca: Archaeogastropoda) in northern Chile. *The Veliger* 21(2):268–273.

———. 1979. Observaciones sobre *Fissurella bridgesii* Reeve, 1849, en Tarapaca, Norte de Chile. *Ciencia y Tecnica del Mar, Cona* 4:53–60.

———. 1980. Age determination in the keyhole limpet *Fissurella crassa* Lamarck (Archaeogastropoda: Fissurellidae), based on shell growth rings. *Biological Bulletin* 159:606–612.

———. 1982. Biología de *Fissurella maxima* Sowerby (Mollusca: Archaeogastropoda) en el Norte de Chile. 1. Caracteres generales, edad y crecimiento. *Cahiers de Biologie Marine* 23:159–170.

———. 1983. The biology of *Fissurella maxima* Sowerby (Mollusca: Archaeogastropoda) in northern Chile. 2. Notes on its reproduction. *Biological Bulletin* 165:559–568.

Bretos, M., and C. Jiron. 1980. Trematodes in Chilean fissurellid molluscs. *The Veliger* 22(3):293.

Bruguière, J. 1789. *Histoire naturelle des vers.* Paris, v. 1, part 1, 344 pp.

Carcelles, A.R. 1950. Catalogo de los moluscos marinos de la Patagonia. *Anales del Museo Nahuel Huapi* 2:41–92, pls. 1–6.

———. 1953. Catalogo de la malacofauna Antartica Argentina. *Anales del Museo Nahuel Huapi* 3:150–250, pls. 1–5.

Carcelles, A.R., and S.I. Williamson. 1951. Catalogo de los moluscos marinos de la provincia Magallanica. *Revista del Instituto Nacional de Investigacion de la Ciencias Naturales, Museo Argentino de Ciencias Naturales "Bernardina Rivadavia," Ciencias Zoologicas* 2(5):225–283.

Castilla, J.C. 1981. Perspectivas de investigacion en estructura y dinamica de comunidades intermareales rocosas de Chile Central. II. Depredadores de alto nivel trofico. *Medio Ambiente* 5(1–2):190–215.

Castilla, J.C., and I. Bahamondes. 1979. Observaciones conducuales y ecológicas sobre *Lutra felina* (Molina) 1782 (Carnivora: Mustelidae) en las zonas Central y Centro-Norte de Chile. *Archivos de Biología y Medicina Experimentale* 112:119–132.

Christiaens, J. 1973. Les Fissurelles Européennes—II. Le genre *Fissurella* Bruguière, 1789. *Informations de la Société Belge de Malacologie,* séries 2, no. 5, pp. 67–98.

Dall, W.H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. *Proceedings of the United States National Museum* 37:147–294.

Dance, S.P. 1966. *Shell collecting: An illustrated history.* Berkeley: University of California Press, 344 pp.

Davila, P.F. 1767. *Catalogue systématique et raisonné des curiosités de la nature et de l'art, qui composent la cabinet de M. Davila.* Paris, 3 vols.

Dayton, P.K., R.J. Rosenthal, L.C. Mahen, and T. Antezana. 1977. Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. *Marine Biology* 39:361–370.

Delessert, B. 1841. *Recueil de coquilles décrites par Lamarck dans son Histoire naturelle des animaux sans vertébrés et non encore figurées.* Paris, 40 pls. (with unnumbered explanations).

Dell, R.K. 1971. The marine Mollusca of the Royal Society Expedition to Southern Chile, 1958–59. *Records of the Dominion Museum (Wellington)* 7(17):155–233.

Deshayes, G.P. 1830–1832. *Encyclopédie Méthodique. Histoire naturelle des vers.* Paris, v. 2, 594 pp.

Dwyer, K.R., and D.R. Lindberg. 1981. The topography, formation, and role of the home depression of the limpet *Collisella scabra* Gould. *13th Annual Report, Western Society of Malacologists,* p. 11.

Fretter, V., and A. Graham. 1962. *British prosobranch molluscs.* London: Ray Society, xvi + 755 pp.

———. 1964. Reproduction. In *Physiology of Mollusca,* ed. K.M. Wilbur and C.M. Yonge, 127–164. New York: Academic Press.

———. 1976. The prosobranch molluscs of Britain and Denmark. Part 1. Pleurotomariacea, Fissurellacea, and Patellacea. *Journal of Molluscan Studies, Supplement* 1, 1–37.

Gallardo, C., and C. Osorio. 1978. *Hiatella solida* (Sowerby, 1834) (Mollusca: Hiatellidae) on *Concholepas concholepas* (Bruguière, 1789) and other substrates. *The Veliger* 20(3):274–278.

Gibson, P.H. 1978. Systematics of *Dodecaceria* (Annelida: Polychaeta) and its relation to the reproduction of its species. *Zoological Journal of the Linnean Society* 63: 275–287.

Gmelin, J.F. 1791. *Caroli a Linné systema naturae per regna tria naturae. Editio decima tertia.* Leipzig, v. 1, part 6, Vermes, pp. 3021–3910.

Gould, A.A. 1846. Descriptions of the shells collected by the United States Exploring Expedition. *Proceedings of the Boston Society of Natural History* 2:148–152.

———. 1852–1856. *Mollusca and shells. United States Exploring Expedition.* Boston, v. 12, 509 pp. [1852]; Atlas, 16 pp., 52 pls. [1856].

Gray, J.E. 1839. Molluscous animals and their shells. In F. W. Beechey, *The zoology of Capt. Beechey's voyage . . . to the Pacific and Behring's Straits in his Majesty's ship "Blossom,"* i–xii, 103–155, pls. 33–44. London.

Herm, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. *Zitteliana* 2:1–158.

Hickman, C.S. 1981. Evolution and function of asymmetry in the archaeogastropod radula. *The Veliger* 23(3):189–194, 2 pls.

———. 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. *Malacologia* 25(1):143–160.

Hupé, L.H. 1854. Fauna Chilena, Moluscos. In *Historia fisica y politica de Chile,* ed. C. Gay. Zoologia, v. 8. Santiago, 499 pp., atlas, v. 2, pls. 1–8.

Ihering, H. 1907. *Les mollusques fossiles du Tertiaire et du Crétacé Supérieur de l'Argentine.* Anales del Museo Nacional de Buenos Aires, ser. 3, v. 7, 611 pp., 18 pls.

Illingworth, J.F. 1902. The anatomy of *Lucapina crenulata* Gray. *Zoologische Jahrbucher, Abtheilung für Anatomie und Ontogenie der Tiere* 16:449–480, pls. 31–33.

Jara, H.F., and C.A. Moreno. 1984. Herbivory and structure in a midlittoral rocky community: A case in southern Chile. *Ecology* 65(1):28–38.

Johnson, R.I. 1964. *The Recent Mollusca of Augustus Addison Gould.* United States National Museum, Bulletin 239, 182 pp., 45 pls.

Keen, A.M. 1971. *Sea shells of tropical west America,* Second edition. Stanford: Stanford University Press, xiv + 1064 pp., 22 pls.

Knight, J.B., L.R. Cox, A.M. Keen, R.L. Batten, E.L. Yochelson, and R. Robertson. 1960. Systematic descriptions (Archaeogastropoda). In *Treatise on invertebrate paleontology. Part I, Mollusca 1,* ed. R.C. Moore, 169–310. Geological Society of America and University of Kansas Press.

Lamarck, J.B.P.A. de M. de. 1815–1822. *Histoire naturelle des animaux sans vertébrés.* Paris, v. 1–7.

———. 1835–1845. *Histoire naturelle des animaux sans vertébrés,* ed. 2, revised by G.P. Deshayes and H. Milne-Edwards. Paris, v. 1–11.

Lesson, R.P. 1830–1831. *Voyage autour du monde . . . sur "la Coquille" pendant . . . 1822–25.* Paris, v. 2, Zoologie, 471 pp., atlas, 157 pls.

Lindberg, D.R. 1976. The homing depression of the limpet, *Collisella scabra* (Gould, 1846). *Bulletin of the American Malacological Union for* 1975:69–70.

Lindberg, D.R., and K.R. Dwyer. 1983. The topography, formation and role of the home depression of *Collisella scabra* (Gould) (Gastropoda: Acmaeidae). *The Veliger* 25(3):229–234.

Lowenstam, H.A. 1954. Faetors affecting the aragonite: calcite ratios in carbonate-secreting marine organisms. *Journal of Geology* 62:284–322.

———. 1964. Coexisting calcites and aragonites from skeletal carbonates of marine organisms and their strontium and magnesium contents. In *Recent researches in the fields of hydrosphere, atmosphere and nuclear geochemistry, editorial committee of Saguawara festival volume,* 374–404. Tokyo.

MacClintock, C. 1963. Reclassification of gastropod *Proscutum* Fischer based on muscle scars and shell structure. *Journal of Paleontology* 37:141–156.

———. 1967. *Shell structure of patelloid and bellerophontid gastropods (Mollusca).* Peabody Museum of Natural History, Yale University, Bulletin 22, 140 pp., 32 pls.

Margolin, A.S. 1964. The mantle response of *Diodora aspera. Animal Behaviour* 12(1):187–194.

Marincovich, L., Jr. 1973. *Intertidal mollusks of Iquique, Chile.* Natural History Museum, Los Angeles County, Science Bulletin 16, 49 pp.

McLean, J.H. 1984a. A case for derivation of the Fissurellidae from the Bellerophontacea. *Malacologia* 25(1): 3–20.

———. 1984b. Shell reduction and loss in fissurellids: A review of genera and species in the *Fissurellidea* group. *American Malacological Bulletin* 2:21–34.

Melvill, J.C., and R. Standen. 1898. Notes on a collection of marine shells from Lively Island, Falklands, with list of species. *Journal of Conchology* 9:97–105.

———. 1907. The marine Mollusca of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 46:119–157.

———. 1914. Notes on Mollusca collected in the northwest Falklands, by Mr. Rupert Vallentin, F.L.S., with descriptions of six new species. *Annals and Magazine of Natural History,* series 8, 13:109–136.

Mermod, G. 1950. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivantes, I. *Revue Suisse de Zoologie* 57(34):687–756.

Métivier, B. 1969. Resultats scientifiques des compagnes de la "Calypso." Campagne au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). Mollusques Prosobranches: Fissurellidae, Acmaeidae et Patellidae. *Annales de l'Institut Océanographique, Monaco* 47(1): 115–125.

Moreno, C.A., and E. Jaramillo. 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. *Oikos* 41:73–76.

Moreno, C.A., J.P. Sutherland, and H.F. Jara. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* 42:155–160.

Odhner, N.H. 1932. Zur Morphologie und Systematik der Fissurelliden. *Jenaische Zeitschrift für Naturwissenschaft* 67:292–309.

Olsen, D.A. 1968a. Banding patterns of *Haliotis rufescens* as indicators of botanieal and animal succession. *Biological Bulletin* 37(1):139–141.

———. 1968b. Banding patterns in *Haliotis* II. Some behavioral considerations and the effect of diet on shell coloration for *H. rufescens, H. corrugata, H. sorenseni,* and *H. assimilis. The Veliger* 11(2):135–139.

Orbigny, A.d'. 1831–1847. *Voyage dans l'Amérique Méridionale.* Paris, v. 5, part 3, pp. 1–758; atlas, v. 9, Mollusques, pls. 1–85.

Paine, R.T., and A.R. Palmer. 1978. *Sicyases sanguineus:* A unique trophic generalist from the Chilean intertidal zone. *Copeia* 1978(1):75–81.

Peña, G.M. 1970. Zonas de distribucion de los gasterópodos marinos del Perú. *Anales Científicos de la Universidad Nacional Agraria (Lima)* 8(3–4):153–170.

Pérez-Farfante, I. 1943. The genera *Fissurella, Lucapina,* and *Lucapinella* in the western Atlantic. *Johnsonia* 1(10): 1–20.

———. 1952. Nuevo gênero y nuevo especie del gênero *Fissurella. Revista de la Sociedad Malacológica "Carlos de la Torre" (Habana)* 9(1):31–33.

Philippi, R.A. 1845. Diagnosen einiger neuer Conchylien. *Archiv für Naturgeschichte* 11(1):50–71, 142–144.

———. 1845–1846. Fissurella. *Abbildungen und Beschreibungen neuer oder wenig bekannter Conchylien.* Kassel, 2 pls. [pl. 1, 1845; pl. 2, 1846].

———. 1857. Ueber die Conchylien der Magellanstrasse. *Malakozoologische Blätter* 3:157–173.

———. 1860. *Reise durch die Wueste Atacama auf Befehl der Chilenischen Regierung im Sommer 1853–54.* Halle: E. Anton, 254 pp., 27 pls. [Also in Spanish edition (1860) "*Viage al Desierto de Atacama . . . .*"]

———. 1887. *Die Tertiären und Quartären Versteinerungen Chiles.* Leipzig, 268 pp., 58 pls. [Also in Spanish edition (1887), Santiago.]

Pilsbry, H.A. 1890. *Stomatellidae, Scissurellidae, Pleurotomariidae, Haliotidae, Scutellinidae, Addisoniidae, Cocculinidae, Fissurellidae. Manual of Conchology,* v. 12. Philadelphia.

Powell, A.W.B. 1951. Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Reports* 26:47–196, pls. 5–10.

Ramirez-Boehme, J. 1974. Nuevas especies chilenas de *Lucapina, Fissurella,* y *Collisella* (Mollusca, Archaeogastropoda). *Boletin Museo Nacional de Historia Natural, Chile* 33:15–34.

Ringuelet, R.A., A. Amor, N. Magildi, and R. Pallares. 1962. Estudio ecologico de la fauna intercotidal de Puerto Deseado, en Febrero de 1961 (Santa Cruz, Argentina). *Physis (Buenos Aires)* 23(64):35–53.

Rathke, M.H. 1833. *Zoologischer Atlas.* Part 5. Berlin, i–vii, 1–28, pls. 21–25. [Completion of work started by J.F. Eschscholtz, 1829–1831.]

Reeve, L. 1849–1850. *Monograph of the genus* Fissurella. *Conchologica Iconica.* London, v. 6, 16 pls. [pls. 1–8, 1849; pls. 9–16, 1850].

Riveros-Zuñiga, F. 1951. Catalogo descriptivo de fisurelidos Chilenos. *Revista de Biología Marina (Universidad de Chile)* 3(1–2):89–148.

Rochebrune, A.T. de, and J. Mabille. 1885. Diagnoses de Mollusques nouveaux, receuillis par les membres de la mission du Cap Horn . . . à Santa Cruz. *Bulletin de la Société Philomathique de Paris* 7(9):100–111.

———. 1889. *Mollusques. Mission Scientifique du Cap Horn* (1882–1883), v. 6, Zoologie. Paris, 126 pp., 8 pls.

Scarabino, V. 1977. Moluscos del Golfo San Matias (Provincia de Río Negro, República Argentina). *Comunicaciones de la Sociedad Malacológica del Uruguay* 4(31–32):177–297.

Sowerby, G.B. 1825. *A catalogue of the shells contained in the collection of the late Earl of Tankerville.* London, vii + 99 + xxxiv pp., 9 pls.

———. 1835a. Shells collected by Mr. Cuming on the western coast of South America, and among the islands of the South Pacific Ocean. *Proceedings of the Zoological Society of London, for* 1834:123–128.

———. 1835b. *A catalogue of the Recent species of* Fissurella. *The conchological illustrations.* London, pp. 1–8, 77 figs. on 12 unnumbered plates.

Sowerby, G.B., II. 1862. *Monograph of the family Fissurellidae, genus* Fissurella. *Thesaurus conchyliorum, or Monographs of genera of shells.* London, v. 3, pp. 183–206, pls. 1–9.

Stearns, R.E.C. 1891. List of shells collected on the west coast of South America, principally between latitudes 7°30′ S. and 8°49′ N., by Dr. W.H. Jones, surgeon, U.S. Navy. *Proceedings of the United States National Museum* 14(854):307–335.

Strebel, H. 1907. Beiträge zur Kenntnis der Mollusken Fauna der Magalhaen-Provinz. 5. *Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie, Jena* 25:79–196.

———. 1908. *Die Gastropoden. Wissenschaftliche Ergebnisse der Schwedische Sudpolar-Expedition, 1901–1903,* v. 6, Zoologie 2. Stockholm, 111 pp.

Stuardo, J. 1964. Distribucion de los moluscos marinos litorales en latinoamerica. *Boletin Instituto Biología Marina (Mar del Plata)* 7:79–91.

Tobler, M. 1902. Zur Anatomie von *Parmophorus intermedius* Reeve. *Jenaische Zeitschrift für Naturwissenschaft* 36:229–274, pls. 13–15.

Tomlinson, J.T. 1969. *The burrowing barnacles (Cirripedia: Order Acrothoracica).* United States National Museum, Bulletin 296, 162 pp.

Vance, R.S. 1978. A mutualistic interaction between a sessile marine clam and its epibionts. *Ecology* 59(4):679–685.

Vermeij, G.J. 1978. *Biogeography and adaptation.* Cambridge: Harvard University Press, xi + 332 pp.

Ward, J. 1966a. Feeding, digestion, and histology of the digestive tract in the keyhole limpet *Fissurella barbadensis* Gmelin. *Bulletin of Marine Science* 16:668–684.

———. 1966b. The breeding cycle of the keyhole limpet *Fissurella barbadensis* Gmelin. *Bulletin of Marine Science* 16:685–695.

Watson, R.B. 1886. *Report on Scaphopoda and Gasteropoda collected by "Challenger." Report on the Scientific Results of the Voyage of the H.M.S. Challenger.* Zoology, v. 15. London, vii + 756 pp., 50 pls.

Wenz, W. 1938–1944. Gastropoda. Allgemeiner Teil und Prosobranchia. In *Handbuch der Paläozoologie,* ed. O.H. Schindewolf. Band 6. Berlin, 1639 pp.

Woodring, W.P. 1965. Endemism in Middle Miocene Caribbean molluscan faunas. *Science* 148:961–963.

———. 1966. The Panama land bridge as a sea barrier. *Proceedings of the American Philosophical Society* 110(6):425–433.

Ziegenhorn, A., and H. Thiem. 1925. Beiträge zur Systematik und Anatomie der Fissurellen. *Jenaische Zeitschrift für Naturwissenschaft* 62:1–78, pls. 1–6.

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CONTRIBUTIONS IN SCIENCE

AN EARLY HEMINGFORDIAN (EARLY MIOCENE) FOSSIL VERTEBRATE FAUNA FROM BORON, WESTERN MOJAVE DESERT, CALIFORNIA

David P. Whistler

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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AN EARLY HEMINGFORDIAN (EARLY MIOCENE) FOSSIL VERTEBRATE FAUNA FROM BORON, WESTERN MOJAVE DESERT, CALIFORNIA

David P. Whistler[1]

ABSTRACT. A small assemblage of fossil vertebrates has been obtained from the Arkose Member of the Kramer Beds in the upper part of the Tropico Group at Boron, California. Known as the Boron Local Fauna (new name), it displays affinities with the Tick Canyon and Phillips Ranch Local Faunas of southern California and the fossil assemblages from the Runningwater and Batesland Formations of Nebraska and South Dakota, respectively, the latter used as the standard for the earlier part of the Hemingfordian land mammal age. These correlations and radiometric dates with a range of 18.3 ± 0.6 ma to 20.3 ± 0.7 ma from the underlying Saddleback Basalt support an early Hemingfordian age for the Boron Local Fauna.

Prior to the discovery of this fossil assemblage, considerable uncertainty existed about the age of scattered occurrences of volcanic flows and volcaniclastic rocks in the western Mojave Desert which were restricted and redefined as the Tropico Group by Dibblee (1958a). Based on lithologic correlations, ages ranging from Middle Miocene to Early Pliocene had been suggested for the Tropico Group. The presence of the early Hemingfordian Boron Local Fauna in the uppermost unit of the Tropico Group limits the age of this entire sequence to pre-Middle Miocene. The well-preserved assemblage contains at least 15 vertebrate taxa. Two new species are described, *Cupidinimus boronensis* n. sp. (Rodentia, Heteromyidae) and *Aletomeryx occidentalis* n. sp. (Artiodactyla, Palaeomerycidae). There are also two lizards which are not diagnostic at the family level, two snakes, cf. *Calamagras* sp. (Boidae) and cf. *Paracoluber* sp. (Colubridae), a lagomorph, *Archaeolagus* sp. or *Hypolagus* sp. (Leporidae), three additional rodents, ?*Miospermophilus* sp. (Sciuridae), *Mookomys* sp. and *Trogomys* cf. *T. rupinimenthae* (Heteromyidae) and five additional artiodactyls, *Merychyus* cf. *M. minimus* and ?*Merychyus* sp. (Merycoidodontidae), cf. *Hesperocamelus* sp. (Camelidae) and two other camels not identified to genus. Conspicuous by their absence are eomyid and large geomyoid rodents, horses, dromomerycine palaeomerycids, and antilocaprids typical of most Middle Miocene assemblages.

INTRODUCTION

In March, 1964, the geology staff of the United States Borax and Chemical Corporation mine at Boron, California, reported uncovering a pocket of fossil bones during operations in the open pit mine (Figure 1). An initial sample collected by the Department of Geology at the University of California at Riverside was recognized as representing a Miocene assemblage older than any previously known from the central Mojave Desert. The fossils were recovered from the Kramer Beds, sediments which were correlated with other scattered continental sequences in the Mojave Desert, all of which were considered to be Late Miocene or Pliocene in age. These fossil vertebrates, hereafter called the Boron Local Fauna, demonstrated that the Kramer Beds were older than the richly fossiliferous deposits of the Barstow Formation which contained the oldest fossil faunas then known from the central Mojave Desert and necessitated re-thinking the geologic history of this area. Subsequent discoveries (Woodburne et al., 1974; Woodburne, Miller, and Tedford, 1982) have led to recognition of even earlier Miocene assemblages, but the Boron Local Fauna was the first well-preserved pre-Barstovian assemblage from the Mojave Desert.

The Boron Local Fauna is markedly different in taxonomic composition from the well-documented faunas of the Barstow Formation and other fairly widespread Barstovian (Middle Miocene) assemblages in southern California. The Boron Local Fauna is dominated by four groups (heteromyid rodents, oreodonts, camels, and palaeomerycids) which, except for camels, are rare or absent in Barstovian assemblages of southern California. In contrast, the Boron Local Fauna lacks three groups (cricetid rodents, horses, and antilocaprids) which are a common element of Barstovian assemblages. The Boron Local Fauna also differs from the less well preserved late Hemingfordian assemblages of southern California which are dominated by small merychippine horses, middle-sized oreodonts, dromomerycines, and antilocaprids, groups lacking at Boron. The Boron Local Fauna appears to

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[1] Vertebrate Paleontology Section, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California, 90007.

