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CONTRIBUTIONS IN SCIENCE

RODENTS, BATS, AND INSECTIVORES FROM THE
PLIO-PLEISTOCENE SEDIMENTS TO THE
EAST OF LAKE TURKANA, KENYA

Craig C. Black and Leonard Krishtalka



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

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RODENTS, BATS, AND INSECTIVORES FROM THE PLIO-PLEISTOCENE SEDIMENTS TO THE EAST OF LAKE TURKANA, KENYA

Craig C. Black¹ and Leonard Krishtalka²

ABSTRACT. Fossil small mammals collected from five Plio-Pleistocene localities in the Koobi Fora Formation along the east side of Lake Turkana, Kenya, are described. The assemblage bears close resemblance to those from Olduvai Bed I in Tanzania and Omo Members F and G in Ethiopia. The most common elements of the assemblage are the murids *Thallomys quadrilobatus* and *Praomys (Mastomys) minor*. The micromammals from one locality, which dates at approximately 1.6 million years, suggest an arid environment with *Acacia* scrub and some riverine forest along intermittent stream channels.

INTRODUCTION

Paleontological investigations have been carried out along the eastern side of Lake Turkana, under the auspices of the Koobi Fora Research Project, National Museums of Kenya, since 1968. Results of these field studies have appeared in many journals and are summarized by Coppens et al. (1976) and Leakey and Leakey (1978). While various studies of the geology, paleoanthropology, and paleontology have been pursued by a number of investigators, there have been no previous studies of microvertebrates from these sediments. Such studies have been undertaken for a sequence of deposits of similar age along the Omo River in Ethiopia (Jaeger and Wesselman, 1976; Wesselman, 1984), for at least Bed I at Olduvai Gorge in Tanzania (Butler, 1969; Butler and Greenwood, 1973, 1976, 1979; Jaeger, 1976), and for a portion of the Hadar Formation in Ethiopia (Sabatier, 1982).

In order to broaden paleontological knowledge of the East Turkana faunas to include the smaller mammals, we began a series of washing and screening operations in the summer of 1974. A primary goal of the project was to identify the ecological conditions prevailing during the early evolution of hominids between 3 and 1 million years ago, a period informally referred to as the Plio-Pleistocene (Harris, 1983: 3), in the Lake Turkana (formerly Lake Rudolf) basin of northern Kenya. An understanding of past environmental

conditions at Turkana would assist in correlating the East African Rift Valley Plio-Pleistocene localities.

Small vertebrates such as rodents, insectivores, snakes, and amphibians are often quite sensitive to local environmental fluctuations. Their occurrence can be used to interpret local climatic conditions in both past and present ecosystems. A history of climatic and environmental change can be reconstructed by studying the species composition of microvertebrate assemblages at each of many fossil localities and comparing these groups of species with Recent assemblages of related species and their environmental requirements. The degree of reliability of such analogies is dependent upon recovery of large samples from temporally restricted horizons and upon the degree of relationship between the fossil and Recent taxa. The more diverse the fossil assemblage, and the closer the fossil taxa are to the Recent species, the greater is their usefulness in making environmental interpretations.

The initial field party consisted of the authors, together with John Sutton, Dan Womachel, and several Kenyan assistants. After becoming familiar with the general geological setting, we sampled eleven localities from the central and northern part of the area, all of which were above the KBS Tuff (Harris, 1983). The amount of sediment processed varied with locality, the smallest sample being 115 kg and the largest, 3700 kg (Table 1). From this initial sampling three potentially productive localities were identified. During the summer of 1975, then again in May and June of 1978, these localities were intensively sampled, but only one proved to be sufficiently rich to warrant a large-scale washing operation. This is our locality 130-A (Figure 1) located below the Okote Tuff in Area 130 (Isaac and Harris, 1978).

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Table 1. Quantities of sediment processed.

| Area | Locality | Sediment processed (kilograms) | | | Species |
|------|----------|--------------------------------|--------|-------|--|
| | | 1974 | 1975 | 1978 | |
| 101 | 101-A | 180 | — | — | None |
| 102 | 102-A | 275 | — | — | None |
| 103 | 103-A | 135 | — | — | <i>Thryonomys</i> sp. |
| | 103-B | 180 | — | — | |
| 104 | 104-A | 115 | 230 | — | <i>Aethomys</i> sp. |
| 130 | 130-A | 700 | 18,000 | 2,400 | <i>Crocidura</i> cf. <i>C. nana</i> <i>Crocidura</i> cf. <i>C. dolichura</i> <i>Scotophilus</i> sp. Pteropodidae <i>Nycteris</i> sp. <i>Tatera</i> sp. <i>Thryonomys</i> sp. Hystricid sp. <i>Arvicanthis</i> sp. <i>Aethomys</i> sp. <i>Praomys</i> cf. <i>P. minor</i> <i>Thallomys quadrilobatus</i> <i>Mus</i> sp. |
| 131 | FxJ,20 | 3,700 | — | — | Chiroptera indet. |
| | 131-A | | | | <i>Jaculus orientalis</i> <i>Thryonomys</i> sp. Hystricid sp. <i>Aethomys</i> sp. <i>Tatera</i> sp. <i>Arvicanthis</i> sp. <i>Aethomys</i> sp. <i>Thallomys quadrilobatus</i> |
| | 131-B | 450 | 450 | 700 | |
| 8 | 8-A | 450 | — | — | |
| | 8-B | 135 | — | — | |
| | 8-C | 115 | — | — | |
| | Total | 6,435 | 18,680 | 3,100 | |

The fossiliferous sediment at 130-A is a brown, sandy silt which changes laterally to a coarse channel sandstone. Within the stratum, there are lenses of brown, silty clay and many calcareous root casts. Lithologically the fossiliferous facies is quite similar to the Type II fossil-bearing facies of Badgley and Behrensmeyer (1980:143). We interpret the sediments as overbank or channel margin deposits. Approximately 28,000 kg of matrix was taken from this locality, and most of the material described here was recovered from this sample. The sediment processed from FxJ,20 (Isaac and Harris, 1978), locality 131-A, was taken from the backdirt of the archaeological excavation, while that from 131-B was taken from a small knoll just to the east of FxJ,20. This archaeological excavation is situated within the Okote Tuff (Leakey and Leakey, 1978:66) and thus lies stratigraphically above locality 130-A. A few isolated teeth were recovered from samples taken from locality 8 in the Ileret Region. These lie

stratigraphically between the samples from 130-A and 131-A. One *Jaculus* molar was recovered in 1984 from 10 meters below the Chari Tuff in Area 3 by Craig Feibel.

All matrix from the various localities was hauled in burlap sacks to the Koobi Fora camp, where it was placed in Lake Turkana to soak. The bags were then hand agitated until only bones, teeth, small calcareous concretions, and a minimum of silt particles remained in the bags. These were dried and the resulting bone concentrate sorted at the Koobi Fora base camp.

Three seasons of fieldwork, approximately 720 man-days of exploration, washing, and sorting, have resulted in the recovery of some eighty specimens of rodents, bats, and insectivores, together with a few fragmentary small bird, amphibian, and reptile bones. Finding fossiliferous horizons that represented suitable depositional environments for the accumulation of small bones and teeth was extremely difficult.

The few concentrations of small vertebrate fossils appear to occur in overbank depressions. Periodic flushing of slow-moving or intermittent small stream channels during intervals of heavy rains and flooding resulted in water spreading over the stream banks to form small pools in which fine-grained sediment and small bones settled out, leaving accumulations of transported small vertebrates. The apparent absence of major permanent rivers east of Lake Turkana in the interval between 1.4 and 1.8 ma was not conducive to the preservation of the microfauna then living in the region. Moreover, the prevailing environment, ephemeral rivers flanked by narrow gallery forest which gave place laterally to open *Acacia* scrub or steppe, offered a limited range of available habitats for small mammals. This might explain the discrepancy in both sample number and diversity between the Koobi Fora microfaunal localities and the much richer but slightly older samples recovered from Olduvai Bed I or Omo Members F and G.

AGE AND CORRELATION

The principal small mammal producing localities, 130-A, 131-A, and 8-A, lie in the lower part of the Upper Member of the Koobi Fora Formation in the *Metridiochoerus andrewsi* and at the base of the *Metridiochoerus compactus* zones of Harris (1983:17). Sediments processed come from the interval between the KBS and Okote tuffs or from within the Okote Tuff itself (131-A). This suggests an age of approximately 1.6 million years for these small mammal assemblages. Harris (1983:18) believes that this portion of the Turkana section was deposited somewhat later than the sediments of Members F to G of the Shungura Formation in the Omo valley based upon the correlation of the Shungura Tuff H2 with the KBS Tuff (Cerling and Brown, 1982). The F and G assemblages would then date at between 2.4 and 2.2 million years. However, the Turkana rodent assemblages from 130-A and 131-A are extremely similar to those from Omo F and G as well as to the rodents from Olduvai Bed I.

While the Turkana material is insufficient to determine which species of *Tatera*, *Arvicanthis*, *Aethomys*, and *Mus* are present, in all cases the material is quite close in size and morphology to that found at the Omo and/or at Olduvai. The Turkana rodent assemblage is not as diverse as that from Members F and G of the Omo, Bed I at Olduvai or the Sidi Hakoma/Denen-Dora section at Hadar. Both Olduvai (Lavocat, 1965) and Laetoli in Tanzania (Denys, in press) have a diverse representation of dendromurine rodents, a group which is not represented in any of the northern faunas. Sciurids are present in the Omo and at both Laetoli and Olduvai but have not been found at Turkana or Hadar.

Based solely on the Muridae, the Turkana assemblages from localities 130-A, 131-A, and 8-A postdate but are most closely comparable to those from the Omo, Members F and G, and from Olduvai Bed I (Table 2).

ENVIRONMENTAL CONSIDERATIONS

The micromammals from 130-A suggest an arid environment with some *Acacia* scrub and perhaps some riverine

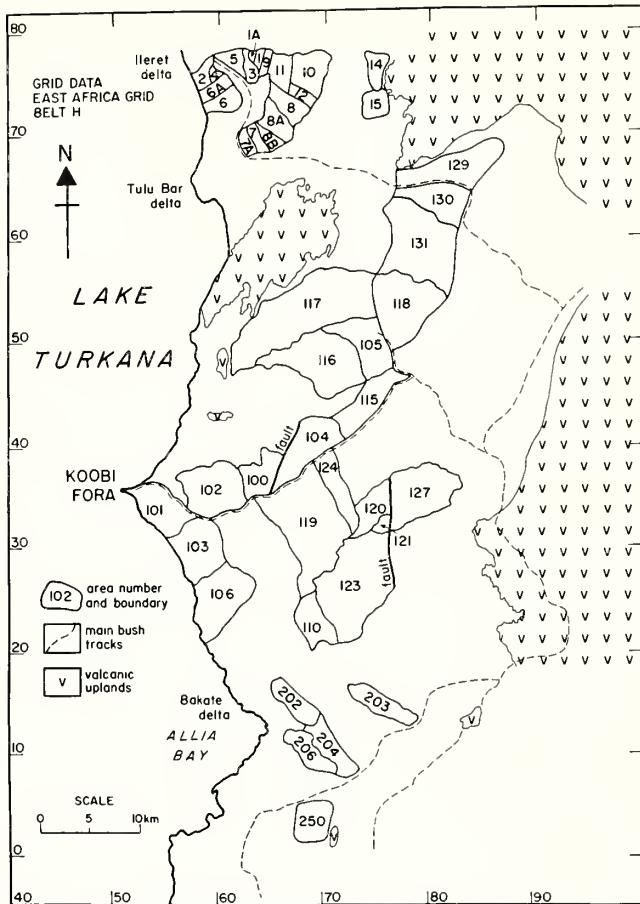


Figure 1. The Koobi Fora region showing location of the paleontological collecting areas. From Harris, 1983.

forest in small patches along intermittent stream channels. The presence of *Thallomys* strongly suggests *Acacia* scrub while *Tatera*, *Arvicanthis*, *Hystrix*, and perhaps *Aethomys* are indicative of dry savanna or river floodplain. *Praomys*, *Mus*, and *Crocidura* all have rather wide ecological tolerance, but require rather thick vegetative cover whether in mesic or arid scrub conditions. This assemblage suggests a limited stream bank forest community rapidly giving place to semi-arid *Acacia* savanna and probably considerable true desert farther removed from the lake shore as indicated by the *Jaculus* specimens from 131-A. A similar environment has been suggested by Wesselman (1984) for the deposition of Members F and G at the Omo. As the Turkana assemblages are younger than those of the Omo perhaps by as much as 500,000–600,000 years, it appears that the arid conditions noted in the Omo F and G members persisted for a considerable period of time.