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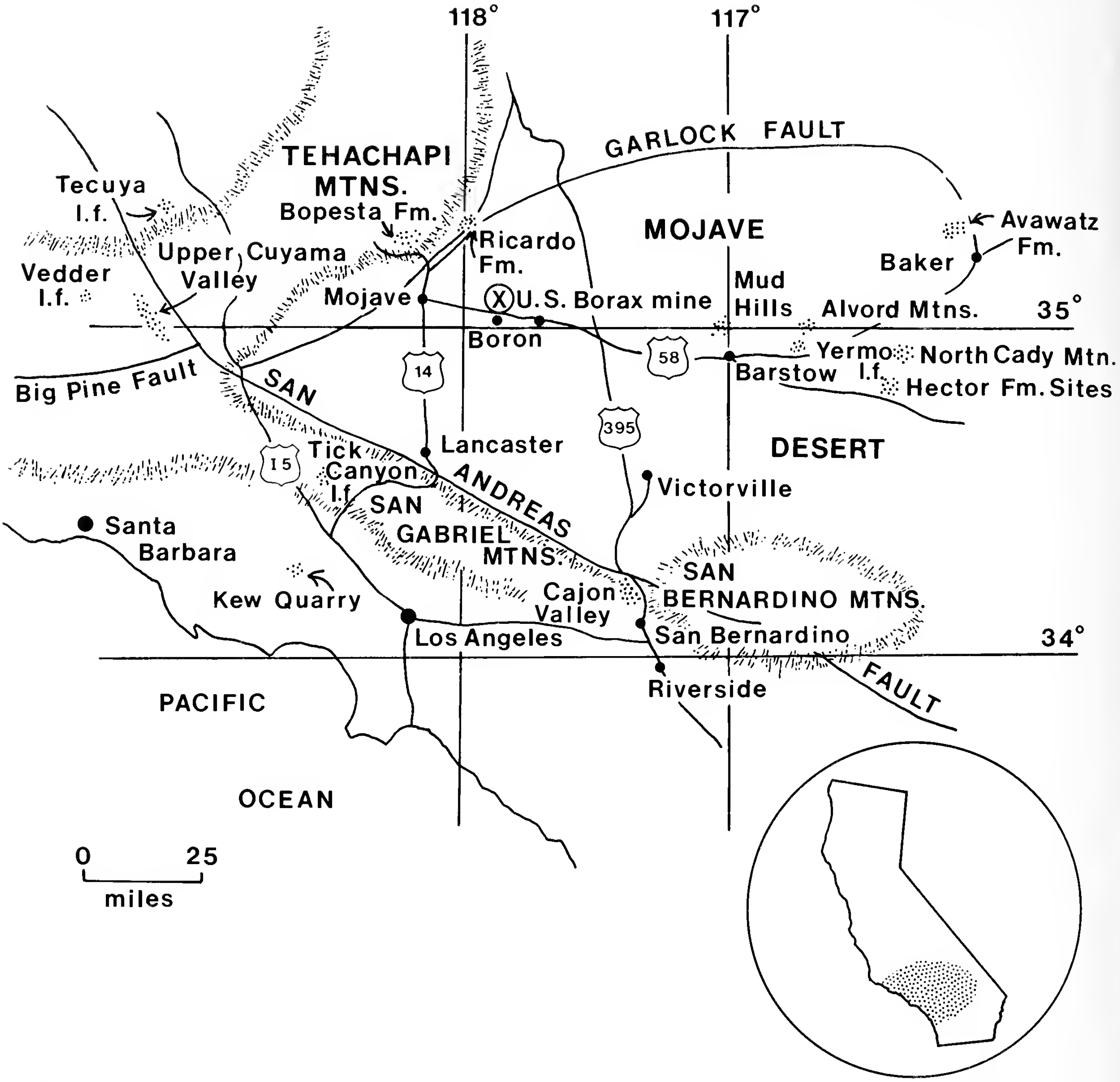


Figure 1. Index map showing location of Boron Local Fauna and other southern California Miocene fossil vertebrate assemblages discussed in this report.

be the first early Hemingfordian fossil assemblage sampled in southern California.

GEOLOGIC SETTING

The western and central Mojave Desert is a broad, fault-bounded block underlain by Mesozoic crystalline rocks which were faulted into many localized basins during the Middle and Late Cenozoic. Deposition in these basins was dominated by volcanics and volcaniclastics during the first half of the Miocene. Volcanism subsided during later Miocene and fluviatile and lacustrine sediments accumulated in the localized basins which persisted due to down-faulting, a process which continues today in some areas. In other areas, faulting has uplifted and exposed Miocene and younger sequences.

Considerable geologic, stratigraphic, and geophysical work has been done in the general area of Boron, much of it per-

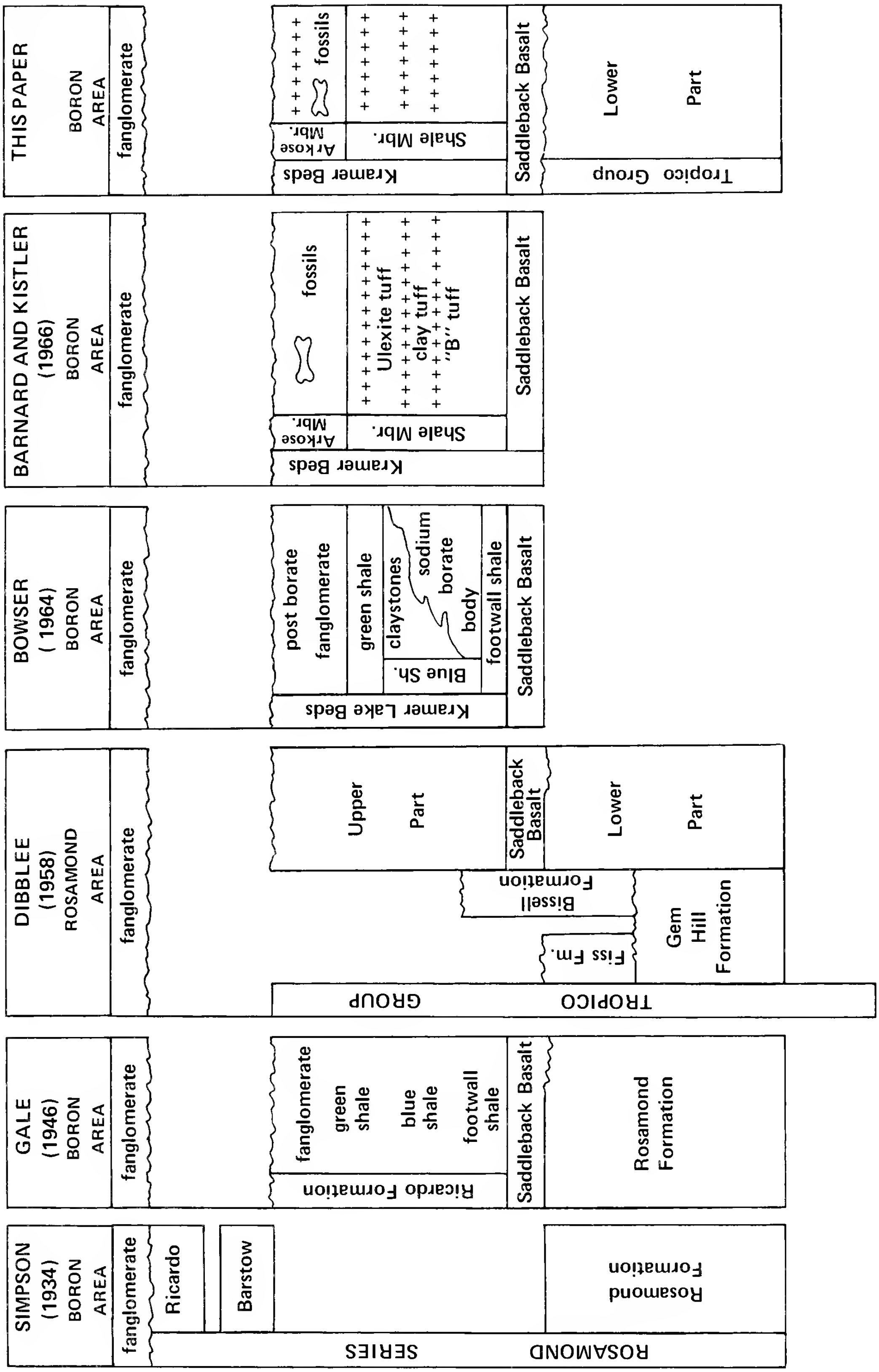


Figure 2. Stratigraphic nomenclature of geologic units at Boron and vicinity.

taining to the deposition and extent of the borate-rich sediments there (Figure 2). The Tertiary rocks at Boron and surrounding hills were originally referred to as the Rosamond Series (Hershey, 1902), a name expanded to include most of the continental sedimentary and volcanic rocks in the Mojave Desert, including such units as the Ricardo Formation of Clarendonian age (Merriam, 1919; Dibblee, 1952) and widely scattered deposits of Hemingfordian and Barstovian age, usually referred to the Barstow Formation (Merriam, 1919; Bowen, 1954). The first mapping of the borate producing beds at Boron was done by Gale (1946). He referred these beds to the Ricardo Formation and defined a new underlying unit, the Saddleback Basalt, which occurs in surface exposures at Saddleback Butte, 5 km to the east of Boron. A similar basaltic flow also occurs as a series of small hills just north of the mine and is found exposed in several areas of the open pit. It is also recognized in many of the drill holes in the general area.

During the 1950's, Dibblee undertook a regional mapping program in the western and central Mojave Desert including the area around Boron. Because of confusion over previous usage of stratigraphic names, Dibblee (1958a) established a new unit, the Tropico Group, to include only some of the Tertiary rocks previously referred to as the Rosamond Series. He included four formations within the Tropico Group (Gem Hill Formation, Fiss Fanglomerate, Bissel Formation, and Saddleback Basalt), but excluded such units as the Ricardo and Barstow Formations which had been included in the Rosamond Series by other workers.

Dibblee (1958a, b) did not give any formational designation to the beds at the open pit mine at Boron but referred to them only as the "Upper Part of the Tropico Group." Following the usage of the geology staff at the Boron mine, Bowser (1965), in his geochemical studies, used the term "Kramer Lake Beds" for the sequence above the Saddleback Basalt. Barnard and Kistler (1966) simplified Bowser's name to the Kramer Beds, included the Saddleback Basalt and published a detailed stratigraphic section which included the location of the Boron Local Fauna. They subdivided the Kramer Beds into three members, the Saddleback Basalt, Shale Member, and Arkose Member in ascending order. The Saddleback Basalt forms the base of the exposed section in the open pit mine and is the only member of the Kramer Beds with natural exposures. This sequence of flows and flow breccias appears to lie unconformably on pyroclastic rocks which may, in part, represent an eastern extension of the Gem Hill Formation, the basal unit of the Tropico Group.

The Shale and Arkose Members of the Kramer Beds overlying the Saddleback Basalt include lacustrine and fluviatile sediments exposed only in the open pit mine and known otherwise from drilling data (Benda et al., 1960; Dickey, 1957). The seemingly local extent of these units has been discussed by several authors (Gale, 1946; Bowser, 1964; Barnard and Kistler, 1966). The Shale Member is lacustrine, composed of dark green to brown, borate-bearing clays, shales, stratified borate ore bodies, and several thin bentonitic tuff beds. The Arkose Member, which produced the Boron Local Fauna, is composed of beds of well-bedded, buff, light tan and dark reddish brown claystone and micaceous siltstone and lenses of coarser, cross-bedded, light brown to yellowish white arkosic sandstone and pebble conglomerate. The Arkose Member contains relatively few volcanic beds, suggesting that the volcanism so commonly represented in the underlying units of the Tropico Group had subsided.

At the time of his original description, Dibblee (1958a) believed that much of the Tropico Group was Late Miocene and Pliocene in age. His conclusion was based on a diatom flora recovered from a limestone in the Tropico Group west of Boron and on Gale's (1946) lithologic correlation of the Saddleback Basalt with andesite breccia flows in the basal part of the Ricardo Formation which produced a fossil vertebrate fauna of Clarendonian age (then considered Pliocene). The discovery of the Boron Local Fauna at first seemed to refute this latter conclusion, but subsequent work in the type area of the Ricardo Formation has shown that a correlation of the basal andesite breccia flows and underlying pyroclastic rocks with the Tropico Group is reasonable. Field studies have shown that these volcanic rocks unconformably underlie the fossil-producing rocks of the Ricardo Formation which are radiometrically dated at a maximum of 10.2 ma (Evernden et al., 1964). These volcanics have subsequently been radiometrically dated at 17.1 ma (Loomis et al., 1983) and thus fall within the age range of the Tropico Group. The Saddleback Basalt has yielded radiometric dates in a range from 18.3 ± 0.6 (R.B. Kistler, personal communication) to 20.3 ± 0.7 ma (Armstrong and Higgens, 1973), somewhat older than, but possibly representing the same volcanic episode as the andesite flows underlying the Ricardo Formation.

Dibblee (1958a) recognized lithologic similarities between the Gem Hill Formation, the basal unit of the Tropico Group, the Middle Miocene Kinnick Formation in the mountains north of Tehachapi and the Pick Handle Formation underlying the Middle and Late Miocene Barstow Formation in the Mud and Calico Hills. The presence of the Boron Local Fauna in the uppermost member of the Tropico Group tends to support Dibblee's conclusions, but also shows that this entire unit is pre-Middle Miocene in age, much older than he had supposed.

FOSSIL OCCURRENCE

Fossils of the Boron Local Fauna were not observed at the original site of deposition by the author. They were first noticed by several mine employees operating heavy equipment removing overburden from the open pit mine. The mine foreman informed the geology staff who had the remaining fossil-bearing matrix dumped in a separate location from the general mine dump so that the fossils could be recovered. It is not certain how much of the fossil-bearing pocket was lost before this action was taken, but 4–5 earthmover loads (12–15 cubic meters) were subsequently recovered before the pocket stopped producing readily visible fossil bone.

According to the location provided by mine employees, the fossil-producing layer was approximately 146 m above the Saddleback Basalt. Observations made in the pit in 1964 and from the fossil-bearing matrix indicate the fossils were restricted to one or more beds of light tan micaceous claystones which locally contain pumice lapilli fragments. These beds were part of a sequence of fluviatile siltstones and sandstones locally cut by channels of coarser arkosic sandstones and pebble conglomerates. About 3 m above the fossil-producing beds were several discontinuous lenses of grayish-pink bentonitic tuff and yellowish-white, medium-grained sandy tuff.

Many of the individual bones were fractured and splintered prior to fossilization, suggesting a period of surface exposure before burial. On the other hand, some fossils are very well preserved and several limb fragments were still partially articulated. There is no evidence of rodent or carnivore gnawing on any of the fossil bone. Several matrix blocks contain small, lenticular concentrations of partially leached small vertebrate bone, apparently representing disassociated owl pellets or carnivore coprolites which undoubtedly are the source of the rich microvertebrate assemblage.

Limited prospecting by the author in the walls of the open pit mine in 1964 did not produce additional fossils, nor did extensive prospecting in all exposed fluviatile facies of the Tropico Group within 15 km of Boron yield further fossil specimens. The entire collection of fossil vertebrates was deposited in the Department of Earth Sciences at the University of California at Riverside.

METHODS

The fossils were obtained from the pile of matrix removed from the open pit mine. Blocks containing natural molds of bones destroyed during excavation were also collected and plaster casts were subsequently made of these molds. All matrix with a lithology similar to known fossil bearing matrix (about 2700 lb) was sieved under water with screens with an average mesh opening of 0.7 mm.

Measurements on larger bones were made with a vernier caliper to the nearest 0.1 mm and the microvertebrates were measured with an EPOI optical micrometer to the nearest 0.01 mm. Measurements are taken at their maximum dimensions unless otherwise indicated. The anteroposterior dimension of the P^4 of heteromyids was measured with the posterior surface of the metaloph oriented vertically.

The stereophotographs were taken by the author using an extension bellows and reversed 50 mm, f 1.4 lens mounted on a stereophotographic bar. The specimens were coated with vaporized magnesium oxide prior to photographing.

Radiometric dates have been converted using the new decay and abundance constants given by Dalrhymple (1979). This has the effect of increasing most later Tertiary dates published before 1979 by about 2.6 percent.

Metric abbreviations and designations of tooth position follow standard usage. Other abbreviations used are as follows:

LACM	Collections of the Natural History Museum of Los Angeles County
LACM(CIT)	Collections formerly at the California Institute of Technology, now at LACM
UCMP	Collections of the University of California, Museum of Paleontology, Berkeley
UCR	Collections of the University of California at Riverside, Department of Geological Sciences
L	Left
R	Right
ma	millions of years before present

FAUNAL LIST

Below is a summary of the fossil vertebrate assemblage of the Boron Local Fauna as recognized in the following systematics section.

- Class Reptilia
  - Order Squamata
    - Suborder Sauria
      - Family Iguanidae or Xantusiidae
        - Iguanidae or Xantusiidae sp. indet.
      - Family undetermined
        - Sauria, *incertae sedis*
    - Suborder Serpentes
      - Family Boidae
        - Subfamily Erycinae
          - cf. *Calamagras* sp.
      - Family Colubridae
        - cf. *Paracoluber* sp.
- Class Mammalia
  - Order Lagomorpha
    - Family Leporidae
      - Subfamily Archaeolaginae
        - *Arachaeolagus* sp. or *Hypolagus* sp.
  - Order Rodentia
    - Family Sciuridae
      - ?*Miospermophilus* sp.
    - Family Heteromyidae
      - Subfamily Perognathinae
        - *Mookomys* sp.
        - *Trogomys* cf. *T. rupinimenthae*
      - Subfamily Dipodomyinae
        - *Cupidinimus boronensis* n. sp.
  - Order Artiodactyla
    - Family Merycoidodontidae
      - Subfamily Merychinae
        - *Merychyus* cf. *M. minimus*
        - ?*Merychyus* sp.
    - Family Camelidae
      - Subfamily Aepycamelinae
        - cf. *Hesperocamelus* sp.
      - Subfamily undetermined
        - Camelidae, small species
        - Camelidae, large species

Family Palaeomerycidae
Subfamily Aletomerycinae
Aletomeryx occidentalis n. sp.

SYSTEMATICS

Class Reptilia

Order Squamata

Lizards and snakes are represented by very fragmentary material, but the presence of two lizards and two snakes can be demonstrated. The lizard identifications are based on the tooth-bearing bones although some postcranial material is also present. One of the lizards may represent the only Middle Miocene record of the family.

At least one boid and one colubrid snake are present. Small boids are common in the middle and late Tertiary, thus the Boron occurrence is not unusual. On the other hand, the colubrid represents one of the earliest records of the family in North America and extends the geographic range of such colubrids to west of the Rocky Mountains. Vertebral terminology follows Auffenberg (1963) and taxonomy follows Holman (1979).

Suborder Sauria

Family Iguanidae or Xantusiidae

Iguanidae sp. indet. or Xantusiidae sp. indet.

MATERIAL. Fragment of right dentary (or splenio-dentary), UCR 21174; anterior left dentary (or splenio-dentary), UCR 21175; premaxilla fragment, UCR 21176; miscellaneous unnumbered edentulous maxillary and dentary fragments.

DESCRIPTION. Small lizard, dentary less than 1 cm long based on estimate from several specimens; Meckelian groove closed and fused except for anterior opening; posterior teeth strongly tricuspate with grooves on both lingual and labial tooth surfaces between main cusp and lateral cusps; anterior teeth single cusped; teeth of similar width along entire tooth row; subdental lingual shelf well developed; dentary thin (dorsoventrally) below subdental lingual shelf; dentary same thickness below subdental lingual shelf for most of length of tooth row; premaxilla with 6 teeth.

DISCUSSION. The Boron lizard material is very fragmentary and the above description is based on a composite of several specimens with the single common character of a fused Meckelian canal, a character restricted to the xantusiids, gekkonids, and some iguanids such as *Dipsosaurus* Hallowell, 1854. The material is too incomplete to precisely estimate the entire tooth row length or the number of teeth. The individual tooth bases are relatively large and uncrowded, typical of xantusiids and some iguanids and in contrast to gekkonids, which usually have large numbers of small teeth. No posterior dentary fragments are preserved, thus the presence or absence of the diagnostic xantusiid character of separate anterior inferior alveolar and anterior mylohyoid foramina (terminology of Schatzinger, 1980) entirely enclosed within the splenio-dentary is not preserved. The teeth are strongly tricuspate, similar to *Paleoxantusia kyrentos* Schatzinger, 1980, but less so than in living *Dipsosaurus* or *Xantusia riversiana* Cope, 1883. The subdental lingual shelf is well developed as in the extinct *Paleoxantusia* Hecht, 1956, and in contrast to most iguanids. The continuously dorsoventrally thin dentary below the subdental lingual shelf is more similar to that of xantusiids than iguanids or gekkonids.

The Boron material does not permit positive identification, but appears to represent an undescribed species of either xantusiid or iguanid. Small iguanids are poorly known in the fossil record but a variety of undescribed material is present in Middle and Late Miocene deposits of the Mojave Desert and Great Basin (collections at the University of California, Berkeley, Museum of Paleontology, Natural History Museum of Los Angeles County and University of California at Riverside). *Paleoxantusia,* an early xantusiid, has been recognized only from the Paleocene and Eocene of western North America. Undescribed xantusiid material is known from Middle and Late Miocene deposits in the Mojave Desert (specimens in same collections as above) and the Middle Pleistocene Palm Springs Formation in San Diego and Imperial Counties of California (M. Norell, personal communication; specimens in the Natural History Museum of Los Angeles County).

Family undetermined

Sauria *incertae sedis*

DISCUSSION. There is a single dentary fragment, UCR 21177, and miscellaneous unnumbered specimens of a small lizard with an unfused Meckelian canal. The tooth morphology of this (or these) lizard(s) is not preserved. This material demonstrates the presence of at least one other small lizard in the fauna.

Suborder Serpentes

Infraorder Henophidia

Family Boidae

Subfamily Erycinae

Calamagras Cope, 1873

cf. *Calamagras* sp.

Figure 3

MATERIAL. Centrum portion of trunk vertebra retaining right diapophysis and portion of right prezygapophysis, UCR 21178; fragment of cotyle, prezygapophysis, and diapophysis, UCR 21179; centrum fragment, UCR 21180.

DESCRIPTION. Size small; vertebral centrum short (2.35 mm from dorsal edge of cotyle to distal end of condyle); ventral surface of centrum smooth with no haemal keel; no subcentral ridges; paradiapophysis subdivided into two distinct articular surfaces of similar size.

DISCUSSION. Although fragmentary, this material is clearly referable to the Family Boidae on the basis of the short vertebral centrum and lack of haemal keel. There are no neural arches or caudal vertebrae necessary for positive subfamily assignment, but the small size favors assignment to the Subfamily Erycinae. Among the fossil North American erycines, only *Calamagras* and *Tregophis* Holman, 1975, completely lack a haemal keel. The diagnostic characters of *Tregophis* occur in the neural arch, a structure not preserved in the Boron sample. *Tregophis* is a peculiar form known only from one Clarendonian locality in Kansas, and thus it appears more reasonable to refer the Boron species to *Calamagras,* a wide ranging taxon in the Middle Miocene.

The cf. *Calamagras* sp. from Boron lacks the haemal keel, the large, more widely separated paradiapophysial articular surfaces and subcentral gutter of *Charina prebottae* Brattstrom, 1958, from the Barstow Formation.

The living *Lichanura* Cope, 1861, also lacks a distinct haemal keel. The characters of the neural spine and caudal vertebrae necessary to distinguish *Calamagras* from *Lichanura* are not preserved in the Boron sample. *Lichanura* has not been recognized in the pre-Pleistocene record, and the Boron species is tentatively referred to *Calamagras* for this reason, not on morphological grounds.

Family Colubridae

Subfamily Colubrinae

Paracoluber Holman, 1970

cf. *Paracoluber* sp.

Figure 4

MATERIAL. Vertebral centrum complete from cotyle to condyle but lacking neural arch and associated structures, UCR 21181; five uncataloged posterior centrum fragments with condyles.

DESCRIPTION. Size small, centrum 3.15 mm long; centrum long compared to width; haemal keel moderately developed, oblanceolate, posterior end flat, not overlapping condyle; keel border straight in lateral view.

DISCUSSION. Although fragmentary, this material is complete enough to permit assignment to the Family Colubridae. These specimens are disinguished from boids, the common pre-Barstovian snakes in North America, by the long centrum and relatively narrow, long haemal keel, from the palaeophids, elaphids, viperids (including crotalids), and natricine colubrids by the absence of hypapophyses, and from the xenodontine colubrids (based on *Heterodon* Latreille, 1802) by the presence of a narrow, relatively high haemal keel.