METHODS

Measurements were made with an ocular micrometer to the nearest 0.01 mm. Measurements were taken at the maximum tooth dimension. Tooth terminology follows that of Butler

Table 2. Distribution of Koobi Fora rodent taxa at other East African Plio-Pleistocene localities.

| | Olduvai Bed I | Omo F and G | Laetoli | Hadar |
|---------------------------------|---------------------|------------------------|-----------------------|---------------|
| <i>Jaculus orientalis</i> | | X | | X |
| <i>Tatera</i> sp. | | X | <i>T. cf. inclusa</i> | |
| <i>Thryonomys</i> spp. | X | X | X | X |
| <i>Hystrix</i> sp. | X | X | X | |
| <i>Arvicanthis</i> sp. | <i>A. primaevus</i> | X | | |
| <i>Aethomys</i> sp. | <i>A. lavocati</i> | <i>A. deheinzelini</i> | | |
| <i>Praomys (Mastomys) minor</i> | X | X | <i>M. cinereus</i> | <i>M. sp.</i> |
| <i>Thallomys quadrilobatus</i> | X | X | n. sp. | |
| <i>Mus</i> sp. | <i>M. petteri</i> | <i>M. minutoides</i> | | X |

(1978) and Missone (1969) except that cingulum is used for both upper and lower teeth following general usage in describing rodent dentition. All specimens are deposited in the National Museum of Kenya.

Abbreviations used are:

KNM-ER—Kenya National Museum, East Rudolf
CMNH—Carnegie Museum of Natural History

W—width

L—length

Tri—trigonid

Tal—talonid

mm—millimeter

SYSTEMATIC PALEONTOLOGY

Order Insectivora

Family Soricidae

Genus *Crocidura* Wagler, 1832

Crocidura sp., cf. *C. nana* Dobson, 1890

Figure 2

REFERRED MATERIAL. RM₂₋₃—KNM-ER 5950, 5953; RM₁—KNM-ER 5951.

LOCALITY. 130-A.

DESCRIPTION. M₁ (L = 1.30; W = 0.80) is relatively unworn and has a high trigonid that is as long as, but narrower than, the talonid. The protoconid, the tallest and largest of the trigonid cusps, is pyramidal, with a long, sloping, anterolabial face, and occupies approximately two-thirds of the trigonid. The metaconid is directly lingual to and about half as high as the protoconid. The well-developed paraconid is lower than the metaconid and juts anterolingually. The posterior walls of the trigonid and talonid are parallel, and perpendicular to the long axis of the tooth. The hypoconid is an angular cusp at the posterolabial corner of the talonid, whereas the entoconid is conical and somewhat laterally compressed. The cristid obliqua meets the trigonid below and labial to the apex of the protoconid, resulting in a shallow hypoflexid notch. The posthypocristid runs directly lingually

to the posterior part of the base of the entoconid where it forms a narrow postentoconid ledge and descends vertically along the posterolingual corner of the talonid. The anterior cingulum is broad; a weak lingual cingulum is discernible along the base of the crown.

M₂ (L = 1.20; W = 0.90) repeats the morphology of M₁, except that it is slightly smaller, and has a slightly longer trigonid than talonid. M₃ (L = 0.80–0.90; W = 0.65) has a well-developed trigonid but a markedly reduced talonid; it is much narrower than the trigonid, unicuspid, and unabashed. The single cusp (?hypoconid) bears a round weak facet. As on M₁ and M₂, a weak cingulum runs along the lingual part of the base of the crown, and a stronger buccal cingulum begins anteriorly below the apex of the paraconid.

DISCUSSION. These teeth most closely resemble comparable parts of the dentition of *C. nana*. They are smaller than those of *C. bicolor*, *C. cyanea*, *C. flavescens*, *C. batesi*, and *C. fumosa*, and slightly smaller than those of *C. dolichura*. M₃, without a talonid basin, differs from that of *C. fumosa*; M₁₋₂, with a posthypocristid that runs directly lingually rather than obliquely, are unlike those in *C. dolichura*.

Referral of this material to *C. nana* is not warranted, however, considering the lack of preserved parts of the upper and anterior dentitions, which are crucial to the identification of crocidurines. P.M. Butler (personal communication) has suggested that this material may belong to a species of *Crocidura* recovered from the Kaffir Beer Cave, Transvaal.