The cf. *Paracoluber* sp. from Boron is distinguished from small fossil North American colubrines (see Holman, 1979) by a combination of the long centrum, absence of subcentral ridges, and structure of the haemal keel. It superficially resembles *Nebraskophis* Holman, 1973, in length of centrum, but has a much deeper haemal keel. The Boron species resembles *Paroxybelis* Auffenberg, 1963, except that the posterior end of the haemal keel is not pointed and does not extend onto the condyle. It differs from *Salvadora paleolineata* Holman, 1973, in lacking strong subcentral ridges. Except for its small size, cf. *Paracoluber* sp. from Boron closely resembles *Paracoluber storeri* Holman, 1970, in structure of the haemal keel and weak subcentral ridges. Holman (1970:1322) indicates that a paratype of *P. storeri* is smaller, but does not give the dimensions.

The incomplete Boron material does not permit species assignment, but it clearly demonstrates the presence of a small colubrid in the fauna.

Class Mammalia

Order Lagomorpha

The lagomorphs are the second most common microvertebrates in the fauna. Because much of the material is from juveniles, positive identification is difficult. Dental terminology and taxonomy follow Dawson (1958).

Family Leporidae

Subfamily Archaeolaginae

Archaeolagus Dice, 1917 or *Hypolagus* Dice, 1917

Archaeolagus sp. or *Hypolagus* sp.

Figures 5–6

MATERIAL. Fragment of left dentary with broken M_1, complete M_2, alveolus for M_3, UCR 10401; isolated, unworn LM^1, UCR 10403; partial LdP^4, UCR 10400; isolated, unworn LP_3 or LdP_4, UCR 10402; isolated tooth and postcranial fragments, UCR 10404–10412.

DESCRIPTION. M^1 with two lophs separated by cement-filled, lingual reentrant; dP^4 bilophed lingually, enamel limited to lingual side, large, labially curved root centered under lingual lophs, labial roots missing; UCR 10402 (unworn P_3 or dP_4) with distinct talonid and trigonid separated by continuous valley instead of separate lingual and labial reentrants; cement only in central part of valley separating talonid and trigonid; trigonid composed of three separate spurs joined at center of tooth, labial spur narrow, bordered anterolingually by deep reentrant.

DISCUSSION. Both the isolated M^1 and UCR 10402 (unworn P_3 or dP_4) are from very young individuals, neither showing wear. Thus, both display distinct, separate cusps in contrast to the lophodont nature typical of lagomorphs. The bases of the teeth are open and both are relatively low crowned, suggesting neither tooth was completely formed. The reentrants of UCR 10402 (P_3 or dP_4) would be persistent in wear for nearly the entire length of the preserved tooth crown. With some wear, the tooth would divide into two lophs and an additional anterolabial reentrant. Such a persistent reentrant is more diagnostic of *Hypolagus* (Dawson, 1958).

Archaeolagus is typically characterized by the loss of the lingual reentrant in the P_3 with wear, but a very young in-

Figures 3–7. Stereophotographs of cf. *Calamagras* sp., cf. *Paracoluber* sp., *Archaeolagus* sp. or *Hypolagus* sp., and ?*Miospermophilus* sp. **Figure 3,** cf. *Calamagras* sp., UCR 21178, ventral view of vertebral centrum. **Figure 4,** *Paracoluber* sp., UCR 21181, ventral view of vertebral centrum. **Figures 5–6,** *Archaeolagus* sp. or *Hypolagus* sp., UCR 10402, unworn LP$_3$ or dP$_4$; **(5)** occlusal view, **(6)** labial view. **Figure 7,** ?*Miospermophilus* sp., UCR 10399, unworn LdP^4 or LP^4, occlusal view. Scale bar = 1 mm.

dividual of *Archaeolagus acaricolus* Dawson, 1958 (specimen LACM(CIT) 5176) exhibits a structure in the P$_3$ similar to UCR 10402. The Boron material appears small, even for *Archaeolagus,* but this is probably due to the juvenile state of most of the specimens. The available material from Boron is not complete enough for certain assignment to either *Hypolagus* or *Archaeolagus.* While the size is more consistent with *Archaeolagus,* the morphology of UCR 10402, if it is indeed a P_3 in extremely early wear, more nearly resembles *Hypolagus.*

Order Rodentia

The rodent fauna is dominated by heteromyids except for a single small squirrel tooth. Compared with other rodents, squirrels are generally uncommon in the fossil record, and although the Boron species appears to have some unique characters, the single specimen is inadequate to make a specific assignment. The dental terminology used for the squirrel follows Black (1963).

At least three heteromyid species representing two subfamilies are present. As recognized by all who work with these forms, heteromyid taxonomy is in great need of revision. The Boron species do not help resolve this problem, but they do indicate intraspecific variation in some characters which have traditionally been used to separate species or even genera.

The most common species in the microfauna, represented by more specimens than all other microvertebrates combined, is a new species of dipodomyine heteromyid referred to *Cupidinimus* Wood, 1935. This species represents the earliest record of this widespread genus but it is already clearly derived with respect to species thought to be ancestral to this and closely related genera. The other heteromyids, one a very low crowned, bunodont species and the other a relatively high crowned perognathine, are each represented by only two teeth but are, nonetheless, identifiable at the generic level. There are several vials of fragmentary postcranial bones from small mammals, but none are clearly assignable to any of the species represented by teeth. Tooth cusp terminology for these heteromyids is given in Figure 8, taxonomy follows Wood (1935) and Korth (1979).

Family Sciuridae

Subfamily Sciurinae

Miospermophilus Black, 1963

?*Miospermophilus* sp.

Figure 7

MATERIAL. Unworn, LdP^4 or LP^4, UCR 10399.

DESCRIPTION. Anteroposterior diameter = 1.65 mm, width = 1.80 mm; outline sub-triangular; lophs and cusps high and distinct; metaloph higher than protoloph, connected to protocone by narrow ridge; connection between protoloph and protcone stronger than connection between metaloph and protocone; protocone large, with separate posterolingual expansion (possibly indicating the position of a separate hypocone) continuous with posterior cingulum; anterior and posterior cingula low but distinct; anterior cingulum continuous from protocone to termination in large parastyle in anterolabial corner of tooth; posterior cingulum running from posterolingual corner of metacone to posteriorly expanded protocone (hypocone); mesostyle large.

DISCUSSION. The small size, sub-triangular outline, relatively high cusps and lophs and presence of a metaconule serve to distinguish this species as a ground squirrel or chipmunk (Black, 1963). The Boron specimen is unusual for either a chipmunk or a ground squirrel in the retention of distinct cusps, the presence of a distinct protoconule, large parastyle, and protocone split into two cusps. All these features might simply be attributable to the unworn condition of this specimen, but they also strongly suggest that it is a deciduous premolar. The roots are missing, but the specimen has the hollowed out base typical of both deciduous teeth and unerupted permanent teeth.

Regardless of permanent versus deciduous designation, the small size favors assignment of the Boron specimen to one of three genera, *Miospermophilus* Black, 1963, *Tamias* Illiger, 1811, or *Ammospermophilus* Merriam, 1892, all represented by Miocene aged species. The size is most consistent with species of *Miospermophilus,* which are larger than those of living and extinct species of *Tamias* and the Miocene species of *Ammospermophilus.*

The dP^4 of these small squirrels is poorly known, making direct comparison difficult. The dP^4 of *M. bryanti* (Wilson, 1960) from the Martin Canyon Quarry in Northeastern Colorado (in Black, 1963:188) and *M. wyomingensis* Black, 1963: 192 from the Split Rock Formation of Wyoming are described as having a strong metaconule and low, distinct anterior and posterior cingula similar to the Boron specimen. *M. bryanti* lacks a mesostyle but *M. wyomingensis* is described as having a small mesostyle similar to the Boron specimen. A partial, isolated dP^4 from the Branch Canyon Formation of California referred to *Miospermophilus* sp. by Lindsay (1974:14) lacks the protoconule and metaconule but does have a small mesostyle. No described dP^4's of *Miospermophilus* have the distinct protoconule present in the Boron specimen, but undescribed specimens from the Thomas Farm faunas of Florida do have a protoconule (D. Webb and A. Pratt, personal communication).

The only described dP^4 of a fossil species of *Tamias* (Black, 1963:129) is reported to bear the conules, large mesostyle, and expanded anterior cingulum found in the Boron specimen.

The dP^4 of fossil species of *Ammospermophilus* has not been described, but specimens of this tooth and the permanent P^4 in a sample of the living species *A. lecurus* (Merriam, 1889) from the LACM Mammalogy collections differ considerably from the Boron specimen. In these, the anterior cingulum of the dP^4 extends only half way along the anterolingual corner of the tooth and there is no hint of a parastyle which is prominent in the Boron ?*Miospermophilus* specimen. The metaloph in both the dP^4 and P^4 is reduced lingually and does not connect to the protocone even in late wear stages in the modern species examined. A further variation was found in specimens of the dP^4 of the subspecies *A. lecurus peninsulae* (Allen, 1893) where the metaloph connects to the posterolingual corner of the lingual end of the protoloph.

Although similar in most features, the permanent P^4 of species of *Miospermophilus, Tamias,* and *Ammospermophilus* is generally even more lophodont, with greater reduction

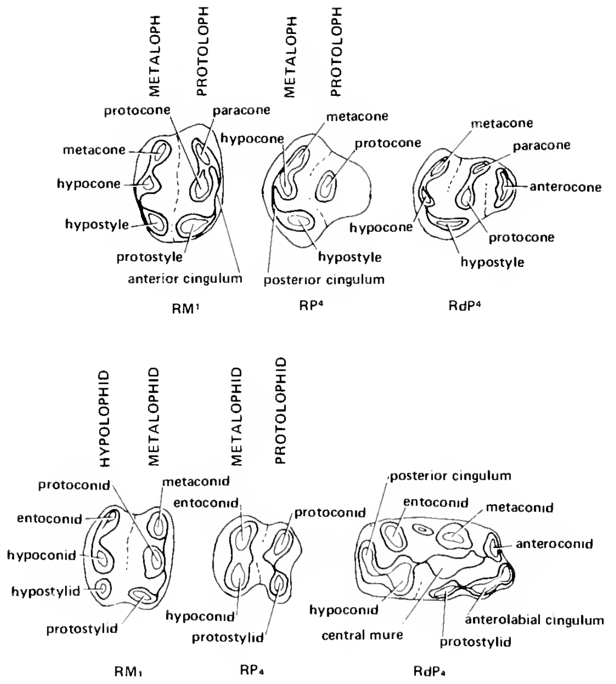


Figure 8. Tooth cusp terminology used in heteromyid rodents.

Table 1. Selected dental measurements of *Mookomys* sp. and *Trogomys* cf. *T. rupinimenthae*. Abbreviations: AP = anteroposterior dimension of tooth, WP = width of protoloph(id), WM = width metaloph(id), X = mean.

	UCR	AP	X	WP	X	WM	X
	Mookomys sp.						
P_4	10421	0.70		0.36		0.73	
M_1 or M_2	10464	0.86		0.78		0.79	
	Trogomys cf. *T. rupinimenthae*						
P^4	21182	1.00				1.15	
P_4	10419	0.83		0.60		0.85	

of the metaconule and protoconule than the dP^4. The cingula are also better developed and nearly as high as the protoloph and metaloph in the P^4. The Boron specimen is similar in size to the P^4 of *Miospermophilus* species, but differs in retention of distinct conules, particularly the protoconule.

Family Heteromyidae

Subfamily Perognathinae

Mookomys Wood, 1931

Mookomys sp.

Figures 9–12, Table 1

MATERIAL. RP_4, UCR 10421; LM_1 or LM_2, UCR 10464.

DESCRIPTION. P_4 triangular in occlusal outline with four subequal low rounded cusps; protostylid very small, lower than protoconid; protostylid and protoconid nearly joined as single cusp with only a shallow anterior groove separating cusps on upper part of tooth crown; connection between protolophid and metalophid central; no posterior cingulum.

UCR 10464 (M_1 or M_2) nearly square in occlusal outline with six low, separate cusps not distinctly connected until late wear; tooth bilophodont with wear; central valley deep; protostylid and hypostylid small, both offset posteriorly relative to protoconid and hypoconid; protostylid anteroposteriorly expanded; no anterior or posterior cingulum; connection of lophids late, central; two roots.

DISCUSSION. The lower premolar, with its reduced protolophid, is more similar to species of *Heliscomys* Cope, 1873, than to the common species of *Mookomys, M. altifluminis* Wood, 1931, and *M. formicorum* Wood, 1935, both with distinctly four-cusped lower premolars. The P_4 of *M. subtilis* Lindsay, 1972, is not known. UCR 10421 lacks the posterior cingulum diagnostic of *Heliscomys* species. A triangular P_4 with four cusps, but with a very small hypostylid and a narrow protolophid, would be expected in an early species of *Mookomys* if, as is generally accepted, this genus is a descendant from *Heliscomys,* which has triangular, three-cusped P_4's.

The lower molar is typical of species of *Mookomys* with a very low crown and low separate rounded cusps which only join in later wear. The Boron specimen is much smaller than that of any species of *Mookomys* except *Mookomys subtilis,* even if the specimen is a M_2 (which is smaller than M_1). It is closer to size to teeth species of *Heliscomys,* but it lacks the characteristic cingula. *Mookomys* sp. from Boron differs from the M_1 of *M. subtilis* in having a smaller anterior cingulum, less posteriorly offset protostylid and hypostylid, and lacking a posterior cingulum. In this latter character and the very low crown height, *M. subtilis* is more similar to species of *Heliscomys* than to species of *Mookomys.* Lindsay (1972) does not compare *M. subtilis* (Barstovian) with *Heliscomys,* but it appears that it is more similar to *Heliscomys,* even though the latter is restricted to the Oligocene.

Mookomys sp. from Boron probably represents a very small species of *Mookomys,* but it could be interpreted as a survivor species of *Heliscomys* in the early Hemingfordian.

Trogomys Reeder, 1960

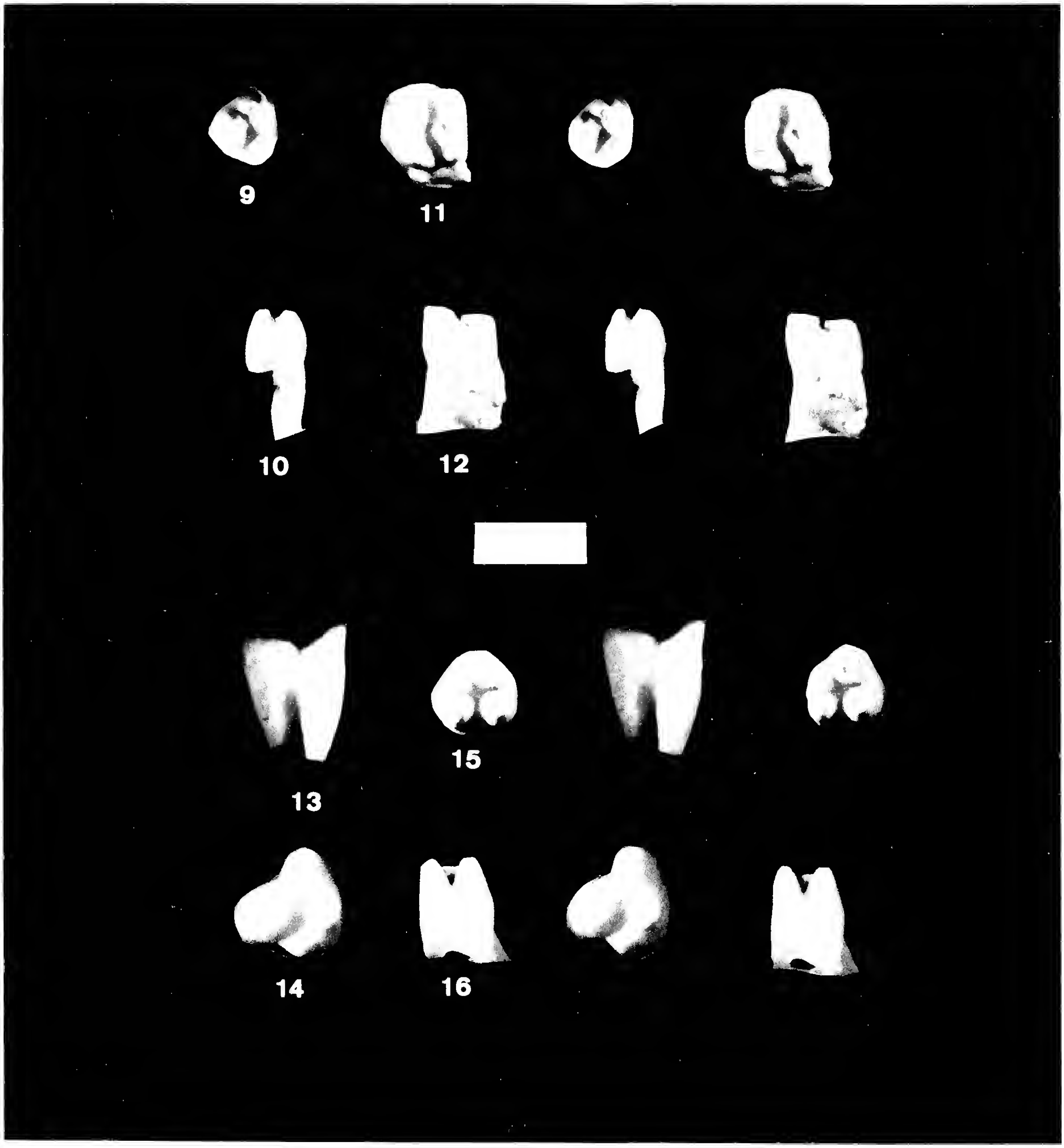
Trogomys rupinimenthae Reeder, 1960

Trogomys cf. *T. rupinimenthae*

Figures 13–16, Table 1

MATERIAL. LP^4, UCR 21182; RP_4, UCR 10419.

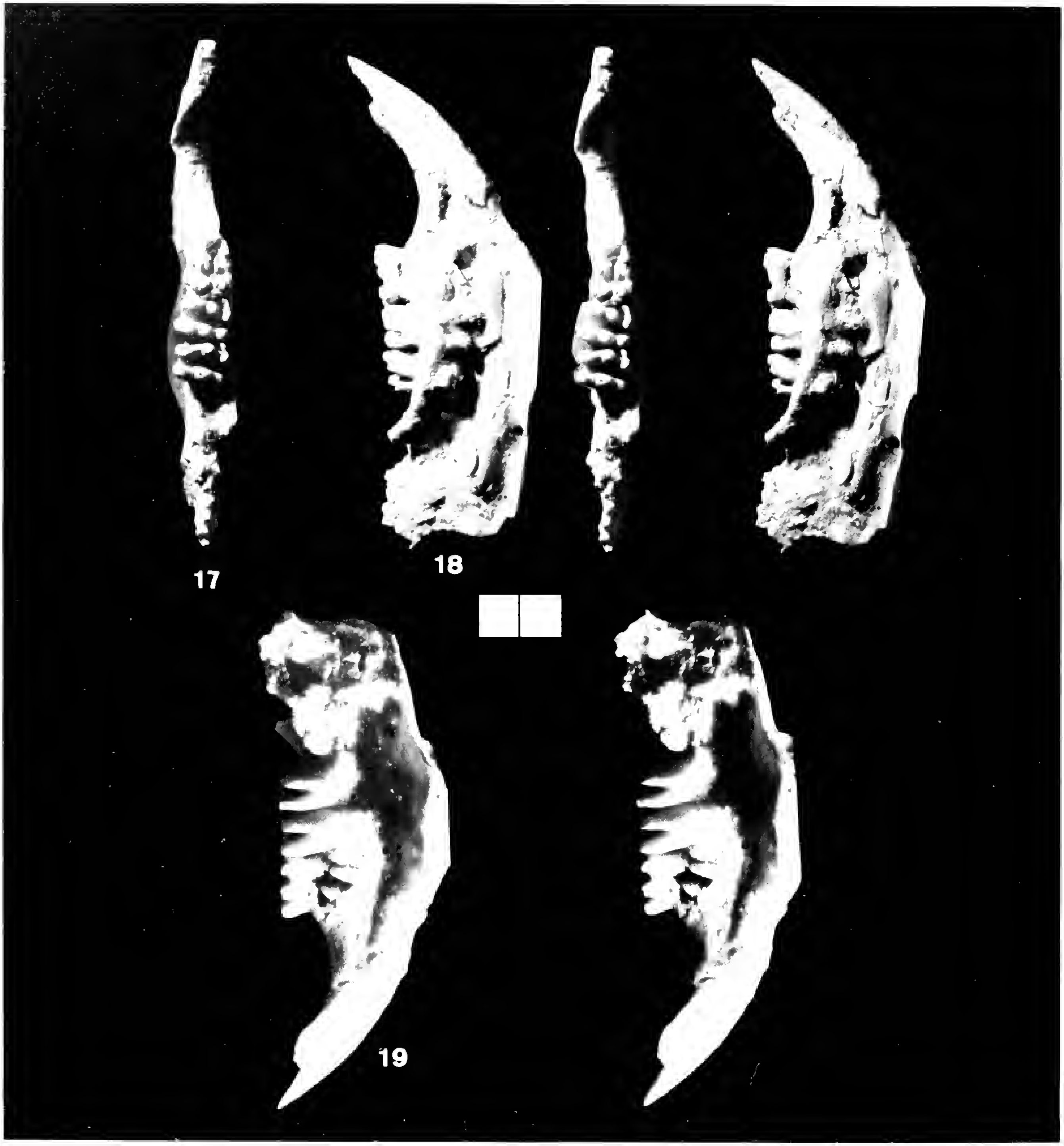
DESCRIPTION. P^4 with transversely expanded protocone but no protostyle; central connection of protoloph to metaloph; metaloph with three cusps, hypocone and metacone closer together than hypocone and hypostyle; hypostyle nearly same size as metacone, not anteroposteriorly expanded, connected to hypocone by posterior cingulum; three roots, separate to base.



Figures 9-16. Stereophotographs of *Mookomys* sp. and *Trogomys* cf. *T. rupinimenthae*. **Figures 9-10,** *Mookomys* sp., UCR 10421, RP_4; **(9)** occlusal view, **(10)** lingual view. **Figures 11-12,** *Mookomys* sp., UCR 10464, LM_1 or LM_2; **(11)** occlusal view, **(12)** lingual view. **Figures 13-14,** *Trogomys* cf. *T. rupinimenthae*, UCR 21182, LP^4; **(13)** labial view, **(14)** occlusal view. **Figures 15-16,** *Trogomys* cf. *T. rupinimenthae*, UCR 10419, RP_4; **(15)** occlusal view, **(16)** lingual view. Scale bar = 1 mm.

P_4 four cusped; no hypostylid; fairly high crowned, clearly more hyposodont than *Perognathus* Wied-Neuwied, 1839; protostylid smaller than protoconid, offset posteriorly; valley between lophids deep lingually, shallow labially; first connection of lophids labial; sulcus between hypoconid and metaconid as deep as between metaconid and protoconid; two roots, separate to base.

DISCUSSION. These premolars are distinctly lower



Figures 17–19. Stereophotographs of *Cupidinimus boronensis* n. sp., UCR 10413, holotype, right dentary with dP$_4$, M$_{1-2}$; (**17**) occlusal view, (**18**) labial view, (**19**) lingual view. Scale bar = 2 mm.

crowned than those of *Cupidinimus,* higher crowned and more lophodont than those of *Mookomys* and somewhat higher crowned than those of the common Barstovian species, *Perognathus furlongi* Gazin, 1930. The diagnostic features of *Trogomys,* the asulcate upper incisor and characters of the molars, are not represented in the Boron sample. The two Boron teeth are within the size range of *P. furlongi,* but are higher crowned, a characteristic of *Trogomys.* They are com-

Table 2. Selected dental measurements of *Cupidinimus boronensis* n. sp. Abbreviations: AP = anteroposterior dimension of tooth, WP = width protoloph(id), WM = width metaloph(id), X = mean.

	UCR	AP	X	WP	X	WM	X
Type M_1	10413	0.98		1.19		1.30	
M_2		0.91		1.15		1.16	
dP_4		1.42		0.97			
P^4	10449	1.30	1.26	1.40	1.31		
	10450	1.31		1.27			
	10451	1.30		1.25			
	10452	1.12		1.31			
	10453	1.20		1.29			
	10454	1.45		1.37			
	10456	1.23		1.36			
	10457	1.13		1.29			
	10458	1.26		1.29			
M^1	10459	0.95	0.99	1.37	1.30	1.23	1.16
	10460	0.95		1.17		1.10	
	10461	1.03		1.36		1.25	
	10462	1.00		1.34		1.20	
	10463	1.02		1.28		1.16	
	21183	1.00		1.25		1.00	
M^2	10465	0.90	0.86	1.23	1.11	1.02	0.99
	10467	0.88		1.04		0.92	
	10468	0.83		1.11		1.04	
	21184	0.83		1.05		0.98	
M^3	10466	0.77		0.87		—	
dP^4	10471	1.08		1.01		—	
	10472	1.19		1.15		—	
P_4	10416	0.95	1.00	0.91	0.88	1.05	1.05
	10417	1.11		0.89		1.13	
	10418	1.02		0.83		1.10	
	10420	0.99		0.90		0.95	
	10422	0.94		0.88		1.03	
M_1	10413	0.98	1.05	1.19	1.17	1.30	1.27
	10423	1.04		1.16		1.29	
	10424	1.06		1.29		1.29	
	10427	1.09		1.15		1.27	
	10429	1.02		1.23		1.27	
	10434	1.15		1.19		1.28	
	10436	1.08		1.19		1.27	
	10438	1.06		1.13		1.19	
	10439	1.00		1.13		1.25	
	10441	1.09		1.05		1.22	
M_2	10413	0.91	0.95	1.15	1.19	1.16	1.10
	10426	0.90		1.17		1.08	
	10430	1.03		1.21		1.09	
	10431	0.89		1.25		1.11	
	10432	0.90		1.19		—	
	10433	1.05		1.23		1.10	
	10435	1.01		1.24		1.07	
	10437	0.87		1.13		1.15	
	10440	1.04		1.23		1.16	
	10444	0.96		1.26		1.07	
	10447	0.88		1.05		1.00	
M_3	10443	0.74	0.73	1.08	0.92	0.77	0.76
	10445	0.74		0.91		0.76	
	10446	0.72		0.76		0.74	
dP_4	10414	1.32		—		0.75	

parable in size, crown height, and cusp morphology to *T. rupinimenthae* from the Arikareean age Tick Canyon Formation of southern California.

Subfamily Dipodomyinae

Cupidinimus Wood, 1935

Cupidinimus Wood, 1935:118.
Perognathoides Wood, 1935:92.
Prodipodomys? *mascallensis* Downs, 1956; sample of Shotwell, 1967:22.
Perognathus saskatchewanensis Storer, 1970:1127.

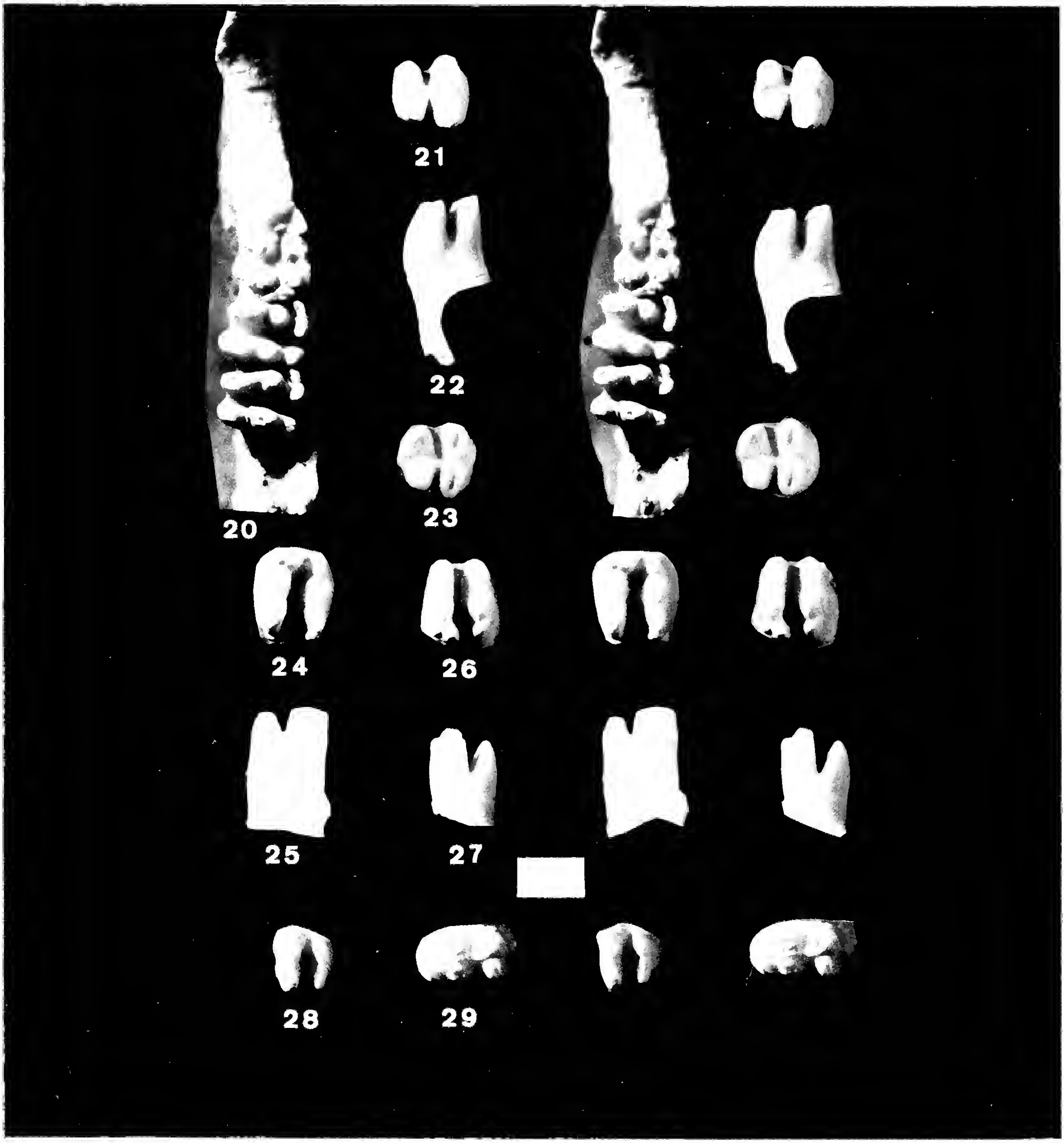
***Cupidinimus boronensis* new species**

Figures 17–39, Table 2

HOLOTYPE. UCR 10413, right dentary with incisor, dP_4, M_{1-2}.

TYPE LOCALITY. UCR locality RV 6421, Arkose Member of the Kramer Beds of Barnard and Kistler (1966), 146 m above the top of the Saddleback Basalt on the third level below the surface in the east wall of the open pit mine of the United States Borax and Chemical Corporation as it existed in March, 1964, 4.8 km northwest of Boron, Section 23, T.11N., R.8W., Boron Quadrangle, United States Geological Survey, 1954, 1:62,500, San Bernardino County, California.

REFERRED MATERIAL. Five RP^4's, UCR 10449, UCR 10450, UCR 10451, UCR 10452, and UCR 10453; five LP^4's, UCR 10454, UCR 10455, UCR 10456, UCR 10457, and UCR 10458; two RM^1's, UCR 10460 and UCR 21183; four LM^1's, UCR 10459, UCR 10461, UCR 10462, and UCR 10463; two RM^2's, UCR 10465 and UCR 21184; two LM^2's, UCR 10467 and UCR 10468; RM^3, UCR 10466; LM^1 or LM^2, UCR 10469; two RdP^4's, UCR 10471 and UCR 10472; two RP_4's, UCR 10418 and UCR 10420; four LP_4's, UCR 10415, UCR 10416, UCR 10417, and UCR 10422; seven RM_1's, UCR 10423, UCR 10424, UCR 10427, UCR 10436, UCR 10438, UCR 10439, and UCR 10441; four LM_1's, UCR 10428, UCR 10429, UCR 10434, and UCR 10470; five RM_2's, UCR 10431, UCR 10437, UCR 10440, UCR 10444, and UCR 10447; six LM_2's, UCR 10425, UCR 10430, UCR 10432, UCR 10433, UCR 10435, and UCR 10442; RM^3, UCR 10445; two LM_3's, UCR 10443 and UCR 10446;



Figures 20-29. Stereophotographs of *Cupidinimus boronensis* n. sp. lower dentition. **Figure 20,** UCR 10413, holotype, occlusal view of dentition only. **Figues 21-22,** UCR 10416, LP$_4$; **(21)** occlusal view, **(22)** labial view. **Figure 23,** UCR 10422, LP$_4$, occlusal view. **Figures 24-25,** UCR 10423, RM$_1$; **(24)** occlusal view, **(25)** labial view. **Figures 26-27,** UCR 10430, LM$_2$; **(26)** occlusal view, **(27)** lingual view. **Figure 28,** UCR 10445, RM$_3$, occlusal view. **Figure 29,** UCR 10414, RdP$_4$, occlusal view. Scale bar = 1 mm.

RdP_4, UCR 10414; all from type locality, UCR locality RV 6421.

DIAGNOSIS. Teeth typical of dipodomyines by being higher crowned than those of perognathines and most heteromyines; further distinguished from heteromyines by lacking a "J" wear pattern in the P^4; distinguished from geomyines by smaller size, lower crown height, retention of cuspidate teeth and central (versus lingual) connection of lophs in P_4; individual teeth larger than those of *C. nebraskensis* Wood, 1935, *C. halli* (Wood, 1936b), *C. cuyamensis* (Wood, 1937), and *C. madisonensis* (Dorr, 1956), smaller than *C. bidahochiensis* (Baskin, 1979); teeth high crowned but retaining individual cusps until moderate wear; roots long, separate to base; premolars lacking accessory cusp(id)s; M^3_3 reduced; dP^4_4 low crowned, with complex cusp pattern; metaloph of P^4 wide compared to width of M^1, hypostyle not greatly elongate and posterior cingulum incomplete; P_4 short anteroposteriorly relative to width of protolophid and length of M_1; anterior cingulum not anteriorly expanded in M_1 or M_2; dP_4 with large anteroconid connected to central mure and lacking hypostylid; in addition to size, differs from *C. halli* and *C. madisonensis* by lack of accessory cusps in P^4_4, anteroposteriorly short P_4, reduced anterior cingula on M_1 and M_2 and large anteroconid connected to central mure and lack of hypostylid in dP_4; in addition to size, differs from *C. nebraskensis* by anteroposteriorly short P_4, relatively unreduced M_2, reduced M^3_3, and strong central mure on dP_4.

ETYMOLOGY. Named after the type locality.

DESCRIPTION. P^4 with transversely expanded protocone; accessory cusps lacking on protocone except for one specimen, UCR 10454, with greater transverse expansion of protoloph suggestive of protostyle; first connection of lophs central; metaloph three cusped; hypocone slightly posterior relative to lateral cusps; hypostyle slightly expanded anteroposteriorly; posterior cingulum small, between posteromedial surface of hypocone and hypostyle; three roots, one each under protoloph, metacone, and hypostyle, separate to base.

M^1 six cusped in early wear, cusps less persistent than in lower molars; anterior cingulum low relative to protocone, continuous between paracone and protostyle, thickening near paracone; protoloph wider than metaloph; anterior face of protoloph flat; small protolophule connecting protocone and paracone in 2 of 3 specimens with early enough wear to show character; transverse valley deep and narrow; first union of lophs lingual, followed by central connection, but no lake formation; median cusps (protocone and hypocone) positioned posteriorly relative to lateral cusps, making metaloph convex posteriorly; no posterior cingulum except for connection between hypocone and hypostyle; one lingual, two labial roots, separate to base.

M^2 smaller than M^1, proportionately more reduced than M_2; anterior face convex; posterior face concave; anterior cingulum reduced to absent; protolophule between protocone and paracone present in one specimen; first union of lophs labial, but transverse valley shallower than in M^1, closed both lingually and labially; metaloph narrower than protoloph due to reduction in metacone; metaloph three cusped, joined into continuous posterior crescent; hypostyle offset relative to hypocone and more anteroposteriorly elongate than in M^1; one lingual, two labial roots, separate to base.

M^3 with no anterior cingulum; protostyle elongate anteroposteriorly; metaloph bearing three cusps joined to posterior crescent which lacks distinct cusps; roots not preserved in available sample.

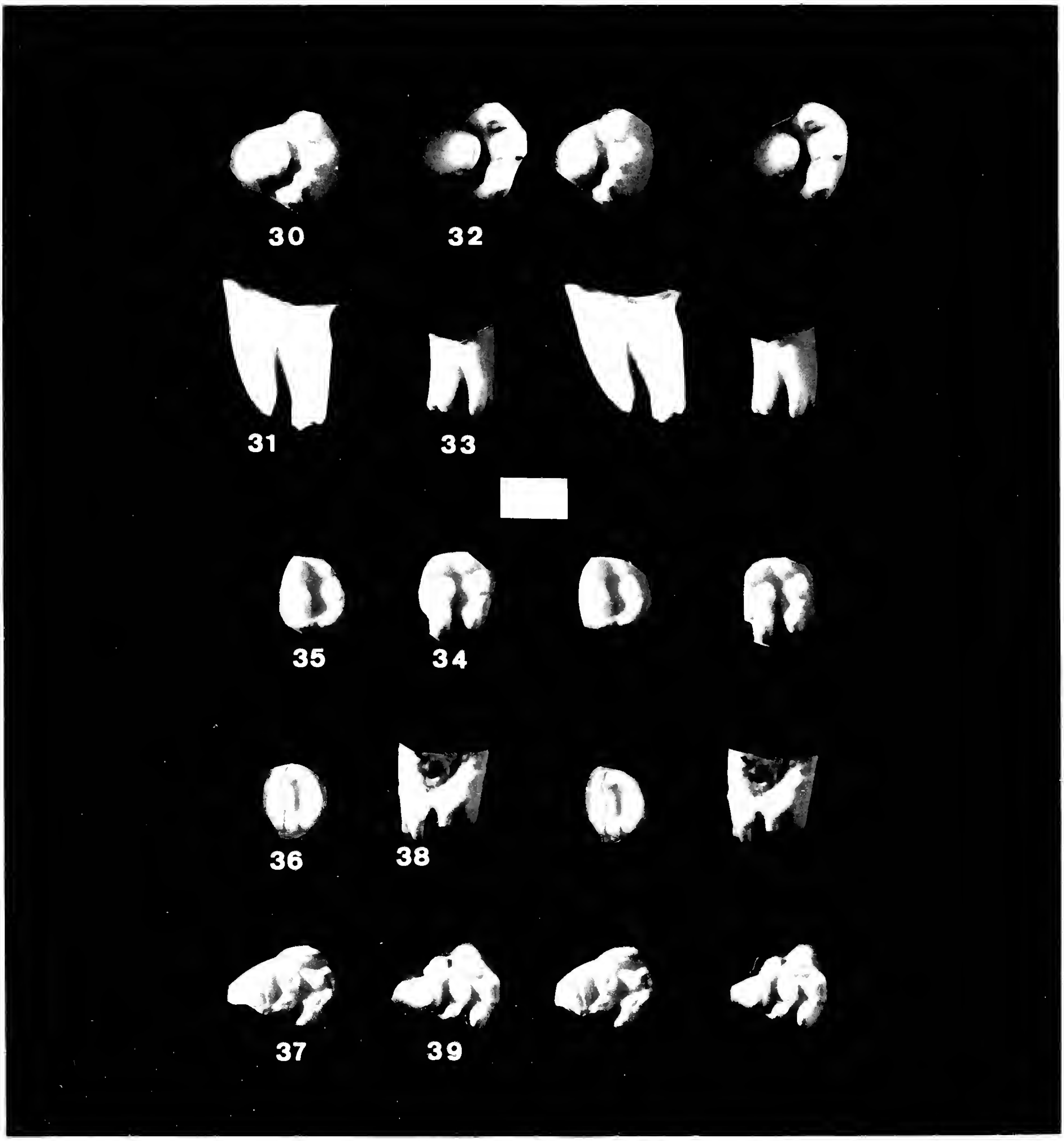
dP^4 low crowned; triangular outline; cusps low but distinct; three lophed; large, transversely expanded anterocone; protoloph with two cusps, larger protocone and smaller paracone; metaloph with three cusps, metacone, hypocone, and anteroposteriorly expanded hypostyle; anterolabial connection between protoloph and anterocone; no connection between protoloph and metaloph; hypostyle extends anteriorly to lingual side of protocone but with no connection to protocone; three roots, one each under anterocone, metacone, and protostyle.

P_4 with four cusps nearly equal in size; protostylid smaller than protoconid, closer to hypoconid than protoconid is to metaconid; protoconid-protostylid connection central; protolophid narrower than metalophid; first connection of lophs either slightly lingual of center, between protostylid and hypoconid, or central; two roots, separate to base.

M_1 six cusped; tooth wider than long; protostylid nearly same size as protoconid, offset posteriorly relative to protoconid, continuous with anterior cingulum which connects to anteromedial surface of protoconid; metalophid convex anteriorly, hypolophid straight; transverse valley deep, narrow, open labially and lingually, deeper on lingual side; first union of lophs both between protostylid and hypostylid and central, probably forming short-lived lake; hypolophid narrower than metalophid due to expanded entoconid; hypostylid smaller than hypoconid; no posterior cingulum; two roots, separate to base.

M_2 six cusped; tooth wider than long; metalophid and hypolophid same width; metalophid less convex anteriorly than in M_1; protostylid small, smaller than in M_1, offset posteriorly relative to protoconid, continuous with anterior cingulum which extends only to anterolabial corner of protoconid; hypostylid smaller than on M_1; transverse valley deep, deeper lingually than labially, labial connection deeper than in M_1; first union of lophs more strongly central than in M_1, labial connection late or lacking; hypolophid straight; two roots, separate to base; two early wear specimens, UCR 10442 and 10444 displaying variation from above by lacking distinct hypostylid (but with hypoconid extending labially toward base, thus forming as broad a hypolophid as an M_2 with hypostylid) and with protostylid separated from anterior cingulum by distinct, shallow groove lost with early wear.

M_3 four cusped, lacking stylids; bilophodont in early wear;



Figures 30-39. Stereophotographs of *Cupidinimus boronensis* n. sp. upper dentition. **Figures 30-31,** UCR 10450, RP^4; **(30)** occlusal view, **(31)** labial view. **Figure 32,** UCR 10449, RP^4, occlusal view. **Figures 33-34,** UCR 10460, RM^1; **(33)** labial view, **(34)** occlusal view. **Figure 35,** UCR 10467, LM^2, occlusal view. **Figure 36,** UCR 10445, RM^3, occlusal view. **Figure 37,** UCR 10472, RdP^4, occlusal view. **Figures 38-39,** UCR 10471, RdP^4; **(38)** lingual view, **(39)** occlusal view. Scale bar = 1 mm.

very small anterior cingulum in early wear, forming anterolabial "corner" on protoconid with wear; metalophid distinctly wider than hypolophid; central valley narrow, deep; single rooted.

dP_4 very low crowned; elongate oval in occlusal view, narrower anteriorly; complex cusp pattern with three main central cusps, metaconid, entoconid, and hypoconid; large anterolingually placed anteroconid nearly continuous with high anterolabial cingulum; anterolabial cingulum and protostylid as high as central cusps, nearly continuous to mid-labial portion of tooth and connecting back lingually to central mure; very small cuspule between hypoconid and posterior end of anterolabial cingulum; low protoconid anterolabial to metaconid; no hypostylid; with wear, hypoconid joins a central mure which runs anteriorly through protoconid to anteroconid; with wear, metaconid joined by short loph to protoconid; entoconid connected by mure either directly to hypoconid or through posterior cingulum to hypoconid; small lingual accessory cuspid between metaconid and entoconid; large posterior cingulum; two roots, one anterior, one posterior.

DISCUSSION. *C. boronensis* is assigned to the genus *Cupidinimus* following the expanded concept of this genus proposed by Korth (1979). As previously noted by Reeder (1956), Lindsay (1972), and Sutton (1977), the genus *Cupidinimus,* represented by the single species *C. nebraskensis,* and at least some of the eight species referred to *Perognathoides,* are nearly indistinguishable in dental morphology. Characters which have been used to distinguish these species were found to be variable as larger samples became available. Thus, Korth (1979) proposed formal synonymy of *Perognathoides* and several other species referred to other genera with *Cupidinimus.*

C. boronensis is typical of this expanded *Cupidinimus* species complex with high-crowned teeth which retain individual cusps until moderate wear. It is unique in combining large size, length (anteroposterior) of P_4 much less than M_1 (a *Perognathus*-like character), high-crowned teeth, relatively unreduced M_2, reduced $M^3{}_3$, and dP_4 with central mure and no hypostylid (*C. halli–C. madisonensis* characters), with a lack of accessory cusps on $P^4{}_4$, a wide metaloph on P^4 compared to M^1, a reduced anterior cingulum on M_1, and dP_4 with large anteroconid connected to central mure (*C. nebraskensis* characters).

C. boronensis is higher crowned than the perognathines *Mookomys, Perognathus,* and *Trogomys.* It is also higher crowned than most species of the heteromyines *Peridiomys* Matthew, 1924, and *Proheteromys* Wood, 1932. These and the higher crowned heteromyine *Diprionomys* Kellogg, 1910, are further distinguished by the "J" wear pattern in the P^4 with the first union of lophs lingually between the protocone and hypostyle. *C. boronensis* is smaller, lower crowned, and lacks the labial connection of protoloph and metaloph in the P^4 of *Mojavemys* Lindsay, 1972, and other geomyines.

C. boronensis is closest in size to *C. halli* and *C. madisonensis* (= *C. halli* according to Lindsay, 1972, but considered distinct by Sutton, 1977, a view I will follow). The molars are as large as or larger than those of *C. halli* and *C. madisonensis. C. boronensis* also differs from these species as follows: 1) the roots are less fused, 2) the length of P_4 is less in comparison to the width of the metalophid and length of M_1, 3) the P^4 lacks an anteroconid, and the connection of protoconid and protostylid is central rather than posterior, 4) the relative shortness of the P_4 is similar to the condition in *Perognathus* and *Trogomys,* in contrast to other species of *Cupidinimus* in which this is the longest tooth in the lower tooth row, 5) the anterior cingulum of *C. boronensis* is smaller and less angular in both M_1 and M_2, connecting only to the protostylid, not the protostylid and metaconid, 6) the hypostylid is lacking in 2 of 12 specimens of M_1, 7) the P^4 lacks accessory cusps on the protocone, the hypocone is less posterior relative to lateral cusps, the hypostyle and posterior cingulum are smaller, and the metalophid is wider relative to the width of M^1, 8) the M^1 lacks a posterior cingulum and the protolophule between protocone and paracone is smaller, 9) compared to specimens referred to *C. halli* by Lindsay (1972), the dP_4 is much lower crowned with a larger anterolabial cingulum, smaller anteroconid, no hypostylid, and a weaker central mure (except that it is fully connected to anteroconid), and 10) the dP^4, even though unworn, is lower crowned, lacks a connection between hypostyle and protocone and has a labial connection between the protoloph and anterocone.