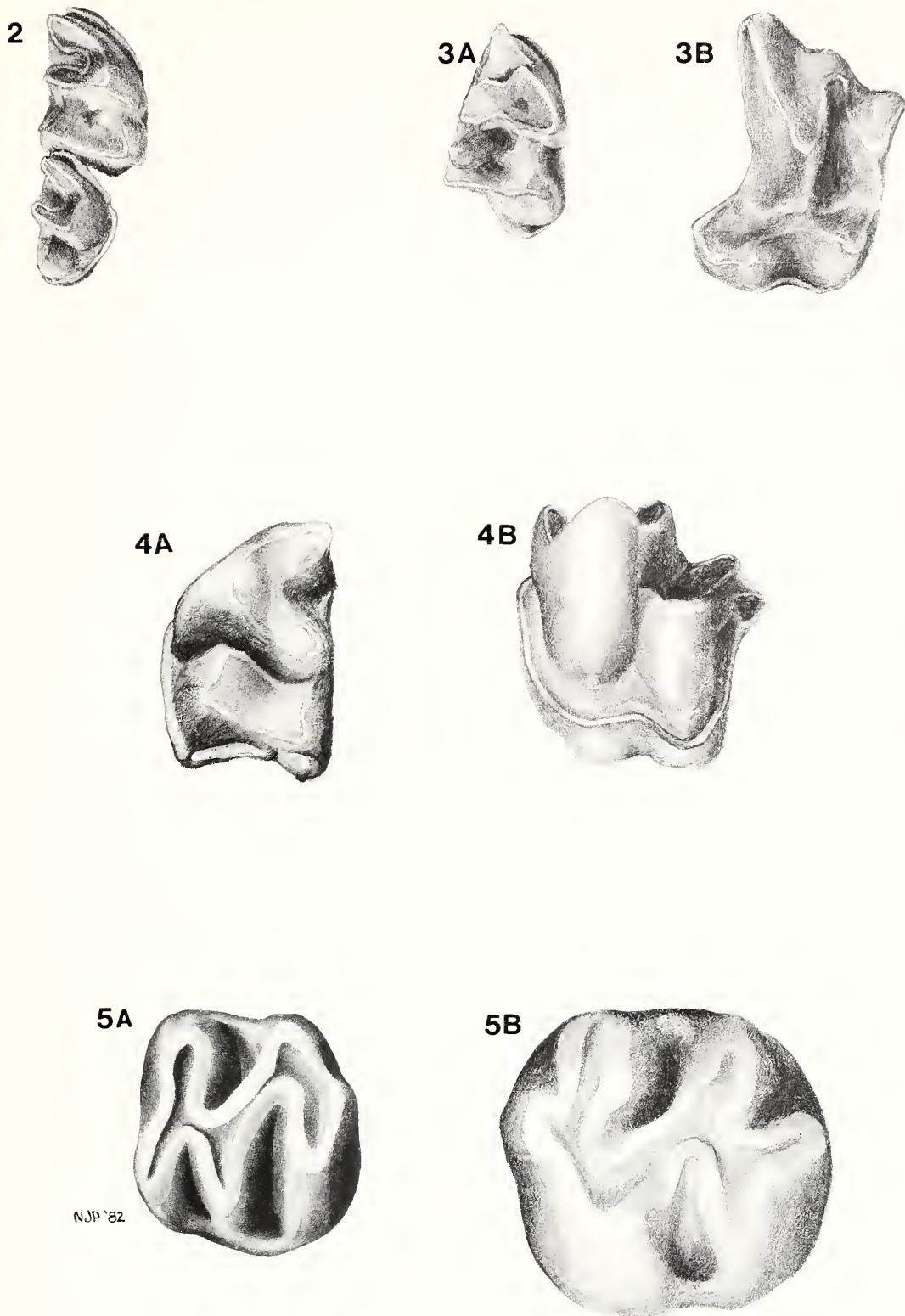
Crocidura sp. cf. *C. dolichura* Peters, 1876

Figure 3

REFERRED MATERIAL. RM₁—KNM-ER 5952; RM¹—KNM-ER 5954.

LOCALITY: 130-A.

DESCRIPTION. KNM-ER 5952 is a right mandibular fragment with M₁ (L = 1.40; W = 1.00), and broken bases of the crowns of P₄ and M₂. The upper half of the protoconid and the posterior portion of the metaconid are broken away from M₁, but it is apparent that these cusps were higher than the paraconid in the undamaged state. On the talonid, which is wider than the trigonid, the entoconid is high, conical, and



Figures 2 through 5. *Crocidura* sp., *Scotophilus* sp., and *Jaculus orientalis*. 2. *Crocidura* sp. cf. *C. nana*. KNM-ER 5953, RM₂₋₃, ×20. 3. *Crocidura* sp. cf. *C. dolichura*. (A) KNM-ER 5952, RM₁; (B) KNM-ER 5954, RM¹, ×20. 4. *Scotophilus* sp. KNM-ER 5955, LM₁, ×20. (A) occlusal view, (B) labial view. 5. *Jaculus orientalis*. (A) KNM-ER 5910, LM₂, ×15; (B) KNM-ER 5911, RM¹, ×20.

somewhat laterally compressed. The hypoconid is V-shaped; the posthypocristid runs lingually and somewhat obliquely to behind the entoconid where it forms a postentoconid ledge. The buccal cingulum is strong, whereas the lingual cingulum—along the entire base of the crown—is weaker. A mental foramen occurs on the mandible below P_4 .

In occlusal view, the crown of M^1 (labial $L = 1.30$; lingual $L = 1.40$; posterior $W = 2.10$) is transverse and trapezoidal: the straight labial and lingual margins diverge posterobuccally and posterolingually from the anterior margin; the posterior border is deeply excavated between the hypoconal shelf and metacone. The latter is approximately twice as large and somewhat higher than the paracone; both cusps are crescentic and form a W-shaped ectoloph with a mesostyle. The hypocone, a cuspule at the anterior end of the hypoconal shelf, is almost directly lingual to the apex of the metacone and is not connected to the postprotocrista. The shelf extends farther posteriorly than does the parastylar salient.

DISCUSSION. This M_1 is slightly larger than that referred to *Crocidura* sp. cf. *C. nana*; both M_1 and M^1 are close in size and morphology to comparative material of *C. dolichura*. Additionally, M^1 is more transverse than in *C. bicolor* and *C. formosa*, and has a less expanded hypoconal shelf than the former.

Order Chiroptera

Family Vespertilionidae

Genus *Scotophilus* Leach, 1821

Scotophilus sp.

Figure 4

REFERRED MATERIAL. LM_1 —KNM-ER 5955; LM^1 or LM^2 —KNM-ER 5956.

LOCALITY. 130-A.

DESCRIPTION. The M_1 ($L = 1.80$; $L_{Tri} = 1.10$; $L_{Tal} = 0.65$; $W_{Tal} = 1.50$) is semi-zalambdodont, with a large trigonid and much lower, shorter, and slightly narrower talonid. The trigonid leans lingually so that, in anterior view, the labial slope of the protoconid is long and inclined approximately 60 degrees to the horizontal. In dorsal view, the occlusal area of the three trigonid cusps occupies only the lingual one-quarter of the basal width of the trigonid. The latter is triangular, with the metaconid and paraconid subequal and situated posterolingual and anterolingual, respectively, to the much higher protoconid. The protoconid is pyramidal, whereas the paraconid and metaconid are somewhat compressed anteroposteriorly. The buccal slope of the hypoconid, like that of the protoconid, is acutely inclined and occupies half of the talonid crown. The hypoconid is V-shaped, with an extremely short cristid obliqua that meets the trigonid below and labial to the apex of the protoconid. The posthypocristid extends posterolingually, parallel to the posterior wall of the trigonid, to the apex of a small, worn entoconid, which, in turn, is linked by a short cristid to the

base of the metaconid. A vertical ridge of enamel on the posterior wall of the talonid below the apex of entoconid may represent an isolated, reduced hypoconulid. A strong basal cingulum is continuous along the anterior, buccal, and posterior surfaces of the crown.