C. boronensis is 18–20 percent larger than *C. nebraskensis* from the type area (Korth, 1979) and the sample from the Barstow Formation (Lindsay, 1972). It resembles the sample from the Barstow Formation in lacking the anteroconid on P_4, but this character is variably developed in the topotypic sample from the Valentine Formation. *C. boronensis* lacks the relative reduction of the M_2 found in *C. nebraskensis* but has a proportionally more reduced M_3.

C. boronensis differs from species of *Cupidinimus* previously referred to *Perognathoides, C. cuyamensis, C. kleinfelderi* (Storer, 1970), and *C. bidahochiensis,* by lacking accessory cusps in the premolars variously developed in all these and differs further from *C. bidahochiensis* by much smaller size. *C. boronensis* also differs from *C. kleinfelderi,* known only from isolated premolars, by lacking an anteriorly drawn out protolph(id) compared to metaloph(id) on $P^4{}_4$.

The types of *C. eurekensis* (Lindsay, 1972), *C. quartus* (Hall, 1930), and *C. tertius* (Hall, 1930), all previously referred to *Perognathoides,* have highly worn teeth which lack diagnostic characters that would facilitate comparison with *C. boronensis,* but *C. eurekensis* is considerably smaller and *C. quartus* and *C. tertius* are larger.

C. boronensis differs from four other species referred to *Cupidinimus* by Korth (1979), a sample of *C.* cf. *C. tertius* from the Avawatz Formation (Wilson, 1939), *C.* cf. *C. cuya-*

Table 3. Selected measurements of *Merychyus* cf. *M. minimus* and ?*Merychyus* sp. from the Boron Local Fauna. Abbreviations: AP = anteroposterior dimension of tooth, TR = width of tooth at anterior loph(id), CH = crown height at mesostyle in uppers, at metaconid in lowers, * = approximate.

	Merychyus cf. *M. minimus*				?*Merychyus* sp.
Skull	**UCR 10319**	**UCR 10320**	**UCR 10321**	**UCR 10322**	**UCR 10331**
Facial length, C to anterior rim orbit	52.8	51.1			54*
Jugal depth below orbit	13.2	12.8			17.7
Length P^1–P^4	30.0	30.8			33*
Length M^1–M^3	38.0				44.7
Length C–M^3	74.3				—
P^2 AP	7.8			8.0	7.8
TR	6.0			6.8	6.6
P^3 AP	8.1	9.6		8.2	9.2
TR	7.6	8.0		7.1	7.5
P^4 AP	7.4	7.3			7.2
TR	9.2	8.6			10.1
CH	10.4				7.6
M^1 AP	—	11.0	12.8		11.5
TR	—	11.1	10.8		11*
CH	—	9.1	10.5		—
M^2 AP	13.5	15.4	—		13.4
TR	11.0	12.5*	—		13.8
CH	—	12.6	—		—
M^3 AP	18.0				21.0
TR	13.0				14.0
CH	14.7				8.9
Length dP^2–dP^4		25.7	26.8		
Length dP^2			7.4		
Length dP^3		8.7	10.1		
Length dP^4		8.7	9.4		

	Merychyus cf. *M. minimus*		?*Merychyus* sp.	
Dentary	**UCR 10323**	**UCR 10325**	**UCR 10332**	**UCR 21270**
Mandible depth below P$_2$	22.6	17.1	24.5	
Length of symphysis	33.8	22.0	32.3	
Length C–M$_3$	79.8		80.1	
Length P$_1$–P$_4$	31.9		29.5	
Length M$_1$–M$_3$	44.2		47.0	
M$_2$ AP	12.6		12.9	
TR	8.0		8.2	
CH	5.5		8.7	
M$_3$ AP	19.8		23*	21.5
TR	8.9		8.8	8.9
CH	—		17.0	
Length dP$_2$–dP$_4$		31.8		

mensis from the Valentine Formation (Klinginger, 1968), a sample referred to as "*Prodipodomys*" ? *mascallensis* (Downs, 1956), from the Quartz Basin in Oregon (in Shotwell, 1967), and *C. saskatchewanensis* (Storer, 1975), by lacking accessory cusps on the premolars. *C. boronensis* is close in size to the Quartz Basin *C. mascallensis* and otherwise similar except that the connection of the protoloph and metaloph in P^4 is lingual rather than central in *C. mascallensis*. *C. boronensis* is also similar in size to *C. saskatchewanensis*, but the latter is lower crowned and the protolophid of its P$_4$ is relatively anteriorly drawn out as in most species of *Cupidinimus*.

C. boronensis is conservative among species of *Cupidinimus* in lacking development of accessory cusps on the premolars. It is even larger than Barstovian species, in contrast to an apparent general trend of size increase from Barstovian to Hemphillian. Although larger than the common Barstovian *C. halli*, it is lower crowned, more like the much smaller, contemporaneous and longer surviving *C. nebraskensis*. This combination of characters would suggest that *C. boronensis* is not directly ancestral to either the smaller, higher crowned *C. halli* or the smaller *C. nebraskensis*. It may represent a separate lineage that increased in size early or, by reversal of the size increase, gave rise to *C. nebraskensis* or similar species.

C. boronensis could easily be derived from any perognathine by a significant increase in crown height and a reduction of cingula. *Trogomys* was suggested as a likely ancestor to the *C. halli*/*C. nebraskensis* complex in the Barstow Formation by Lindsay (1972). *C. boronensis* is much higher crowned and has much reduced cingula compared to the type of *Trogomys*, and it is only separated from the latter by a short geologic interval. However, *Trogomys* is the most likely candidate among the perognathines.

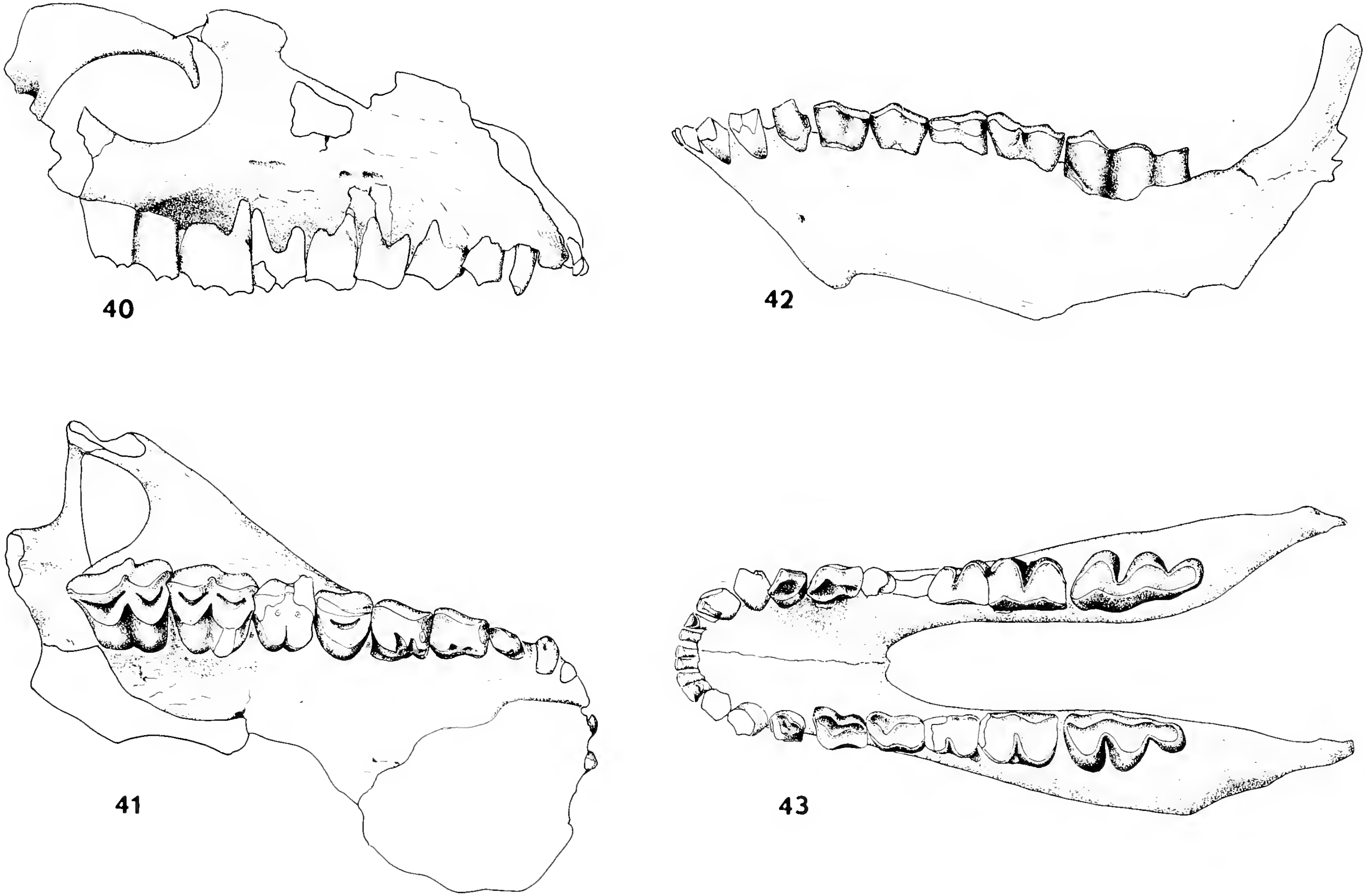
C. boronensis is the earliest species in the *Cupidinimus* species group and the only Hemingfordian representative of this successful group. In general, Hemingfordian heteromyids are poorly known, and as such, *C. boronensis* provides a rare look at these small rodents in the time span between Arikareean faunas dominated by pleurolicine, primitive-perognathine, and *Proheteromys* spp. heteromyid assemblages and Barstovian faunas dominated by *Cupidinimus* spp. and advanced-perognathine heteromyid assemblages.

Order Artiodactyla

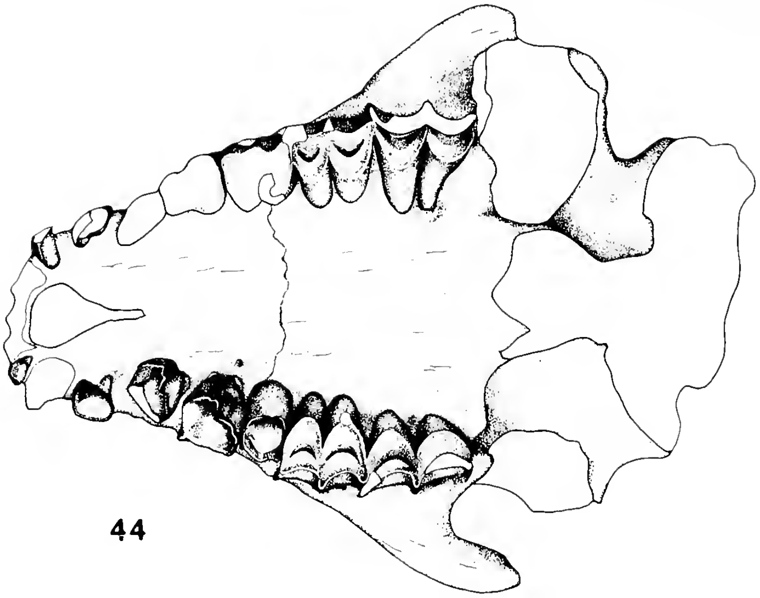
The artiodactyls are represented by three families, oreodonts, camels, and palaeomerycids. More than half the specimens are juveniles, making positive identifications difficult in some cases.

The oreodonts, represented by one or more small, subhypsodont species, are more common than the camels. Oreodont taxonomy is in need of revision and the material from Boron sheds little light on this vexing problem. Taxonomy used follows Schultz and Falkenbach (1947) and Stevens (1977).

As is typical of Miocene faunas, the Boron Local Fauna contains at least three camel taxa. Most of the material is



Figures 40–43. *Merychyus* cf. *M. minimus.* **Figures 40–41,** UCR 10319, partial cranium with right facial region, RI^{1-3} (roots only) and $RC–RM^3$; **(40)** lateral view, **(41)** occlusal view. **Figures 42–43,** UCR 10323, lower mandible with complete dentition; **(42)** left lateral view, **(43)** occlusal view. All actual size.



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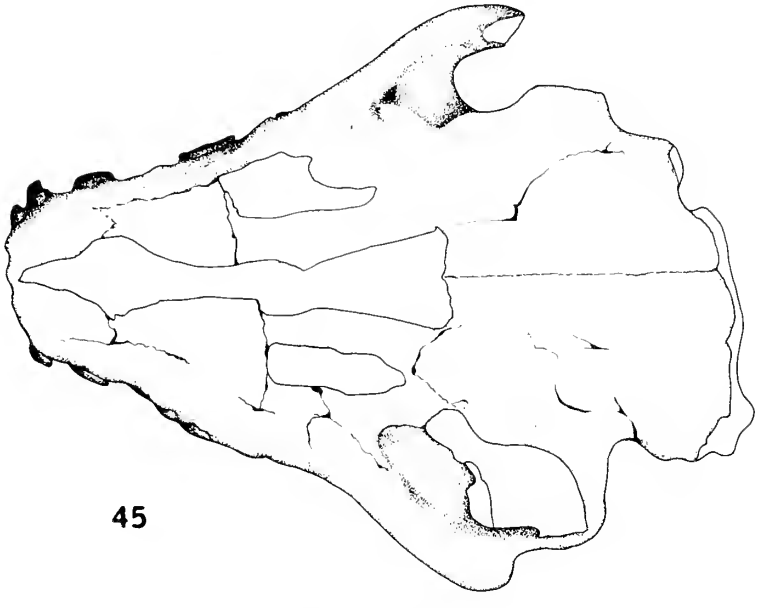

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Figures 44-45. *Merychyus* cf. *M. minimus*, UCR 10320, juvenile cranium with C, P^1, LdP^{3-4}, M^{1-2}, unerupted RP^{2-4} exposed by removing deciduous right premolars; (**44**) dorsal view, (**45**) occlusal view. All actual size.

poorly preserved. Only two species are represented by partial dentitions (one only by juvenile dentition) and associations with postcranial elements have been made on size alone. Thus, only one camel is tentatively identified at the generic level. The other two cannot even be confidently assigned to subfamily level. The taxonomy follows Macdonald (1949), Webb (1965), and Honey and Taylor (1978); osteological terminology follows Webb (1965).

The unique artiodactyl in the Boron Local Fauna is a new species of hypsobrachyodont aletomerycine palaeomerycid. Whereas palaeomerycids are relatively uncommon in fossil assemblages of the Great Basin and southern California when compared to other artiodactyls, this species is the most abundant large animal at Boron and is exceeded in numbers of specimens only by *Cupidinimus boronensis.* Palaeomerycid taxonomy is traditionally based on the orbital horns common in this group. The new species from Boron is represented by one horn fragment, but, in this case, the more diagnostic characters are in the dentition. This new species is noteworthy because it is the first well-documented aletomerycine found west of the Rocky Mountains, thus demonstrating a broader distribution than previously recognized for these small, hypsobrachyodont "horned ruminants." Dental terminology used is given in Figure 50 and taxonomy follows Frick (1937).

Family Merycoidodontidae

Subfamily Merychyinae

Merychyus Leidy, 1858

Merychyus minimus Peterson, 1906

Merychyus cf. *M. minimus*

Figures 40–45, Table 3

MATERIAL. Fragment of cranium with right orbit and facial region, RI$^{1-3}$ (roots only), and RC–M^3, UCR 10319; juvenile cranium lacking posterior portion behind orbits, with moderately worn C, P^1, dP$^{3-4}$, M$^{1-2}$, and unerupted P$^{2-4}$ exposed on right side, UCR 10320; juvenile palate with well worn dI$^{1-3}$, dC, P^1, dP$^{2-4}$, and slightly worn M$^{1-2}$, UCR 10321; partial left maxilla with moderately worn I^3, C, P$^{1-3}$, UCR 10322; isolated LM^3, UCR 21185; mandibular fragment with complete dentition, lacking ascending ramus, angle and condyles, UCR 10323; natural mold of right dentary with condyle, P$_4$–M$_3$, UCR 10324; juvenile mandible with partially erupted P$_1$ slightly worn dC, dP$_{1-3}$, and M$_1$, UCR 10325; unworn LM$_1$ in maxilla fragment, UCR 10326.

DESCRIPTION. Size (based on length of upper tooth row) slightly larger than average *Merychyus crabilli* Schultz and Falkenbach, 1947, and *Merychyus calaminthus* Jahns, 1940, within size range of average *Merychyus minimus;* skull with shallow antorbital fossa and narrow lacrimal vacuity; jugal shallow; orbit large; two infraorbital foramina with posterior one above P^4; dentition sub-hypsodont (ratio of height of enamel of paracone of M^3 to width of M^3 = 0.9); molars appear narrow in relation to length even in late wear giving teeth less robust appearance than typical in oreodonts; premolars large; ratio of length of P$^{1-4}$ to length of M$^{1-3}$ = 0.81 (premolar diameter of Stevens, 1977); premolars lacking complexity of spurs typical in *Merychyus* (*Metoreodon*) *relictus* Matthew and Cook, 1909; upper premolar spacing closed but not crowded; lower premolar spacing somewhat open; anterior margins of P$^{1-3}$ slant backward; upper C and P$_1$ not enlarged.

DISCUSSION. Historically, oreodont taxonomy has been based on samples of complete skulls. The fragmentary material from Boron does not permit such an analysis, and the study is further complicated by the large amount of juvenile material. Oreodonts appear to be evolutionarily conservative in dental characters. Even generic and subfamily differences are difficult to distinguish using only the dentition and there is little agreement among workers on evolutionary lineages. *Merychyus* cf. *M. minimus* from Boron is assignable to the genus *Merychyus* on the basis of the large orbit, presence and size of facial fossa and prelacrimal vacuity, relatively high-crowned teeth with large, posteriorly inclined upper premolars, and small upper C and P$_1$ (P$_1$ is the lower caniniform tooth in oreodonts).

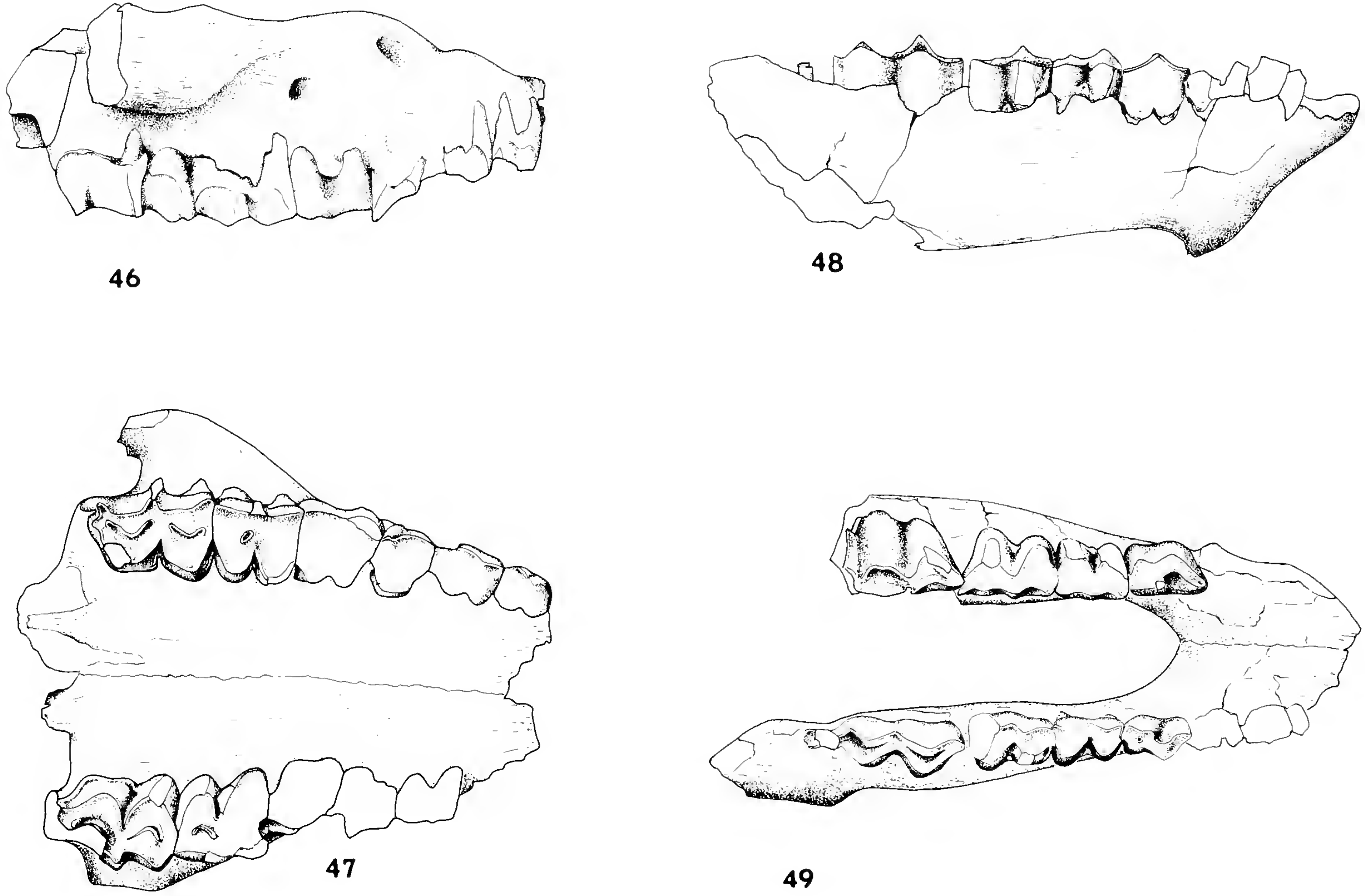
Based on length of upper dentition, the Boron species is 15 percent smaller than *M.* (*Metoreodon*) *relictus* but only 3 percent smaller than *M.* (*Metoreodon*) *relictus fletcheri* Schultz and Falkenbach, 1947, from the Barstow Formation. The subgenus *Metoreodon,* based on *M.* (*Metoreodon*) *relictus,* is distinguished from the subgenus *M.* (*Merychyus*) primarily by its more complex and crowded premolars, P$_{2-4}$ well grooved externally, P$_{1-3}$ set obliquely in the jaw, teeth higher crowned, and several other skull characters not preserved in the Boron sample. *Merychyus* cf. *M. minimus* from Boron has a shallow lacrimal fossa and fairly high crowned teeth, but it lacks the premolar complexity and crowding typical of *M.* (*Metoreodon*).

The length of the upper dentition of the Boron *Merychyus* is 25 percent smaller than *Ticholeptus calimontanus* (Dougherty, 1940), from the Temblor Formation, but it is as high crowned. The genus *Ticholeptus* Cope, 1878, although placed in a different subfamily, is very similar to *Merychyus,* but differs by having a proportionally smaller orbit, a deeper jugal, larger upper canine and P$_1$, and more anterior infraorbital foramen above P$^{3-4}$.

Merychyus cf. *M. minimus* from Boron is larger and more hypsodont than *M. calaminthus* (type series) and material referred to *M. calaminthus* from the type area of the Hector Formation (specimen UCR 10914—Woodburne et al., 1974), a specimen from the Hector Formation in the northern Cady Mountains (specimen UCR 10840—Miller, 1980) and a specimen from the Orocopia Mountains (specimen LACM 27026—Woodburne and Whistler, 1973). In overall size, the Boron material falls between *M. calaminthus/M. crabilli* and *M. minimus* but it is closer to the latter. Stevens (in Woodburne et al., 1974:19) has suggested that *M. calaminthus* and *M. crabilli* are the same species, a suggestion she reaffirmed in a later work (Stevens, 1977:37), but stopped short of proposing a formal synonymy, thus they are considered distinct in this study.