The upper molar is a lingual fragment that preserves the protocone, part of the metacone, and the basolingual wall of the paracone. Like the lower molar, the protoconal portion of this tooth is semi-zalambdodont: the protocone is extremely high, and compressed anteroposteriorly, with a long, oblique lingual slope; its occlusal surface is subcrescentic and small, with very short protocristae. The postprotocrista ends at the lingual wall of the metacone, which is subcrescentic, anteroposteriorly compressed, and approximately one-third higher than the protocone. The V-shaped occlusal surface of the metacone and the preserved portion of the paracone imply that the two cusps were dilambdodont. There are no conules. A strong, basal postcingulum is slightly expanded at the posterolingual part of the base of the protocone, whereas the anterior cingulum is much weaker.

DISCUSSION. These two isolated molars cannot be assigned with confidence to a particular species of *Scotophilus*. The slope of the protocone on the upper molar is higher than in *S. viridus* and also more compressed laterally than in *S. nux* and *S. nigritellus*. The structure of the protocone most closely resembles that in *S. leucogaster* and *S. dinganii*, species that in addition to *S. viridus* also show the development of a hypoconulid on M^1 . However, this cusp on KNM-ER 5955 is more strongly developed.

These two teeth mark the first fossil record of *Scotophilus* (cf. Butler, 1978).

Family Pteropodidae

Genus and species indet.

REFERRED MATERIAL. KNM-ER 5958, RM₁.

LOCALITY. 130-A.

DESCRIPTION. This isolated tooth ($L = 2.50$; $W = 1.40$) corresponds to M_1 of pteropodids in being rectangular in occlusal outline and in having a high, sectorial labial wall, a parallel and much lower lingual wall, and a low, median, longitudinal valley. In external view, the labial wall resembles a triangle in which the anterior slope rises steeply to an apex situated approximately one-third of the distance from the anterior border of the crown. The posterior slope of the labial wall descends more gradually to the posterior edge of the tooth. In medial view, the lingual wall mirrors the shape of the labial one, but its apex, directly opposite that on the labial wall, is only a third as high as the latter. A weak crest joins the two apices and forms the highest point of the median valley where it crosses the crown. The anterior and posterior borders of the crown are gently rounded and the median valley is weakly rugose.

DISCUSSION. This tooth closely resembles M_1 in a number of pteropodid genera, especially *Epomops*, *Epomophorus*,

rus, and *Myonycteris*. A more precise identification is not possible.

?Family Nycteridae

Genus *Nycteris* Geoffroy and Cuvier, 1795

?*Nycteris* sp.

REFERRED MATERIAL. KNM-ER 5957, RC₁.

LOCALITY. 130-A.

DESCRIPTION. This isolated canine ($L = 1.10$; $W = 1.00$) leans posterolingually and is three sided in occlusal cross section: an arc-shaped anterolabial face and flat posterior and lingual faces. A broad, continuous cingulum, which is highest anteriorly, descends sharply ventrolabially and more gently ventrolingually from that point to rim the base of the crown. A cuspule is developed on the posterolingual corner of the cingulum.

DISCUSSION. Referral of this canine to the Nycteridae and *Nycteris* is tentative, although the size of the canine and the structure of the cingulum closely resembles that in the latter.

Chiroptera indet.

REFERRED MATERIAL. KNM-ER 5959, LM₁.

LOCALITY. 131-A.

DESCRIPTION. This isolated lower molar ($L = 2.70$; $W = 1.90$) is worn and much of the enamel on the external faces of the talonid has been eroded. The tooth is rectangular in occlusal outline, with the trigonid approximately as long and wide as the talonid, but twice as high. With the roots oriented vertically, the labial slope of the protoconid is severely canted (approximately 40 degrees to the horizontal), so that the occlusal area bounded by the three trigonid cusps is restricted to the lingual one-third of the basal width of the trigonid. The paraconid, larger and slightly lower than the metaconid, is a pyramidal cusp that forms the anterolingual corner of the crown. The metaconid, more nearly conical than the paraconid, occurs lingual and slightly posterior to the protoconid and directly posterior to the paraconid. As a result, the posterior wall of the trigonid is oriented obliquely posterolingually; the trigonid basin is large and open lingually, whereas it is closed anteriorly and posteriorly by V-shaped cristids that join the protoconid to the paraconid and metaconid.

In posterior view, the external slope of the hypoconid is more nearly vertical than that of the protoconid (approximately 60 degrees to the horizontal), so that the occlusal surface of the talonid occupies approximately the lingual two thirds of the basal width of the crown. The hypoconid, at the posterolingual corner of the talonid, is large, broad at the base and was subcrescentic (if not crescentic) in the unworn, undamaged condition. The entoconid, directly lingual to the hypoconid, was much smaller and conical, judging from its wear facet. A tiny (and mostly eroded) hypoconulid is just posterior to and twinned with the entoconid. The cristid obliqua from the hypoconid meets the trigonid medially,

below and slightly labial to the apex of the protoconid. The posthypocristid runs directly lingually toward the entoconid, but deflects near its base to join the hypoconulid. A strong basal cingulum appears to have been present and continuous along the anterior, labial and posterior aspects of the crown.

DISCUSSION. This tooth most closely resembles M₁ of some Rhinolophidae and Hipposideridae in the open trigonid, the posterolingual orientation of the posterior wall of the trigonid, the trigonid-talonid proportions, and the twining of the entoconid and hypoconulid. However, first and second lower molars in these groups are more nearly dilambodont in that the cristid obliqua meets the posterior wall of the trigonid lingually, near the metaconid, rather than medially as in KNM-ER 5959. Some specimens of *Hipposideros commersoni* and *Rhinolophus eloquens* in the CMNH collections approach KNM-ER 5959 in size and in the orientation of the cristid obliqua, but the similarities are not sufficient to warrant positive referral to these taxa.

Order Rodentia

Family Dipodidae

Genus *Jaculus* Erxleben, 1777

Jaculus orientalis Erxleben, 1977

Figure 5

REFERRED MATERIAL. KNM-ER 5911, RM¹ ($L = 2.45$, $W = 2.35$); K84-2093a, LM₁; KNM-ER 5910, LM₂ ($L = 2.25$, $W = 2.10$).

LOCALITY. 131-A.

DESCRIPTION. The upper molar is moderately worn but shows all occlusal features clearly. The protocone is somewhat larger than the other principal cusps. The protocone and hypocone are set slightly behind the paraeone and metacone to which they are connected by strong crests. A short anterior loph passes from the protocone to the anterointernal margin of the paraeone, forming a shallow notch between the loph and the protoloph. The valley between the paracone and metacone and that between the protocone and hypocone is deep. A short posterior loph passes posteromedially from the hypocone defining a short valley between it and the metacone.

The first lower molar is fragmentary. The second lower molar is somewhat worn and moderately high crowned. The protoconid and hypoconid are set behind the metaconid and entoconid so that the metalophid and hypolophid slant anterolingually. There is a strong lophid from the metaconid that passes anterior to the protoconid with a deep, narrow valley between the lophid and the protoconid. The lingual valley is broad and deep and passes anterobuccally in front of the protoconid-entoconid lophid. The central buccal valley passes posterolingually to the base of the entoconid.

DISCUSSION. The M₂ is similar to that of *Jaculus orientalis*. *Jaculus* has been reported from the Omo Members F and G, again on very few teeth (6), but is unknown at Olduvai, Laetoli, and Hadar.

The M¹ is similar to that figured by Wesselman (1984:

159). In an earlier publication (Black, 1984:113) this tooth was mistakenly identified as that of a ctenodactylid; however, it clearly represents a jerboa. The three teeth from Turkana compare well with those from the Omo.

Family Cricetidae

Genus *Tatera* Lataste, 1882

Tatera sp.

MATERIAL. KNM-ER 2399, LM¹; 2394, RM³.

LOCALITIES. 131-A and 131-B.

DESCRIPTION. The upper first molar ($L = 2.34$; $W = 1.60$) is extremely well worn but still shows the pattern of three cross lophs or crests. The anterior loph is the narrowest; the central loph, the widest. There is the faintest suggestion of an anteroposterior connection between the three lophs in the midline of the tooth. The third upper molar ($L = 1.22$; $W = 1.33$) is not as heavily worn and is about as high crowned as a similar tooth in *Tatera afra* and is of approximately the same size. The first molar is not as broad as that of *T. afra* but is of the same length.

DISCUSSION. With only two isolated teeth of this taxon from the entire Turkana sample, it is impossible to identify accurately the species present. Both teeth come from locality 131, one from the backdirt of the archaeological site FxJ20, and the other from a sample taken 50 meters to the north. Species of *Tatera* are also reported from Olduvai Bed I, Omo Shungara Members B and F, and Hadar.

Family Thryonomyidae

A number of specimens of *Thryonomys*, the cane rat, have been found over the years by others prospecting for hominids and other larger vertebrate fossils. Our field parties recovered several isolated teeth while prospecting in area 8-A, near Ileret, but did not recover any other specimens during our washing operations. *Thryonomys* is known to occur at localities 131, 130, 8, 103, 1-A, and 1. This material has not been studied in detail but only a single species of *Thryonomys* appears to be present.

Family Hystricidae

Hystricids are known from only a few rather fragmentary specimens from Areas 106, 130, and 131. Whether both

Xenohystrix and *Hystrix* are present, as they are at the Omo, has not been determined.

Family Muridae

Genus *Arvicanthis* Lesson, 1842

Arvicanthis sp.

Figure 6

REFERRED MATERIAL. KNM-ER 2396, partial LM¹; 5949, LM¹; 5944, 5945, LM₁₋₂; 5946, 5947, M₂; 5948, RM₃.

LOCALITIES. 8-A and 130-A.

DESCRIPTION. The M¹ has the principal cusps arranged in transverse crests, separated by shallow valleys. T1 and T3 are set only slightly behind T2; they are both smaller than T4 and T6. There is no T7 while T9 is broadly connected to T8.

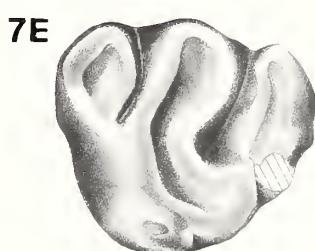
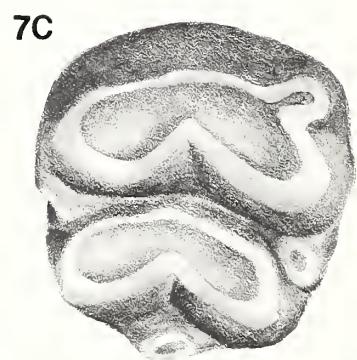
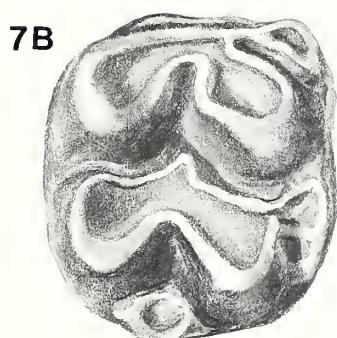
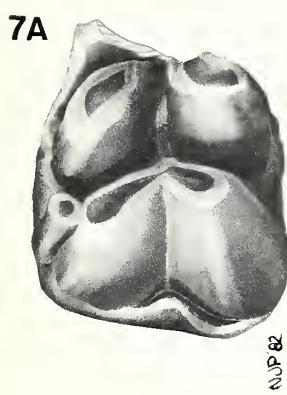
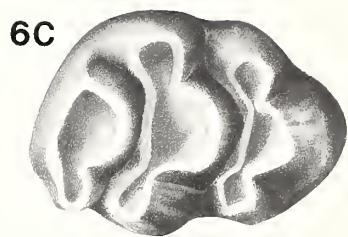
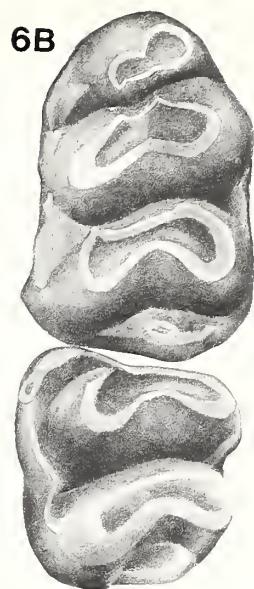
The lower first molars show some variation in the development of the labial cingulum and cingular cusps with Cv5 prominent on 5944, but absent on 5945. On each tooth there is a small cingular ridge between the first and second cross crests. There is no anterior Sm cusp and the posterior cingulum is reduced. The SV and SI cusps form an oblique crest separated from the Epd and Eod crest which shows a weak central ridge directed anteriorly. On M₂, Sv is small and there is no Cv5 on 5945, whereas it is quite small on 5944. The posterior cingulum cusp, Z, is small. M₃ has two transverse crests, the anterior composed of Epd and Eod while the posterior appears to be formed by a single transversely elongate cusp.