Stevens (1977) has suggested two evolutionary trends in *Merychyus*—decrease in "premolar diameter" (the ratio of the length of the P$^{1-4}$ to the length of M$^{1-3}$) and an increase in hypsodonty. The material from Boron (especially UCR 10319) has large premolars that are less reduced than in *M. calaminthus* or *M. crabilli,* but has cheek teeth that are more hypsodont than even higher crowned individuals of *M. minimus* and *Merychyus elegans* Leidy, 1858. The jugal depth (as a ratio of tooth row length) is shallow, more similar to that of *M. calaminthus* and *M. crabilli* than that of *M. minimus* or *M. elegans.*

Merychyus cf. *M. minimus* from Boron appears distinct from *M. calaminthus* and *M. crabilli,* but it falls within the



Figures 46–49. ?*Merychyus* sp. **Figures 46–47,** UCR 10331, adult palate with well worn P^2–M^3 and part of right side of face; **(46)** right lateral view, **(47)** occlusal view. **Figures 48–49,** UCR 10332, lower mandible with alveolus of I_{1-3}, partially complete C, P_{1-3}, complete P_4–M_3; **(48)** right lateral view, **(49)** occlusal view. All actual size.

Table 4. Selected measurements of cf. *Hesperocamelus* sp. and an indeterminate species of small camel from the Boron Local Fauna. Abbreviations: AP = anteroposterior dimension of tooth, TR = width of tooth at anterior loph(id), * = approximate.

		cf. *Hesperocamelus*		Camelidae, small sp.	
		UCR 10366	UCR 10367	UCR 10365	
Width palate, anterior end P^2		27.3			
Length P^2–M^3		115*		Length dP_2–M_1	47.0
P^2	AP	9.0		M_1 AP	16.2
	TR	L6.1, R6.3		TR	6.2
P^3	AP	L16.0, R16.5		Length dP_2	5.9
	TR	9.8		Length dP_3	9.0
M^1	AP	19.6		Length dP_4	16.8
	TR	16.3			
M^2	AP	L27.7, R27.7			
	TR	L21.1, R22.0			
M^3	AP	29.3*			
	TR	23.5*			
M_3	AP		29.9		
	TR		10.0		
Width distal radioulna		50.9 (UCR 10384) 47.7 (UCR 10385)		35.0 (UCR 10374)	
Width proximal metacarpal				31.3 (UCR 21189)	
Width distal tibia		42.0 (UCR 10339) 42.0 (UCR 10387) 37.0 (UCR 10388)		34.0 (UCR 10371)	
Width proximal metatarsus				27.9 (UCR 10376)	
Length calcaneum		117.7 (UCR 21186)		69* (UCR 10379)	
Length astragalus		48.0 (UCR 10392)		36.8 (UCR 10378)	

considerable range of variation of *M. minimus* in many characters. *Merychyus* cf. *M. minimus* from Boron is probably distinct from *M. minimus,* but larger samples and more completely preserved material are needed before this can be conclusively demonstrated.

?*Merychyus* sp.

Figures 46–49, Table 3

MATERIAL. Adult palate with well-worn P^2–M^3 and part of right side of face, UCR 10331; lower mandible bearing alveolus of I_{1-3}, partially complete C and P_{1-3}, complete P_4–M_3, UCR 10332; fragment of left dentary with P_4–M_1, UCR 10333, fragment of right dentary with M_3, UCR 21270.

DESCRIPTION. Size similar to *Merychyus* cf. *M. minimus* described above; jugal deep; infraorbital foramen above posterior root of M^1, suggesting a shorter face; upper molars broad; M^3 with split metastyle and prominent posterior cingulum on metaconule; ratio of length of P^{1-4} to length of M^{1-3} approximately 0.73, considerably smaller than the *Merychyus* cf. *M. minimus* described above; lower premolars crowded, P_3 10 percent larger and more complex than *Merychyus* cf. *M. minimus* described above.

DISCUSSION. Although these three specimens may simply be larger, shorter faced, more robust individuals of *Merychyus* cf. *M. minimus* described above, they are separated because of the more robust teeth, deep jugal, and large P_3. Specimen UCR 10322 is a young adult which may account for the crowding of the lower premolars. The infraorbital foramen is clearly more posteriorly located than in the three specimens of *Merychyus* cf. *M. minimus* described above, suggestive of the condition found in species of *Brachycrus* Matthew, 1901. None of the Boron specimens preserves the nasal region of the cranium which is diagnostic of *Brachycrus.* The split metastyle and strong posterior cingulum of M^3 and jugal depth are variable characters in oreodonts (Lander, personal communication). The jugal, although deep for species of *Merychyus,* is nowhere near as deep as in *Brachycrus,* but is similar to species referred to *Ticholeptus.* The Boron specimens are much smaller than any species of *Brachycrus,* but only slightly smaller than some specimens referred to *Ticholeptus calimontanus.*

These three specimens may be variants of the associated *Merychyus* cf. *M. minimus,* but there is more difference between them and the *Merychyus* cf. *M. minimus* than between the latter and *M. minimus* from Nebraska. Thus, they are considered distinct until larger samples are available to more clearly demonstrate individual variation. There is some suggestion of convergence with features characteristic of both *Brachycrus* and *Ticholeptus.*

Family Camelidae

Subfamily Aepycamelinae

Hesperocamelus Macdonald, 1949

cf. *Hesperocamelus* sp.

Table 4

MATERIAL. Palate with RP^{1-2}, RM^2 and part of RM^3, LP^{2-3}, LM^{1-3}, isolated ? upper incisor, UCR 10366; LM_3, UCR 10367; posterior portion, RM_3, UCR 10368; associated left distal radioulna, scaphoid and lunar, UCR 10384; distal epiphysis, left radioulna, UCR 10385; right distal tibia, UCR 10388; two left distal tibiae, UCR 10387 and UCR 10389; left astragalus, UCR 10392; left calcaneum, UCR 21186; left proximal metacarpal, UCR 21187; right proximal metatarsal, UCR 21188; proximal phalanx, UCR 10391.

DESCRIPTION. Size (length of dentition from P^1 to M^3) larger than the aepycamelines *Oxydactylus* Peterson, 1904, and *Paratylopus* Matthew, 1904, the camelines *Dyseotylopus* Stock, 1935, and *Priscocamelus* Stevens, 1969, and most protolabines; about same size as the aepycameline *Hesperocamelus alexandrae* (Davidson, 1923); smaller than smallest species of *Aepycamelus* Macdonald, 1956; rostrum fairly narrow at anterior root of P^2 but not constricted as in protolabines; teeth relatively low crowned with 80–90 percent of external enamel of paracone of M^3 exposed when this tooth enters occlusion; premolars large in comparison to molars; P^1 large, blade-like, two rooted; P^2 long, blade-like, with weak, discontinuous lingual cingulum; P^3 long, parastyle large, lingual cingulum well developed, with distinct central gap; M^{1-3} with weak, but distinct vertical ribs on paracone, ribs nearly lacking on metacone, metastyle and parastyle strong; M^3 not elongated anteroposteriorly compared to M^1; M_3 with strong metastylid and reduced hypoconulid; metacarpals and metatarsals fused; calcaneum long and slender.

DISCUSSION. Camel taxonomy is usually based on associated skulls and postcranial material. Tentative association of the palate UCR 20366 with some of the postcranial material provides for a composite picture of this medium sized camel. The palate is broken anterior to the P^2 so that the degree of palatal constriction and length of the rostrum are lacking (key characters in distinguishing protolabines from aepycamelines). Although the palate is fairly narrow between the anterior roots of the P^2, these teeth are not turned inward anteriorly as is typical in protolabines.

The premolars are unreduced and large in comparison to the molars, a feature typical of many Early Miocene camels, but they lack the robustness typical of *Miolabis* Hay, 1899 (Aepycamelinae). The large, blade-like P^1 is similar to that of most protolabines and aepycamelines, but P^1 in *Hesperocamelus* is typically more caniniform. The P^2 in the cf. *Hesperocamelus* sp. from Boron is larger in comparison to the other cheek teeth than in most protolabines or aepycamelines. The P^3 is also large. The discontinuous lingual cingulum of the P^3 is a variable character but is similar to the primitive protolabine *Michenia* Frick and Taylor, 1971, and *Hesperocamelus.* The crown of P^4 is missing on both sides of the palate.

The molars are low crowned as is characteristic of aepycamelines and most protolabines and in contrast to the higher crowned cameline *Procamelus* Leidy, 1858, and the notably high-crowned stenomylines (Frick and Taylor, 1968). The vertical ribs on the paracone and metacone are more reduced than those of the primitive protolabines *Michenia* and *Tanymykter* Honey and Taylor, 1978, and the primitive aepycamelines *Oxydactylus* and *Miolabis.* They are more like those of stenomylines and the more derived aepycamelines *Hesperocamelus* and *Aepycamelus.* However, the strong mesostyle is more like that of *Michenia, Tanymykter,* and *Oxydactylus.* The M^3 is not anteroposteriorly lengthened in relation to the length of the M^1 as is common in many derived protolabines. Two isolated M_3's bear relatively strong metastylids which are typical of most protolabines and aepycamelines, otherwise these referred specimens provide little additional information.

Fragments of a fused metacarpal and fused metatarsal occur in the fauna, but neither are complete enough to obtain an estimate of their length. The degree of fusion distinguishes this Boron material from *Miolabis, Paratylopus,* most species of *Oxydactylus* and all species of *Michenia* except *M. exilis* (Matthew, 1960) all of which have unfused metapodials. There is one partial calcaneum which is quite long and slender, a condition common in stilt-legged (aepycameline) camels.

In most observable characters, cf. *Hesperocamelus* sp. from Boron is not clearly distinguishable from early protolabines (*Michenia, Tanymykter*) or early aepycamelines (*Oxydactylus*). As clearly pointed out by Honey and Taylor (1978: 377), it is difficult to distinguish these taxa on cheek teeth alone. However, the Boron cf. *Hesperocamelus* sp. seems to lack the restricted rostrum characteristic of all protolabines and it is larger than any species of *Oxydactylus.* Thus, it is referred to the larger aepycameline with fused metapodials, *Hesperocamelus.* Except for the blade-like P^1 and slightly smaller size, it closely resembles *Hesperocamelus alexandrae* from the Barstow Formation.

Subfamily undetermined

Camelidae, small species

Table 4

MATERIAL. Juvenile dentaries with LdP_{2-4}, RdP_4, RM_1, and LM_1, UCR 10365; proximal right metacarpals III and IV, UCR 21189; proximal right metatarsal, UCR 10376; proximal right scapula, UCR 10370; proximal end right radioulna, UCR 10371; proximal end left radioulna, UCR 10372; proximal articular facet right radioulna, UCR 10373; distal epiphysis right radioulna, UCR 10374; right lunar UCR 21190; right entocuneiform, UCR 10382; distal left tibia, UCR 10377; right malleolus, UCR 21191; right juvenile calcaneum, UCR 10379; right astragalus, UCR 10378; two right cuboids, UCR 10393 and UCR 10394; right navicular, UCR 10395; proximal end, proximal phalanx, UCR 10381.

DISCUSSION. This small camel is represented by a pair of juvenile dentaries with the M_1 the only erupted permanent tooth and with the dP_{3-4} moderately worn. The specimen is broken at the symphysis, but there is an alveolus for a large P_1. Additional small, postcranial camelid elements may also belong to this taxon. One fragment represents the proximal ends of metacarpals III and IV which are closely appressed but unfused; a fragment of the proximal end of the metatarsal is fused.

The material is too incomplete to permit even a subfamilial assignment, but clearly demonstrates the presence of a small camel in the fauna. Based on postcranial elements, this is the most common camel. This small camel could be any of several protolabines that are common in Miocene assemblages of the western United States or a species of *Oxydactylus. Priscocamelus* or *Paratylopus,* all less common.

Camelidae, large species

DISCUSSION. A large camel is represented by a left distal femur fragment, UCR 10386, and a left proximal scapular fragment, UCR 10383. These specimens suggest an animal about half again as large as the species referred to cf. *Hesperocamelus* sp. They could represent one of several small species of *Aepycamelus* which are common in Miocene assemblages of the Great Basin.

Family Palaeomerycidae

Subfamily Aletomerycinae

Aletomeryx Lull, 1920

***Aletomeryx occidentalis* new species**

Figures 51–59, Table 5

HOLOTYPE. UCR 10335, partial young adult right dentary with P_2 (natural cast in part) and complete P_3 through M_3.

TYPE LOCALITY. UCR locality RV 6421 (see complete description under *Cupidinimus boronensis* above).

REFERRED MATERIAL. Portion of right frontal and horn base, UCR 10348; partial left dentary with I_2, well worn P_2–M_2 and roots for I_1, I_3, and C, UCR 10336; partial right dentary with little worn P_2–M_2, UCR 10337; partial subadult right dentary with dP_2, unworn P_3–M_2, UCR 10338; fragment of right dentary with moderately worn M_{2-3}, UCR 10339; fragment of right dentary with moderately worn M_1, UCR 10340; partial right juvenile dentary with symphysis, early wear dP_{2-4}, M_1, UCR 10341; partial right juvenile dentary with early wear dP_{2-4}, M_1 UCR 10342; partial left juvenile dentary with early wear dP_{2-4}, UCR 10343; partial right maxilla with early wear M^{1-3}, UCR 10344; partial young adult right maxilla with alveolus for P^{1-2}, partially complete P^4 and M^{1-2}; UCR 10345; isolated fragment LdP^2, UCR 10347; isolated fragment $?RP^2$, UCR 10398; left proximal scapula, UCR 10352; two right distal humeri, UCR 10356 and UCR 10357; left proximal radius, UCR 10351; distal half right radioulna, UCR 10349; associated distal end left radioulna, scaphoid, lunar, unciform, fused magnum-trapezoid, proximal metacarpal, UCR 10350; left cuneiform, UCR 21192; associated right tibia lacking proximal articulation, astragalus, calcaneum, naviculocuboid, entocuneiform, and proximal fused metatarsals III and IV, UCR 21193; four left distal tibiae, UCR 10358, UCR 10359, UCR 10360, and UCR 10364; right calcaneum, UCR 10361; associated left naviculocuboid, entocuneiform, fused metatarsals III and IV, vestiges of metatarsus II and V, UCR 10355; two left naviculocuboids, UCR 10362 and UCR 10363; left entocuneiform, UCR 10354; proximal phalanx UCR 21194.

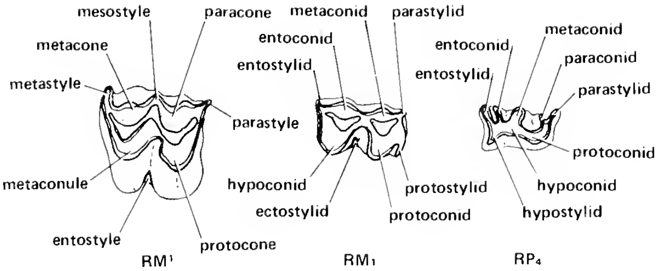


Figure 50. Tooth cusp terminology used in *Aletomeryx*.

DIAGNOSIS. Slightly larger (1.5 percent) than *Aletomeryx marslandesis* Frick, 1937, the largest species of *Aletomeryx*, but smaller (about 2 percent than the smallest species of *Sinclairomeryx* Frick, 1937; horn *Aletomeryx*-like, situated over posterior part of orbit with slight forward tilt; dentition hypsobrachyodont; P_2 large for species of *Aletomeryx;* premolars with simple pattern compared to common palaeomerycids such as *Dromomeryx* Douglass, 1909, but more complicated pattern than that of described species of *Aletomeryx;* lower premolars with relatively straight crests and lacking expanded metaconid; posterior labial corner (hypostylid) of P_{3-4} expanded into distinct cuspid that connects to hypoconid by short crest in moderate wear; labial end of central crest (metaconid) slightly expanded anterolabially in P_4 but much less developed than in dromomerycines and giraffids; opening of lingual flexids of P_4 not directed posteriorly as in dromomerycines; M_{1-2} with well-developed anterior cingula and anterolabial buttresses which join in wear; hypoconulid of M_3 formed by closed lingual crescent or crescent in combination with smaller lingual cusp; post-symphysial diastema short; limbs lightly constructed, proximal ends of metatarsals II and V retained as vestiges.

ETYMOLOGY. From *occidentalis* Latin, of the west, in reference to the occurrence of this species in far western range of distribution of the genus.

DESCRIPTION. Orbital Horn. Single broken pedicel, UCR 10348, situated over posterior portion of orbit, with slight forward tilt and some suggestion of forward curves; external central ridge, leading to postorbital process thinner than in the small species, *Aletomeryx gracilis* Lull, 1920; cross section of horn pedicel at base broadly triangular in outline; internal surface broadly convex, not flat as *Sinclai-*

Table 5. Selected measurements of *Aletomeryx occidentalis* n. sp. Abbreviations: AP = anteroposterior dimension of tooth, TR = width of tooth at anterior loph(id), CH = crown height at paracone in upper molars, at protoconid in lower premolars, at metaconid in lower molars (figures given only for unworn specimens), * = approximate.

Dentary		UCR 10335	UCR 10336	UCR 10337	UCR 10338	UCR 10339	UCR 10341	UCR 10342	UCR 10343
Length P_2–M_3		75.2	69.0						
Length P_2–P_4		24.0	23.9	27.4	25.0				
Length M_1–M_3		48.8	45.7						
P_2	AP	5.5*	6.4	7.8	7.0				
	TR	3.0*	3.5	3.7	3.5				
P_3	AP	8.4	7.5	9.1	8.0				
	TR	4.8	4.4	4.9	4.7				
	CH			6.7*	7.7				
P_4	AP	9.9	10.0	11.1	10.1				
	TR	6.0	5.2	5.0*	4.5				
	CH			10.2	10.5				
M_1	AP	11.5	9.1	14.0	13.8		13.1		
	TR	7.0	6.2	6.5	6.5		6.2		
	CH						8.6		
M_2	AP	14.2	14.0	16.0	17*	15*			
	TR	8.8	8.0	8.5	8.0	—			
	CH			13.1	11.7				
M_3	AP	20.0	21.7			21.0			
	TR	8.8	8.1			8.4			
	CH	12.2							
Length dP_2–dP_4							28.0	26.6	27.0
dP_2	AP						6*	5.5	5.4
	TR							3.1	2.6*
dP_3	AP						7.0	6.1	8.0
	TR						3.6	4.8	4.0
dP_4	AP						14.4	14.1	12.5
	TR						5.4	5.8	5*

Maxilla		UCR 10344	UCR 10345	UCR 10347
Length P^2–M^2			58*	
Length P^2–P^4			28*	
P^2	AP			7.5
	TR			4.6
P^4	AP		9.1	
	TR		9.5*	
M^1	AP	12*	14.1	
	TR		11.2	
M^2	AP	14.6	18.0	
	TR	14.0	14.2	
	CH		15.0	
M^3	AP	14.8		
	TR	14.6		
	CH	12.0		

Table 5. Continued.

Axial skeleton	UCR 10349	UCR 10350	UCR 10356	UCR 10357
Width distal humerus			25.0	23.3
Width distal radioulna	22.8	21.4		
Width proximal metacarpal		18.3		

	UCR 10355	UCR 10358	UCR 10360	UCR 10361	UCR 10362	UCR 10363	UCR 10364	UCR 21193
Width distal tibia		23.8	23.5				23.0	21*
Width naviculocuboid	20.0				19.0	21.4		20.6
Length calcaneum				54.6				51*
Length astragalus								23.8
Width prox. metatarsal	20.0							19.0

romeryx; horn pedicel becomes triangular along posterior border above base; two foramina separated by a small bridge of bone present in frontal above orbit; suggestion of third foramen at frontal-lacrimal suture.

Upper Dentition. Enamel more rugose than in lower dentition; styles well developed, but not greatly enlarged; alveolus for P^2 in UCR 10345 suggests broader tooth than in other species of *Aletomeryx;* alveolus for P^3 about same size as in other species of *Aletomeryx* or *Sinclairomeryx;* P^2 in UCR 10398 with well developed lingual cingulum; P^4 only partially preserved, but with fossette divided posteriorly; M^{1-3} with well-developed styles and accessory folds in fossettes; weak anterior cingulum; small pillar (entostyle) in M^{1-2} lacking in M^3.

Upper Deciduous Dentition. dP^2 similar to permanent P^2 with single high labial crest; continuous lingual cingulum around anterior end of tooth with shallow groove below high portion of labial crest (protocone); small spur leading from center of anterior portion of cingulum to base of protocone.

Dentaries and Lower Dentition. Lower jaws lightly built, with slight inward curve in region of symphysis; post-symphysial diastema proportionally shorter than in smaller species of *Aletomeryx;* molars high crowned with less than half the entire crown height of M_3 exposed when this tooth comes into occlusion; enamel lightly rugose; premolars, particularly P_2, less reduced than in other described species of *Aletomeryx* or *Sinclairomeryx.*

I_{1-3} and lower canine all about the same size judging from roots, all directed anteriorly.

P_2 (based on UCR 10327 and UCR 10336) larger, with more complicated pattern than in previously known *Aletomeryx* species; with well-developed anterior cusp (paraconid) that persists in wear; paraconid connected by labial crest to high central cusp (protoconid); separate entoconid and entostylid present in early wear.

P_3 with more complicated cusp pattern than P_2; paraconid and parastylid well developed, becoming more separate near base of crown; protoconid most prominent cusp; entoconid and entostylid well developed with intervening flexid opening more labially than in most *Aletomeryx* species; suggestion of low postero-labial enlargement (hypostylid) which occludes only in late stage of overall tooth wear.

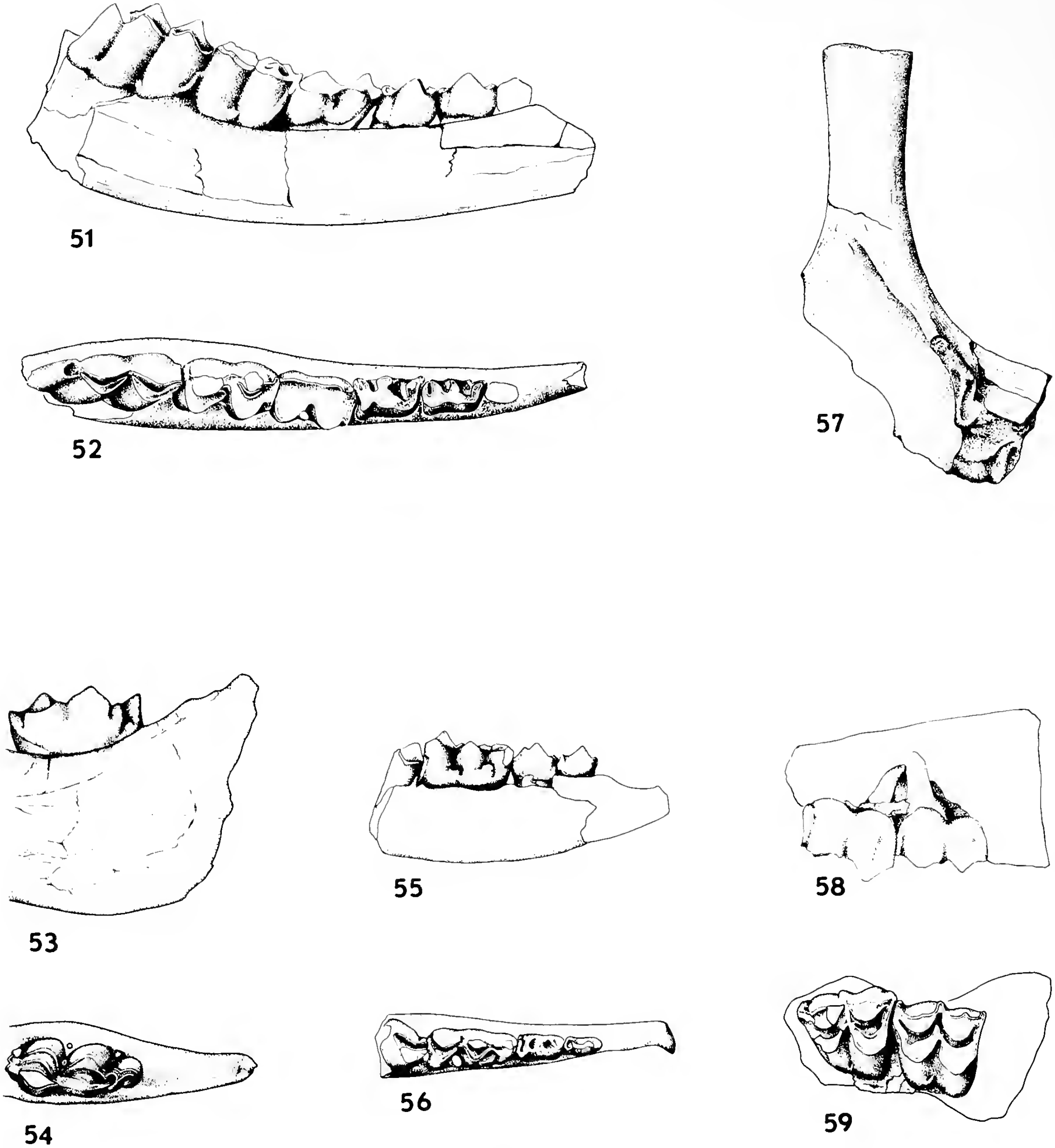
P_4 with separate and distinct paraconid and parastylid; parastylid an isolated cusp in early wear; metaconid beginning as isolated cusp but strongly connected to protoconid by central crest; metastylid absent; posterior portion of P_4 distinctly bifurcate with separate entoconid and entostylid; flexid between entoconid and entostylid opens more posteriorly than in P_3; posterolabial corner (hypostylid) well developed to mid height of tooth crown.