DISCUSSION. The oblique posterolabial orientation of the anterior crest on M₁ relates this sample to *Arvicanthis* as does the arrangement of the cusps of M¹ in essentially transverse laminae. These specimens are similar in most respects to those assigned to *Arvicanthis primaevus* (Jaeger, 1976:71)

Table 3. Measurements in mm of molars of *Arvicanthis* sp.

| KNM-ER | | L | W | L | W | L | W |
|--------|------------------|------|------|------|------|------|------|
| 5949 | M ¹ | 2.10 | 1.47 | | | | |
| 5944 | M ₁₋₂ | 2.25 | 1.55 | 1.55 | 1.70 | | |
| 5945 | M ₁₋₂ | 2.21 | 1.47 | 1.47 | 1.50 | | |
| 5947 | M ₂ | | | 1.81 | 1.68 | | |
| 5948 | M ₃ | | | | | 1.50 | 1.42 |

Figures 6 and 7. *Arvicanthis* sp. and *Aethomys* sp. 6. *Arvicanthis* sp. (A) KNM-ER 5944, LM₁₋₂; (B) KNM-ER 5945, LM₁₋₂; (C) KNM-ER 5949, LM¹, $\times 20$. 7. *Aethomys* sp. (A) KNM-ER 5941, LM₁; (B) KNM-ER 2397, M₂; (C) KNM-ER 5942, M₂; (D) KNM-ER 5939, RM¹; (E) KNM-ER 5940, RM³, $\times 20$.



except that they are somewhat smaller and differ in having a more variably developed labial cingulum and Cv5 on M₁.

The Turkana species is closely related to *A. primaevus* from Olduvai but may prove to be specifically distinct when more adequate material is discovered.

Measurements of molars of *Arvicanthis* sp. are given in Table 3.

Genus *Aethomys* Thomas, 1915

Aethomys sp.

Figure 7

REFERRED MATERIAL. KNM-ER 5939, RM¹; 5940, RM³; 5941, partial LM₁; 2395, 2397, 2400, 5942, M₂; 5943, LM₃.

LOCALITIES. 8-A, 104, 131-A.

DESCRIPTION. In the upper molars all of the cusps are inclined toward the rear with the transverse lophs separated by relatively wide valleys. On M¹, T1, T3, T4, and T6 are of similar size and smaller than T2, T5, and T8. T9 is smaller than the other cusps and is slightly anterior to T8. T4 to T9 are strongly connected, while T3 is only connected to T6 at its base. There is a small cingulum around the base of T2 bearing a small internal cusp. The third upper molar is quite large. T1 is large and T3 is absent. T4, T5, and T6 are fused into a strong central crest which is deeply separated from a smaller but still quite strong T8 and T9 crest.

There is only a partial M₁, preserving the posterior two-thirds of the tooth, that may be assigned to *Aethomys*. The four principal cusps are inclined anteriorly with Eod and Epd not joined, whereas Td and End are joined near their summits to form a transverse crest. The lingual cusps are set somewhat ahead of the buccal ones. The buccal cingulum is discontinuous. Cv5 is large, while Z is small. M₂ is a robust tooth with prominent Sv, Cv3, and Z cusps. The transverse crests are strong, with broad fusion of Eod-Epd and Td-End. M₃ is also stout and displays two transverse crests with little sign of individual cusps.

DISCUSSION. These specimens most closely resemble *Aethomys deheinzelini* from Omo Members F and G (Wesselman, 1984:133) but they are somewhat larger. As he noted both the Omo and Turkana species lack any indication of stephanodonty on M¹ such as is seen in *Aethomys lavocati* from Olduvai. The posterior cingulum of M₁ is reduced as in *Aethomys deheinzelini*. However, without additional and more complete specimens of M¹ and M₁ in the Turkana sample it is difficult to determine its exact relationships.

Measurements of molars of *Aethomys* sp. are given in Table 4.

Genus *Praomys* Thomas, 1915

Subgenus *Mastomys* Thomas, 1915

Praomys (Mastomys) cf. *P. (M.) minor*

Jaeger, 1976

Figure 8

REFERRED MATERIAL. KNM-ER 2392, LM₁-M₂; 2393, RM₁-M₃; 5912, RM₁-M₃; 5913, LM₁-M₃; 5914, LM₁-M₃; 5915, RM₂; 5916-5920, M₂; 5921-5922, M₂; 5923, RM¹-M²; 5924-5930, M¹; 5931-5932, M²; 5933, M³.

LOCALITY. 130-A.

DESCRIPTION. As in the material from Bed I at Olduvai, the valleys on M¹ between T2 and T3, and between T5 and T6, are deeply notched, much more so than between T1 and T2 and between T4 and T5. T1 and T4 are set well behind T2 and T5. T9 is large. There are no cingular cusps. On M², T3 is quite small, as is T9.

On the mandible the masseteric crest is a strong ridge which rises from the ventral border of the mandible below M₂ to terminate in a prominent shelf just below the anterior root of M₁. There is a single, large mental foramen just anterior to this shelf and just below the symphysis.