M_1 small in proportion to P_4 compared to other species of *Aletomeryx* or *Sinclairomeryx;* parastylid, anterior cingulum, and anterolabial buttress (protostylid) well developed.

M_2 with well-developed anterior cingulum bearing distinct anterolabial cusp or buttress (protostylid) in unworn tooth, cusp joins cingulum after moderate wear, persists to late wear; suggestion of metastylid present as inflection in enamel in UCR 10337 and UCR 10338, but not persistent in wear; ectostylid developed as small, low pillar; connection between posterior end of entoconid and posterolingual extension of hypoconid (= entostylid) delayed until moderate wear, forming a shallow enamel infolding in posterolingual corner of tooth.

M_3 with hypoconulid formed by completely closed labial loop in the type, UCR 10335, and UCR 10336; UCR 10339 (Figures 47–48) with additional small, lingually projected spur and small lingual cusp; anterior cingulum not as well developed as in M_1 or M_2; ectostylids variably developed between protoconid and hypoconid, hypoconid and hypoconulid.

Lower Deciduous Dentition. dP_2 very similar to the P_2, except with deeper posterior flexid more persistent with wear; dP_3 with better developed paraconid, parastylid, and bifurcation of the anterior cingulum; posterior flexid of dP_3 opening more directly lingually than in P_3, with small cusp in anterior labial corner (protostylid) that forms anteriorly opening flexid after moderate wear; dP_4 three lobed, resembling reversed M_3, but with stronger ectostylids.



Figures 51-59. *Aletomeryx occidentalis* n. sp. **Figures 51-52,** Holotype, UCR 10335, right adult mandible with early wear P_2 (in part natural cast) and complete P_3–M_3; **(51)** labial view, **(52)** occlusal view. **Figures 53-54,** UCR 10339, RM_3; **(53)** lingual view, **(54)** occlusal view. **Figures 55-56,** UCR 10342, juvenile right dentary fragment with early wear RdP_{2-4}, part of M_1; **(55)** labial view, **(56)** occlusal view. **Figure 57,** UCR 10348, right horn fragment. **Figures 58-59,** UCR 10344, RM^{2-3}; **(58)** labial view, **(59)** occlusal view. All actual size.

Limbs. Long and lightly built; front and hind metapodials well fused; principal metatarsal with vestiges of proximal ends of both metatarsals II and V; vestigial metatarsal II elongate, triangular, fused to central metatarsal; vestigial metatarsal V stubby, broad, unfused; vestige of metacarpal II also present as suggested by flattened, rugose area on metacarpal III.

Discussion. The dentition of *Aletomeryx occidentalis* is high crowned, more so than most taxa referred to Palaeomerycidae. The high-crowned teeth and narrow P_{3-4} distinguish *Aletomeryx occidentalis* from all the more deer- or giraffe-like palaeomerycids: *Dromomeryx, Rakomeryx* Frick, 1937, *Cranioceras* Matthew, 1918, *Barbouromeryx* Frick, 1937, *Drepanomeryx* Sinclair, 1915, and *Yumaceras* Frick, 1937, of North America, *Palaeomeryx* Von Meyer, 1834, *Procervulus* Gaudry, 1878, *Heterocemas* Young, 1937, and *Triceromeryx* Villalta, Crusafont and Lavocat, 1946, from Europe and Asia and *Climacoceras* MacInnes, 1936, *Canthumeryx* Hamilton, 1973, and *Propalaeoryx* Stromer, 1926, from Africa. *Aletomeryx occidentalis* is distinguished from the smaller, hornless, North American leptomerycine *Leptomeryx* Leidy, 1853, *Pseudoparablastomeryx* Frick, 1937, and *Pronodens* Koerner, 1940 (see Taylor and Webb, 1976), from the blastomerycines *Blastomeryx* Cope, 1877, and *Machaeromeryx* Matthew, 1926, and from the palaeomerycid *Longirostromeryx* Frick, 1937, by the high-crowned teeth and presence of orbital horns.

Only three palaeomerycids, *Aletomeryx,* "*Dyseomeryx,*" and *Sinclairomeryx,* have high-crowned, antilocaprid-like teeth. The relatively large premolars, particularly P_2, and the greater complexity of P_{3-4}, with a well-developed metaconid on P_4 and hypostylid on P_{3-4}, are characters derived with respect to any previously described species of *Aletomeryx* or *Sinclairomeryx.*

There is little clear distinction between species of *Aletomeryx,* "*Dyseomeryx,*" and *Sinclairomeryx* because many characters overlap. However, the structure of the horn pedicel, the development of the anterolabial buttress and anterior cingulum on M_2, and the hypoconulid crescent of M_3 favor assignment of the Boron species to the genus *Aletomeryx.* Some smaller specimens of *Aletomeryx gracilis* approach the crown height of *Aletomeryx occidentalis,* but these lack the lower premolar complexity.

There is also confusion as to the validity of the generic (or subgeneric) names *Aletomeryx, Dyseomeryx,* and *Sinclairomeryx* within the Subfamily Aletomerycinae. According to Stirton (1944) in his sort discussion of the Family Palaeomerycidae, the genus *Aletomeryx* Lull, 1920, is distinct but the genera (or subgenera) *Dyseomeryx* Matthew, 1924, and *Sinclairomeryx* Frick, 1937, are synonymous, *Dyseomeryx* with priority. He did not thoroughly discuss his reasons for this synonymy, however. On the other hand, Frick (1937) stated that *Dyseomeryx* is in part synonymous with *Aletomeryx.*

Matthew (1924:196) defined the subgenus *Dyseomeryx,* choosing *Blastomeryx marshi* Lull, 1920, as the type, which then became *Blastomeryx* (*Dyseomeryx*) *marshi* (Lull) as recombined by Matthew (1924). But, according to Frick (1937: 152), *Blastomeryx* (*Dyseomeryx*) *marshi* (Lull) actually belongs in the genus *Aletomeryx,* and therefore *Blastomeryx* (*Dyseomeryx*) *marshi* became *Aletomeryx marshi* (Lull) as recombined by Frick (1938). Because Frick (1937) found it necessary to refer the type of the subgenus (*Dyseomeryx*) to *Aletomeryx,* while he considered other forms referred to (*Dyseomeryx*) generically distinct, he defined the new genus *Sinclairomeryx,* naming as the type species *Sinclairomeryx sinclairi* Frick, 1937. Frick also questionably assigned another of Matthew's species, *Blastomeryx* (*Dyseomeryx*) *riparius* Matthew, 1924, to *Sinclairomeryx.* The type of this species is a left maxilla fragment, and certain assignment to *Sinclairomeryx* by Frick would necessitate an associated horn core, which was not present. Based on comparisons of dentitions, later workers (Skinner et al., 1977) have indicated *S. riparius* and *S. sinclairi* are synonymous, with *S. riparius* having priority.

Although I have not reviewed the original material, it would seem that Frick (1937) substantiated his view and I have accepted the genera *Sinclairomeryx* (= *Dyseomeryx* in part) and *Aletomeryx.*

AGE AND BIOSTRATIGRAPHY

RADIOMETRIC CORRELATION

There are three radiometric dates on different outcrops of the Saddleback Basalt: 18.3 ± 0.6 ma, 19.7 ± 0.6 ma (R.B. Kistler, personal communication), and 20.3 ± 0.7 ma (Armstrong and Higgens, 1973). The Saddleback Basalt occurs 146 m below the Boron Local Fauna in the open pit mine and thus these radiometric dates provide a maximum age for the fossil assemblage. Based on biostratigraphic correlations (see below), the Boron Local Fauna is distinctly older than the typical fossil vertebrate assemblages of the Barstow Formation which have a maximum age of at least 16.3 ± 0.3 ma (Woodburne and Tedford, 1982) and the Early Barstovian Dry Canyon fauna of the Caliente Formation dated at 16.5 ± 1.3 ma (Turner, 1970, KA 2127). These dates provide a minimum age for the Boron Local Fauna. On biostratigraphic grounds, the Boron Local Fauna appears close to the Phillips Ranch Local Fauna which is underlain by a 17.6 ma date (Evernden et al., 1964, KA 478). All these form a consistent pattern with the Boron Local Fauna falling between approximately 16.5 and 18.5 ma.

BIOSTRATIGRAPHIC CORRELATIONS

Generally, correlation of southern Californian Arikareean and Hemingfordian faunas with the classical sequence in Nebraska and neighboring states has been difficult because the fossil assemblages in these widely separated areas usually have had little in common. The Boron Local Fauna presents a rare exception to this generality for it contains two taxa very similar to species in Nebraska, *Merychyus* cf. *M. minimus* and *Aletomeryx occidentalis. Merychyus minimus,* restricted to the early Hemingfordian of the central United States, is a quite variable species and *M.* cf. *M. minimus* from Boron falls within this variation. *A. occidentalis,* although distinct at the species level and probably representing a separate lineage from the *Aletomeryx/Sinclairomeryx* lineage in the central United States, is close to *A. marslandensis* from the early Hemingfordian of Nebraska. Taken as a whole, the Boron Local Fauna is best considered early Hemingfordian in age, but probably near the transition to the late Hemingfordian.

Compared to mid-continent assemblages, the Boron Local Fauna is not particularly diverse, and may lack "key" taxa which were not preserved or may not have been present. To

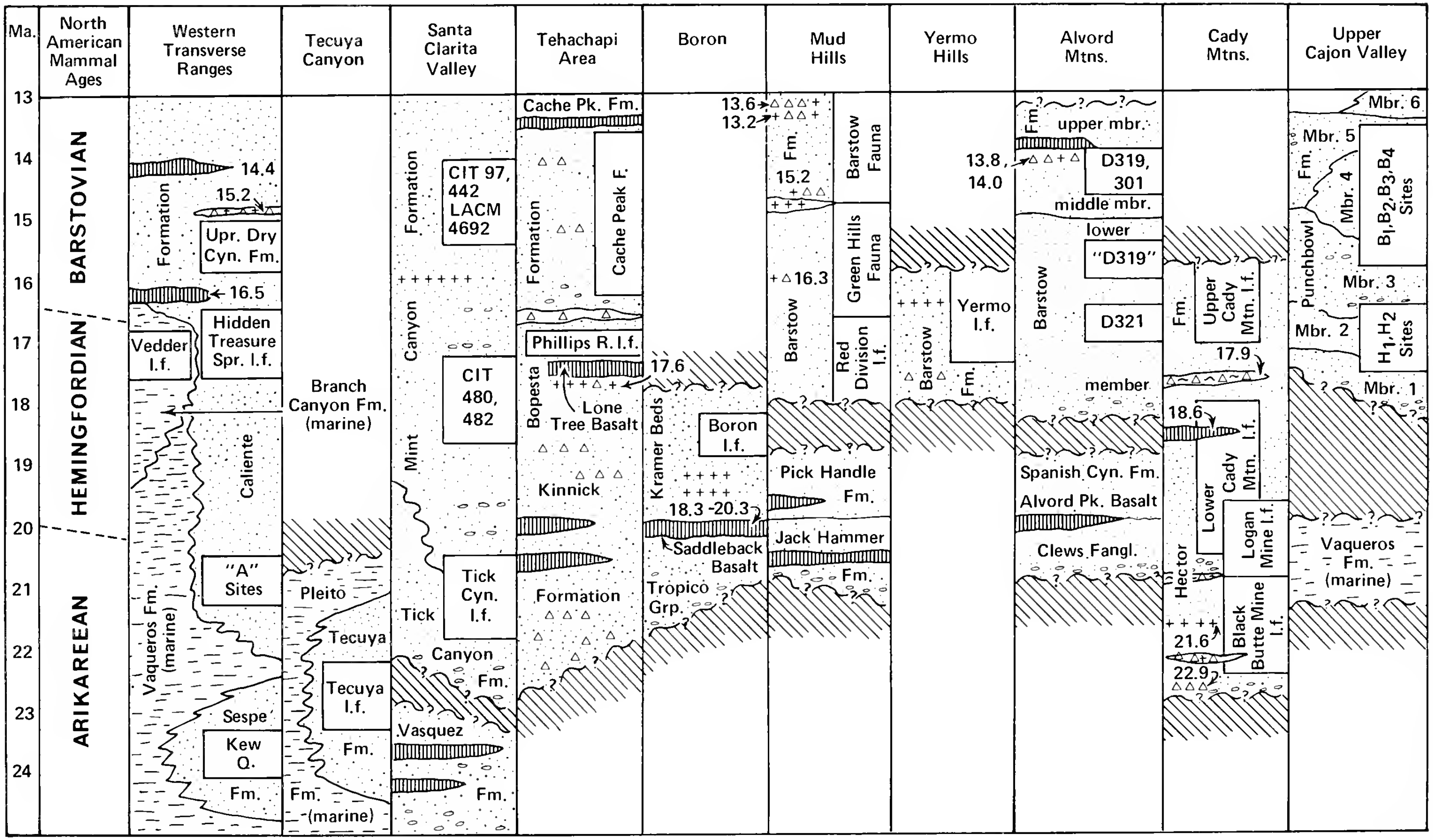


Figure 60. Stratigraphic diagram of lithologic sequences and stratigraphic position of associated fossil vertebrate localities, fossil assemblages, and radiometrically dated units discussed in this report. Sources for interpretations presented in columns as follows: Western Transverse Ranges, Repenning and Vedder (1961), James (1963), Munthe (1979); Tecuya Canyon, Stock (1920, 1932); Santa Clarita Valley, Maxson (1930), Jahns (1940), personal observations by author; Tehachapi area, Dibblee, 1967, J. Quinn, personal communication, personal observations by author; Boron, Barnard and Kistler (1966), R.B. Kistler, personal communication, field observations by author; Mud Hills and Yermo Hills, Woodburne et al. (1982), Woodburne and Tedford (1982); Alvord Mountains, Byers (1960), Woodburne et al. (1982); Cady Mountains, Miller (1980), Woodburne et al. (1982); Upper Cajon Valley, Woodburne and Golz (1972), R. Reynolds, personal communication.

some extent, the Boron Local Fauna represents a unique combination of taxa, with a rodent (*Trogomys*) previously thought to be Arikareean, a palaeomerycid genus (*Aletomeryx*) and an oreodont species (*Merychyus* cf. *M. minimus*), elsewhere restricted to the early Hemingfordian, and a dipodomyine rodent genus (*Cupidinimus*) and camel (cf. *Hesperocamelus* sp.) the latter genus previously restricted to the Barstovian and later.

Absent at Boron are taxa which are generally typical of late Hemingfordian: small merychippines, middle sized oreodonts larger than *Merychyus* (*Brachycrus, Ticholeptus*), dromomerycids (*Bouromeryx* Frick, 1937), and antilocaprids. Conclusions based on absent taxa are always questionable, but the lack of these taxa found in common association in other late Hemingfordian faunas of southern California and Nebraska strongly suggest a real absence in the Boron Local Fauna, not just an artifact of the record and further supports a slightly older age than late Hemingfordian. Camel biostratigraphy is not well documented, and thus the cf. *Hesperocamelus* sp., a genus previously restricted to Barstovian and later, is not considered particularly significant.

The microfauna, although seemingly well preserved, lacks the common Arikareean/Hemingfordian genus *Proheteromys* and the eomyid/geomyoid/zapodid elements common in earlier Miocene assemblages. *Cupidinimus*, the most common taxon in the Boron Local Fauna and a common rodent in the earliest Barstovian, is absent in the only other Hemingfordian microvertebrate assemblage in southern California (Vedder Local Fauna; Lindsay, 1974) and thus may seem out of place at Boron. However, its absence may be environmentally controlled and its presence at Boron merely provides an earlier link between this common Barstovian taxon and its presumed ancestor, *Trogomys*.

The Boron Local Fauna displays greatest similarity with the central United States fossil assemblages of the Runningwater Formation (Cook, 1965; McKenna, 1965), Rosebud Formation (Macdonald, 1963, 1970; Macdonald and Harksen, 1968), Batesland Formation (Harksen and Macdonald, 1967; Martin, 1976), and Martin Canyon "beds" (Galbreath, 1953; Wilson, 1960). These fossil assemblages are considered typical of early Hemingfordian (Tedford et al., 1973). In addition to *M. minimus* and *Aletomeryx* species, these faunas also contain taxa similar to the Boron forms such as *Archaeolagus, Hypolagus, Miospermophilus, Mookomys,* primitive aepycamelines (*Oxydactylus*) and primitive protolabines (*Tanymykter, Protolabis*), even though none of these taxa are limited to the early Hemingfordian.

There is less similarity between the Boron Local Fauna and the later Hemingfordian fossil assemblages of the Sheep Creek Formation (Skinner et al., 1977) and the Box Butte Formation (Galusha, 1975), the latter containing a diversity of horses, including *Merychippus* spp., larger oreodonts (*Brachycrus, M.* (*Metoreodon*), *Ticholeptus*), *Sinclairomeryx* spp. (but no *Aletomeryx*), dromomerycines, and antilocaprids.

The Boron Local Fauna can also be correlated with southern California fossil assemblages (Figure 60). However, such correlations present some difficulty because of the seemingly unusual assemblage of taxa in the Boron Local Fauna. The Arikareean/Hemingfordian interval is not well represented in southern California. Most fossil assemblages referred to this time span are poorly preserved, lack taxonomic diversity and most correlations with the central United States standard have been tenuous. In addition, the Boron Local Fauna appears to sample a restricted time interval not previously seen in southern California or the southern Great Basin.

Most Arikareean fossil assemblages from southern California have been derived from sedimentary basins west of the San Andreas Fault, which, by currently accepted plate tectonic models, places these basins from 100–300 km to the southeast at their time of development (see Crowell, 1975). Whether such a distance would result in significantly different paleoenvironmental conditions than those east of the San Andreas Fault is impossible to resolve. Pyroclastic volcanic deposition dominated in the few basins in existence east of the San Andreas Fault in the Mojave Desert and only one area has yielded fossils. By later Hemingfordian, this volcanism had subsided considerably, but most of the basins east of the San Andreas Fault were dominated by coarse clastic deposition as these volcanics were removed from areas of higher topographic relief. Fossils in these coarse sediments are scattered and poorly preserved. The earlier Hemingfordian was not previously sampled (or recognized, if sampled). The Boron Local Fauna samples this interval for the first time.

Among those southern California assemblages referred to the Arikareean, the Boron Local Fauna shows some similarity to the Tick Canyon Local Fauna (Maxson, 1930; Jahns, 1940) in sharing *Trogomys. Merychyus* cf. *M. minimus* from Boron is derived with respect to *M. calaminthus* from the Tick Canyon Local Fauna. The camel referred to *Miolabis californicus* Maxson, 1930, from the Tick Canyon Local Fauna has unfused metapodials and is considerably larger than the small camelid from Boron with unfused metapodials.

Merychyus cf. *M. minimus* from Boron is also derived with respect to the *M. calaminthus* from the Late Arikareean Black Butte Mine Local Fauna in the Hector Formation (Woodburne et al., 1974) and the *Merychyus* cf. *M. calaminthus* from the Cady Mountain Local Fauna (Woodburne, Miller, and Tedford, 1982). The fused, proximal metatarsal from the small camelid species from Boron is considerably larger than the *Michenia* cf. *M. agatensis* from the latest Arikareean Logan Mine Local Fauna of the Hector Formation.

The Boron Local Fauna shows little similarity to other Arikareean assemblages in California such as the Tecuya Local Fauna (Stock, 1920, 1932a), Kew Quarry (Stock, 1932b, 1935; Wilson, 1934, 1949), and other localities in the upper Sespe Formation (Wilson, 1949).

Among southern California fossil assemblages referred to the late Hemingfordian, the Boron Local Fauna closely resembles the poorly documented Phillips Ranch Local Fauna (localities LACM(CIT) 305, UCMP V2577) in the Kinnick Formation (or the basal Bopesta Formation, James Quinn, personal communication). Buwalda (1916) and Buwalda and Lewis (1955) recognized *Merychippus tehachapiensis* Buwalda and Lewis, 1955 (= *M. carrizoensis* Dougherty, 1940—see Munthe, 1979), small and large camelids, *Moropus* Marsh, 1877, *Merycodus* Leidy, 1854, canids, and felids from this local fauna. Although not published, the Phillips Ranch Local Fauna also contains an oreodont, peccary, and palaeomerycid. The oreodont is a small, high-crowned species probably referable to *Merychyus.* It is slightly larger than the Boron oreodonts but otherwise similar to *M.* cf. *M. minimus.* The palaeomerycid (represented only by upper teeth) is a small, high-crowned species similar in size and morphology to *A. occidentalis* or a small species of *Rakomeryx.* The small camel from Phillips Ranch is intermediate in size between the cf. *Hesperocamelus* sp. and the small camel species from Boron but appears to have fused metatarsals like the cf. *Hesperocamelus* sp. from Boron.

The oreodont from the Late Hemingfordian Red Division Local Fauna in the type section of the Barstow Formation in the Mud Hills (Woodburne and Tedford, 1982), *Merychyus* (*Metoreodon*) *relictus fletcheri* Schultz and Falkenbach, 1947, is based on a heavily worn, poorly preserved specimen. About all that can be said is that this individual is larger than the oreodonts from Boron. The Red Division Local Fauna also produces *Merychippus carrizoensis* which is absent at Boron.

Among other late Hemingfordian fossil assemblages in southern California, the Boron Local Fauna shares no taxa with the Alvord Mountain faunas from the lower member of the Barstow Formation (localities D"319," D321) (Byers, 1960; Lewis, 1968), the Yermo Hills Local Fauna from sedimentary rocks in the Yermo Hills also referred to the Barstow Formation (Woodburne, Miller, and Tedford, 1982), the fauna of the basal Punchbowl Formation in the Cajon Valley (Woodburne and Golz, 1972), Hidden Treasure Spring Local Fauna of the Caliente Formation in the upper Cuyama Valley (Dougherty, 1940b; Repenning and Vedder, 1961; James, 1963), the Vedder Local Fauna of the Branch Canyon Formation (Hutchison and Lindsay, 1974; Lindsay, 1974; Munthe, 1979) or the Upper Cady Mountain Local Fauna in the northern Cady Mountains (Miller, 1980; Woodburne, Miller, and Tedford, 1982). All these have been referred to the late Hemingfordian and all contain the small *Merychippus carrizoensis,* middle sized oreodonts (except the Cady Mountain Local Fauna) referred either to *Ticholeptus calimontanus, Merychyus* (*Metoreodon*) *relictus* or *Brachyus buwaldi,* and small camelids (except the Alvord Mountain area), often referred to Protolabinae. Although the taxonomic assignments may be erroneous, all these oreodonts are derived with respect to those from Boron. The only palaeomerycids in any of these faunas are brachyodont dromomerycines.

The Vedder Local Fauna is the only one of these late Hemingfordian assemblages to also contain microvertebrates except for 5 isolated specimens of *Proheteromys sulculus* from the Cady Mountain Local Fauna. The Vedder Local Fauna shares only one taxon (*Mookomys*) at the generic level with the Boron Local Fauna, but the Boron species is distinctly smaller. The Boron Local Fauna lacks the squirrels, eomyids, and *Proheteromys* species found in the Vedder Local Fauna, and the *P. sulculus* found in the Cady Mountain Local Fauna. On the other hand, the Vedder Local Fauna lacks *Trogomys* and *Cupidinimus* of the Boron Local Fauna, even though the latter is a common element in earliest Barstovian and later Miocene faunas. The Vedder Local Fauna is from near shore or possibly even marine rocks, and perhaps the absence of *Cupidinimus* is environmentally controlled.

Taken on balance, the Boron Local Fauna is best considered early Hemingfordian, a view consistent with the available radiometric data and biostratigraphic correlations with the reference fossil assemblages in Southern California and the central United States.

CONCLUSIONS

Based on the above discussions, the Boron Local Fauna:

1. is the first diverse early Hemingfordian fossil vertebrate assemblage from southern California,
2. is the only diverse Hemingfordian microvertebrate assemblage in southern California east of the San Andreas Fault,
3. contains two new mammalian species, *Cupidinimus boronensis* n. sp. (Mammalia, Rodentia, Heteromyidae) and *Aletomeryx occidentalis* n. sp. (Mammalia, Artiodactyla, Palaeomerycidae),
4. contains one of the earliest North American records of the Family Colubridae (Reptilia, Squamata) and the first Hemingfordian record west of the Rocky Mountains,
5. contains the earliest species of the genus *Cupidinimus,*
6. contains the second occurrence of *Trogomys* (Mammalia, Rodentia, Heteromyidae), extending the range of this genus from the Arikareean into the Hemingfordian,
7. contains the first association of *Cupidinimus* and *Trogomys,* the assumed ancestor of *Cupidinimus,*
8. contains the first Hemingfordian record of a Great Plains species of merychyine oreodont, *Merychyus minimus* (Mammalia, Artiodactyla, Merycoidodontidae), west of the Rocky Mountains,
9. contains the oldest record of the genus *Hesperocamelus* (Mammalia, Artiodactyla, Camelidae),
10. contains the first aletomerycine palaeomerycid, *Aletomeryx occidentalis,* west of the Rocky Mountains,
11. provides a correlative link to the classical early Hemingfordian assemblages of the mid-continent because of the occurrence of *Merychyus* cf. *M. minimus* and *Aletomeryx* (both common mid-continent taxa), and
12. provides a minimum age of Early Miocene for the Tropico Group.

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LITERATURE CITED

Armstrong, R.L., and R.E. Higgens. 1973. K-Ar dating of the beginning of Tertiary volcanism in the Mojave Desert, California. Bulletin, Geological Society of America 84:1095–1100.

Auffenberg, W. 1963. The fossil snakes of Florida. Tulane Studies in Zoology 10(3):131–216.

Barnard, R.M., and R.B. Kistler. 1966. Stratigraphic and structural evolution of the Kramer sodium borate ore body, Boron, California. In J.L. Rau, Editor. *Second Symposium on Salt.* Northern Ohio Geological Society 1:133–150.

Baskin, J.A. 1979. Small mammals of the Hemphillian age White Cone local fauna, northeastern Arizona. Journal of Paleontology 53(3):695–708.

Benda, W.K., R.C. Erd, and W.C. Smith. 1960. Core logs from five holes near Kramer, in the Mojave Desert, California. United States Geological Survey Bulletin 1045F:1–22.

Black, C.C. 1963. A review of the North American Tertiary Sciuridae. Bulletin, Museum of Comparative Zoology, Harvard University 130(3):113–248.

Bowen, C.E. 1954. Geology and mineral resources of the Barstow quadrangle, California. California Division Mines Bulletin 165:7–185.

Bowser, C.J. 1965. Geochemistry and petrology of the sodium borates in the non-marine evaporate environment. Unpublished Master's Thesis, University California at Los Angeles.

Brattstrom, B.H. 1958. New records of Cenozoic amphibians and reptiles from California. Bulletin, Southern California Academy of Sciences 57(1):5–12.

Buwalda, J.P. 1916. New mammalian faunas from Miocene sediments near Tehachapi Pass in the southern Sierra Nevada. University of California Department of Geological Sciences Bulletin 10:78–85.

Buwalda, J.P., and G.E. Lewis. 1955. A new species of *Merychippus.* Geological Society of America Professional Paper 264G:147–152.

Byers, F.M., Jr. 1960. Geology of the Alvord Mountain Quadrangle, San Bernardino County, California. United States Geological Survey Bulletin 1089-A:1–71.

Cook, H.J. 1933. Faunal lists of the Tertiary Vertebrata of Nebraska and adjacent areas. Nebraska Geological Survey Paper 5:1–58.

———. 1965. Runningwater Formation, Middle Miocene of Nebraska. American Museum of Natural History Novitates 2227:1–8.

Cope, E.D. 1873. Synopsis of new vertebrates from Colorado obtained during the summer of 1873. Miscellaneous Publications, United States Geological Survey of the Territories I:1–19.

———. 1878. Descriptions of new extinct Vertebrata from the Upper Tertiary and Dakota formations. Bulletin, United States Geological and Geographic Surveys of the Territories IV:379–396.

———. 1883. Notes on the geographical distribution of Batrachia and Reptilia in western North America. Proceedings of the Academy of Natural Sciences of Philadelphia 1883:10–35.

Crowell, J.C. 1975. The San Andreas Fault in southern California. In J.C. Crowell, Editor. *San Andreas Fault in southern California, a guide to the San Andreas Fault from Mexico to the Carrizo Plain.* California Division Mines Special Report 118:7–27.

Dalrhymple, G.B. 1979. Critical tables for conversion of K-Ar ages from old to new constants. Geology 7(11): 558–560.

Davidson, P.W. 1923. *Alticamelus alexandrae,* a new camel from the Barstow Upper Miocene of the Mojave Desert. University of California Publications, Bulletin Department of Geological Sciences 14:397–408.

Dawson, M.R. 1958. Later Tertiary Leporidae of North America. University of Kansas Paleontological Contributions 6:1–75.

Dibblee, T.W., Jr. 1952. Geology of the Saltdale Quadrangle, California. California Division Mines Bulletin 160: 1–66.

———. 1958a. Tertiary stratigraphic units of the western Mojave Desert, California. Bulletin, American Association Petroleum Geologists 42(1):135–144.

———. 1958b. Geologic map of the Boron Quadrangle, Kern and San Bernardino Counties, California. United States Geological Survey, Mineral Investigations Field Studies Map MF-204.

———. 1967. Areal geology of the western Mojave Desert, California. United States Geological Survey Professional Paper 522:1–153.

Dickey, D.D. 1957. Core logs from two test holes near Four Corners, San Bernardino County, California. United States Geological Survey Bulletin 1045B:63–79.

Dorr, J.A. 1956. Anceney local mammal fauna, latest Miocene, Madison Valley Formation, Montana. Journal of Paleontology 30(1):62–74.

Dougherty, J.F. 1940a. Skull and skeletal remains of the camel *Paratylopus cameloides* (Wortman) from the John Day deposits, Oregon. Carnegie Institution of Washington Publications, Contributions in Paleontology 514:49–58.

———. 1940b. A new Miocene mammalian fauna from Caliente Mountain, California. Carnegie Institution of Washington Publications 514:109–143.

Douglass, E. 1909. *Dromomeryx,* a new genus of American ruminants. Annals Carnegie Museum V:457–479.

Downs, T. 1956. The Mascall fauna from the Miocene of Oregon. University of California Publications, Department of Geological Sciences 31(5):199–354.

Evernden, J.F., D.E. Savage, G.H. Curtis, and G.T. James. 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. American Journal of Science 262:145–198.

Frick, C. 1937. Horned ruminants of North America. Bulletin, American Museum of Natural History 69:1–669.

Frick, C., and B.E. Taylor. 1968. A generic review of the stenomyline camels. American Museum of Natural History Novitates 2353:1–51.

———. 1971. *Michenia,* a new protolabine (Mammalia, Camelidae) and a brief review of the early taxonomic history of the genus *Protolabis.* American Museum of Natural History Novitates 2444:1–24.

Galbreath, E.C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata 5:1–120.

Gale, H.S. 1946. Geology of the Kramer borate district, Kern County, California. California Journal of Mines and Geology 42(4):325–379.

Galusha, T. 1975. Stratigraphy of the Box Butte Formation, Nebraska. Bulletin, American Museum of Natural History 156(1):1–68.

Gazin, C.L. 1930. A Tertiary vertebrate fauna from the upper Cuyama drainage basin, California. Carnegie Institution of Washington Publications, Contributions in Paleontology 404:55–76.

Hall, E.R. 1930. Rodents and lagomorphs from the later Tertiary of Fish Lake Valley, Nevada. University of California Publications, Bulletin Department of Geological Sciences 19(12):295–312.

Hamilton, W.R. 1978a. Cervidae and Palaeomerycidae. In V.J. Maglio and H.B.S. Cooke, Editors. *Evolution of African Mammals.* Harvard University Press.

———. 1978b. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. Philosophical Transactions, Royal Society of London, Biological Sciences 283(999):165–229.

Harkson, J.C., and J.R. Macdonald. 1967. Miocene Batesland Formation named in southwestern South Dakota. South Dakota Geological Survey, Report of Investigation 96:1–10.

Hay, O.P. 1899. On the names of certain North American fossil vertebrates. Science 9(2):593–594.

Hecht, M.K. 1956. A new xantusiid lizard from the Eocene of Wyoming. American Museum of Natural History Novitates 1174:1–8.

Hershey, H.O. 1902. Some Tertiary formations of southern California. American Geologist 29:349–372.

Holman, J.A. 1970. Herpetofauna of the Wood Mountain Formation (Upper Miocene) of Saskatchewan. Canadian Journal of Earth Science 7(5):1317–1325.

———. 1973. Reptiles of the Egelhoff local fauna (Upper Miocene) of Nebraska. Contributions, University of Michigan Museum of Paleontology 24(12):125–134.

———. 1975. Herpetofauna of the Wakeeney local fauna (Lower Pliocene: Clarendonian) of Trego County, Kansas. In G.R. Smith, and N.E. Friedland, Editors. *Studies on Cenozoic Paleontology and Stratigraphy.* University of Michigan, Museum of Paleontology:49–74.

———. 1979. A review of North American Tertiary snakes. Publications of the Museum, Michigan State University, Paleontological Series 1(6):203–260.

Honey, J.G., and B.E. Taylor. 1978. A generic revision of the Protolabidini (Mammalia, Camelidae), with a description of two new protolabidines. Bulletin, American Museum of Natural History 161(3):369–425.

Hutchison, J.H., and E.H. Lindsay. 1974. The Hemingfordian mammal fauna of the Vedder locality, Branch Canyon Formation, Santa Barbara County, California. Part 1: Insectivora, Chiroptera, Lagomorpha and Rodentia (Sciuridae). PaleoBios 15:1–19.

Jahns, R.H. 1940. Stratigraphy of the easternmost Ventura Basin, California, with a description of a new Lower Miocene mammalian fauna from the Tick Canyon Formation. Carnegie Institution of Washington Publications, Contributions in Paleontology 514:145–194.

James, G.T. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley Badlands, California. Part 1. Geology, faunal interpretations and systematic descriptions of Chiroptera, Insectivora and Rodentia. University of California Publications Geological Sciences 45: 1–162.

Kellogg, L. 1910. Rodent fauna of the late Tertiary beds of Virgin Valley and Thousand Creek, Nevada. University of California Publications, Bulletin Department of Geological Sciences 5:411–437.

Klininger, D. 1968. Rodents of the Mio-Pliocene Norden Bridge local fauna, Nebraska. The American Midland Naturalist 80(1):65–74.

Korth, W.W. 1979. Geomyoid rodents from the Valentine Formation of Knox County, Nebraska. Annals Carnegie Museum 48(16):287–310.

Leidy, J. 1858. Notice of remains of extinct Vertebrata from the valley of the Niobrara River, collected during the exploring expedition of 1857, in Nebraska. Proceedings of the Academy of Natural Sciences of Philadelphia 10: 20–29.

Lewis, G.E. 1955. A new species of *Merychippus.* Geological Society Professional Paper 364-G:147–151.

———. 1968. Stratigraphic paleontology of the Barstow Formation in the Alvord Mountain area, San Bernardino County, California. United States Geological Survey Professional Paper 600-C:C75–C79.

Lindsay, E.H. 1972. Small mammal fossils from the Barstow Formation, California. University of California Publications Geological Sciences 93:1–104.

———. 1974. The Hemingfordian mammal fauna of the Vedder locality, Branch Canyon Formation, Santa Barbara County, California. Part II. Rodentia (Eomyidae and Heteromyidae). PaleoBios 16:1–20.

Loomis, D.P., B.F. Cox, and D.P. Whistler. 1983. Basin analysis of the Ricardo Formation and implications for Miocene history of the Garlock Fault. Geological Society America, Abstract, Cordilleran Meeting, May, 1983.

Loomis, F.B. 1924. Miocene oreodonts in North America. Bulletin, American Museum of Natural History 51(1): 1–37.

Lull, R.S. 1920. New Tertiary artiodactyls. American Journal of Science 50:83–130.

———. 1921. New camels in the Marsh collection. American Journal of Science 50:392–404.

Macdonald, J.R. 1949. A new Clarendonian fauna from northeastern Nevada. University of California Publications, Geological Sciences 28(7):173–194.

———. 1956. A new Clarendonian Mammalian Fauna from the Truckee Formation of western Nevada. Journal of Paleontology 30(1):186–202.

———. 1963. The Miocene faunas from Wounded Knee area of western South Dakota. Bulletin, American Museum of Natural History 125:139–238.

———. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bulletin, Los Angeles County Museum of Natural History, Science 8:1–82.

Macdonald, J.R., and J.C. Harksen. 1968. Rosebud Formation in South Dakota. South Dakota Geological Survey, Report of Investigations 97:1–13.

Martin, J.E. 1976. Small mammals from the Miocene Batesland Formation of South Dakota. Contributions to Geology, University of Wyoming 14(2):69–98.

Matthew, W.D. 1901. Fossil mammals of the Tertiary of northeastern Colorado. Memoirs, American Museum of Natural History I:355–448.

———. 1904. Notice of two new Oligocene camels. Bulletin of the American Museum of Natural History 20:211–215.

———. 1924. Third contribution to the Snake Creek fauna. Bulletin American Museum of Natural History 50(2): 59–210.

Matthew, W.D., and H.J. Cook. 1909. A Pliocene fauna from western Nebraska. Bulletin American Museum of Natural History 26:361–414.

Matthew, W.D., and J.R. Macdonald. 1960. Two new species of *Oxydactylus* from the middle Miocene Rosebud formation in western South Dakota. American Museum of Natural History Novitates 2003:1–7.

Maxson, J.H. 1930. A Tertiary mammalian fauna from the Mint Canyon Formation of southern California. Carnegie Institute of Washington Publications, Contributions in Paleontology 404:77–112.

McKenna, M.C. 1965. Stratigraphic nomenclature of the Miocene Hemingford Group, Nebraska. American Museum of Natural History Novitates 2228:1–21.

Merriam, J.C. 1911. The Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada; part II, vertebrate fauna. University of California Publications, Bulletin Department of Geological Sciences 6: 199–304.

———. 1919. Tertiary mammalian faunas of the Mojave Desert. Bulletin, University of California Department of Geological Sciences 11:437–585.

Miller, S.T. 1980. Geology and mammalian biostratigraphy of a part of the northern Cady Mountains, California. United States Geological Survey Open File Report 80-978:1–121.

Munthe, J. 1979. The Hemingfordian mammal fauna of the Vedder locality, Branch Canyon Sandstone, Santa Barbara County, California. Part III: Carnivora, Perissodactyla, Artiodactyla and summary. PaleoBios 29:1–22.

Peterson, O.A. 1904. Osteology of *Oxydactylus*. Annals Carnegie Museum 2(3):434–475.

———. 1906. The Miocene beds of western Nebraska and eastern Wyoming and their vertebrate fauna. Annals of the Carnegie Museum IV:21–72.

———. 1911. A new camel from the Miocene of western Nebraska. Annals of the Carnegie Museum 7(2):260–266.

Reeder, W.G. 1956. A review of Tertiary rodents of the Family Heteromyidae. Unpublished Ph.D. Dissertation, University of Michigan.

———. 1960. A new rodent genus (Family Heteromyidae) from the Tick Canyon Formation of California. Bulletin Southern California Academy Sciences 59(3):121–132.

Repenning, C.A., and J.G. Vedder. 1961. Continental vertebrates and their stratigraphic correlation with marine mollusks, eastern Caliente Range, California. United States Geological Survey Professional Paper 424:C235–C239.

Schatzinger, R.A. 1980. New species of *Palaeoxantusia* (Reptilia: Sauria) from the Unitan (Eocene) of San Diego County, California. Journal of Paleontology 54(2):460–471.

Schultz, C.B. 1938. The Miocene of western Nebraska. American Journal Science 35:441–444.

Schultz, C.B., and C.R. Falkenbach. 1940. Merycochoerinae, a new subfamily of oreodonts. Bulletin Museum of Natural History 77(5):213–306.

———. 1941. Ticholeptinae, a new subfamily of oreodonts. Bulletin American Museum of Natural History 79(1):1–105.

———. 1947. Merychyinae, a subfamily of oreodonts. Bulletin, American Museum of Natural History 88(4):161–285.

Shotwell, J.A. 1967. Later Tertiary geomyoid rodents of Oregon. University of Oregon, Museum of Natural History Bulletin 9:1–51.

Sinclair, W.J. 1915. Additions to the fauna of the Lower Pliocene Snake Creek beds (results of the Princeton University 1914 expedition to Nebraska). Proceedings, American Philosophical Society 54:73–95.

Skinner, M.F., S.M. Skinner, and R.J. Gooris. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western Nebraska. Bulletin, American Museum of Natural History 158(5):265–371.

Stevens, M.S. 1977. Further study of Castolon local fauna (Early Miocene), Big Bend National Park, Texas. Pearce-Sellards Series, Texas Memorial Museum 28:1–69.

Stevens, M.S., J.B. Stevens, and M.R. Dawson. 1969. New Early Miocene formation and vertebrate local fauna, Big Bend National Park, Brewster County, Texas. Pearce-Sellards Series, Texas Memorial Museum 15:1–53.

Stirton, R.A. 1944. Comments on the relationships of the cervoid Family Palaeomerycidae. American Journal Science 242:633–655.

Stock, C. 1920. An early Tertiary vertebrate fauna from southern Coast Ranges of California. Bulletin, Department Geology, University of California 12:267–276.

———. 1932a. Additions to the mammalian fauna from the Tecuya beds, California. Carnegie Institution Washington 418:87–93.

———. 1932b. An Upper Oligocene mammalian fauna from southern California. Proceedings, National Academy of Sciences 18:550–554.

———. 1935. Artiodactyla from the Sespe of the Las Posas Hills, California. Carnegie Institution Washington Publications, Contributions in Paleontology 453:119–125.

Storer, J.A. 1970. New rodents and lagomorphs from the Upper Miocene Wood Mountain Formation of southern Saskatchewan. Canadian Journal of Earth Sciences 7(4): 1125–1129.

———. 1975. Tertiary mammals of Sasakatchewan, Part III: the Miocene fauna. Royal Ontario Museum, Life Sciences Contributions 103:1–134.

Sutton, J.F. 1977. Mammals of the Anceney local fauna (Late Miocene) of Montana. Unpublished Ph.D. Dissertation, Texas Tech University.

Taylor, B.E., and S.D. Webb. 1976. Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. American Museum of Natural History Novitates: 2566: 1–22.

Tedford, R.H., T. Galusha, M.F. Skinner, B.E. Taylor, R. Fields, J.R. Macdonald, T.H. Patton, J.M. Rensberger, and D.P. Whistler. 1973. Faunal succession and biochronology of the Arikareean through Clarendonian interval (Miocene Epoch), North America. Geological Society of America, Abstracts with Programs 5(7):837–838.

Thorpe, M.R. 1937. The Merycoidodontidae, an extinct group of ruminant mammals. Memoirs, Peabody Museum of Natural History III(4):1–428.

Turner, D.L. 1970. Potassium-argon dating of Pacific Coast Miocene foraminiferal stages. Geological Society of America Special Paper 124:91–129.

Webb, S.D. 1965. The osteology of *Camelops*. Bulletin, Los Angeles County Museum of Natural History 1:1–54.

Webb, S.D., and B.E. Taylor. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. Bulletin, American Museum of Natural History 167(3):121–157.

Wilson, R.W. 1934. Two rodents and a lagomorph from the Sespe of the Las Posas Hills, California. Carnegie Institution Washington Publications, Contributions in Paleontology 453:11–17.

———. 1939. Rodents and lagomorphs of the Late Tertiary Avawatz fauna, California. Carnegie Institution Washington Publications, Contributions in Paleontology 514: 31–38.

———. 1949. Rodents and lagomorphs of the upper Sespe. Carnegie Institution Washington Publications, Contributions in Paleontology 584:51–65.

———. 1960. Early Miocene rodents and insectivores from northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata 7:1–92.

Wood, A.E. 1931. Phylogeny of the heteromyid rodents. American Museum Novitates 501:1–19.

———. 1932. New Miocene rodents from the Miocene of Florida. Florida State Geological Survey Bulletin 10:43–51.

———. 1935. Evolution and relationship of the heteromyid rodents with new forms from the Tertiary of western North America. Annals Carnegie Museum 24:73–262.

———. 1936a. Geomyid rodents from the middle Tertiary. American Museum of Natural History Novitates 866: 1–23.

———. 1936b. Fossil heteromyid rodents in the collections of the University of California. American Journal of Science, Fifth Series 32(188):112–119.

———. 1937. Additional material from the Tertiary of the Cuyama basin of California. American Journal of Science 33:29–43.

Woodburne, M.O., and D.J. Golz. 1972. Stratigraphy of the Punchbowl Formation, Cajon Valley, southern California. University of California Publications Geological Sciences 92:1–57.

Woodburne, M.O., and R.H. Tedford. 1982. Litho- and biostratigraphy of the Barstow Formation, Mojave Desert, California. In *Guidebook, Geologic Excursions in the California Desert.* Cordilleran Section, 78th Annual Meeting, Geological Society of America:47–64.

Woodburne, M.O., and D.P. Whistler. 1973. An Early Miocene oreodont (Merychyinae, Mammalia) from the Orocopia Mountains, southern California. Journal of Paleontology 47(5):908–912.

Woodburne, M.O., S.T. Miller, and R.H. Tedford. 1982. Stratigraphy and geochronology of Miocene strata in the central Mojave Desert, California. In *Guidebook, Geologic Excursions in the California Desert.* Cordilleran Section, 78th Annual Meeting, Geological Society of America:47–64.

Woodburne, M.O., R.H. Tedford, M.S. Stevens, and B.E. Taylor. 1974. Early Miocene mammalian faunas, Mojave Desert, California. Journal of Paleontology 48(1): 6–26.

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