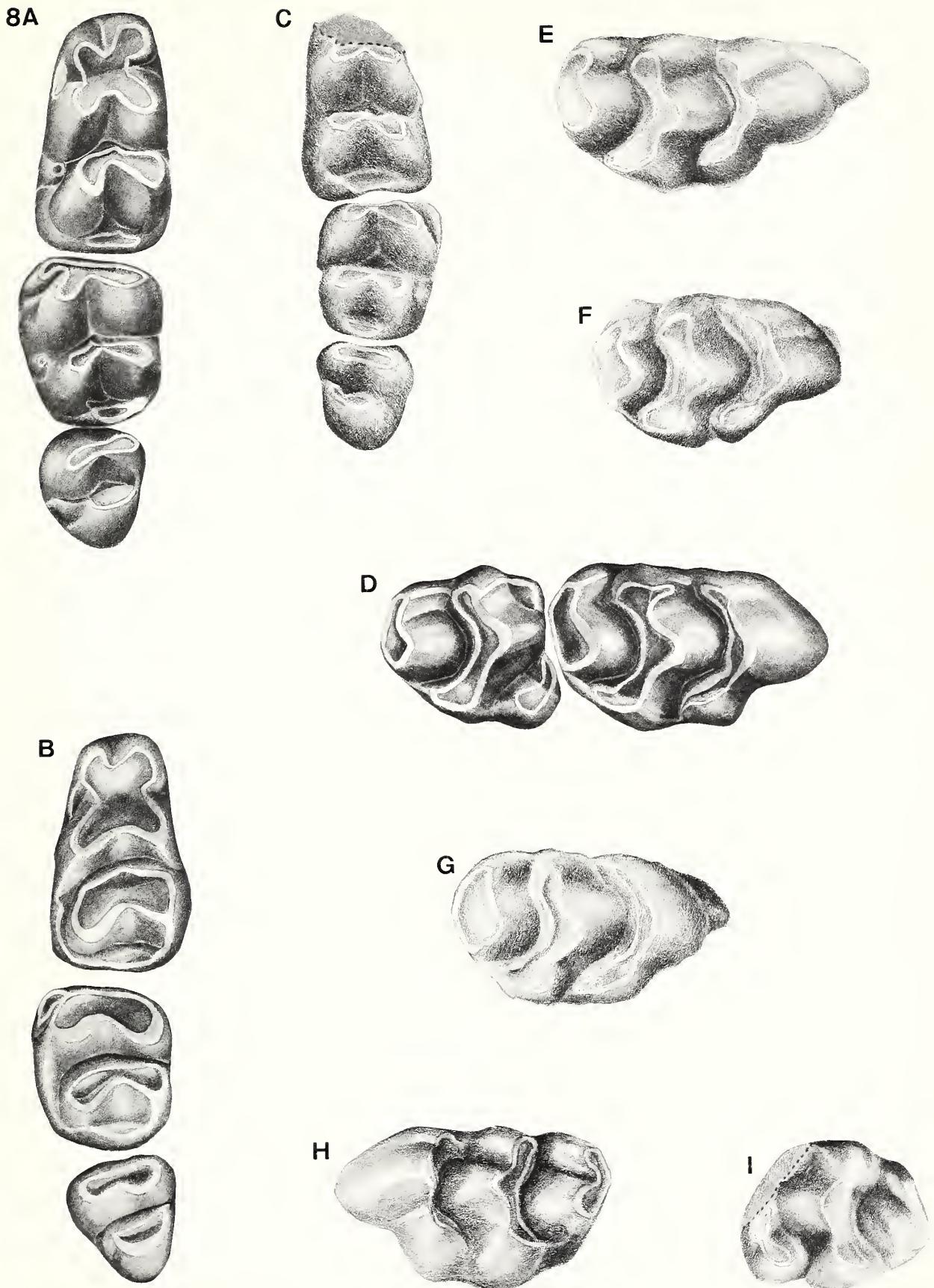
The lower first molar has no Sm and only a trace of the buccal cingulum between Sv and Eod. C5 is present, but small on M₁ and M₂. Z is not present as a distinct cusp, but is merely a thickened posterior shelf on both M₁ and M₂. The four anterior cusps of M₁ form an X pattern with S1 displaced anteromesially. Sv is prominent on M₂.

DISCUSSION. The upper molars from 130-A appear to be somewhat smaller than those of *Praomys (Mastomys) minor* from Olduvai Bed I (Jaeger, 1976:89). The lower molars from the two localities, however, agree quite well in size

Table 4. Measurements in mm of molars of *Aethomys* sp.

| KNM-ER | | L | W |
|----------|----------------|------|------|
| Specimen | | | |
| 5939 | M ¹ | 2.81 | 2.36 |
| 5940 | M ³ | 2.14 | 1.88 |
| 5941 | M ₁ | — | 1.00 |
| 5942 | M ₂ | 2.06 | 2.00 |
| 2395 | M ₂ | 2.13 | 2.15 |
| 5943 | M ₃ | 1.55 | — |

Figure 8. *Praomys (Mastomys)* cf. *P. (M.) minor* (A) KNM-ER 5913, LM₁₋₃; (B) KNM-ER 5914, LM₁₋₃; (C) KNM-ER 2393, LM₁₋₃; (D) KNM-ER 5923, RM₁₋₂; (E) KNM-ER 5928, RM¹; (F) KNM-ER 5930, RM¹; (G) KNM-ER 5927, RM¹; (H) KNM-ER 5929, LM¹; (I) KNM-ER 5932, LM², × 20.



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and the difference in the upper molars may be due simply to a difference in technique of measurement. *Praomys* sp. from Hadar (Sabatier, 1982) is quite close in size to the Turkana sample but differs significantly in morphology. The Omo Member B and Member F *Mastomys* is also referred to *M. minor* (Wesselman, 1984). There is certainly nothing in the occlusal morphology on which to separate the Turkana and Olduvai samples.

Measurements of molars of *Praomys* (*Mastomys*) cf. *P. (M.) minor* are given in Table 5.

Genus *Thallomys* Thomas, 1920

Thallomys quadrilobatus Jaeger, 1976

Figure 9

REFERRED MATERIAL. 5900, 5901, M¹; 2398, 5902, 5903; 5908, M²; 5909, M³; 5904, 5905, M₁; 5906, M₂–M₃; 5907, M₂.

LOCALITIES. 130-A and 8-A.

DESCRIPTION. All teeth are quite similar in occlusal

Table 5. Measurements in mm of molars of *Praomys* (*Mastomys*) cf. *P. (M.) minor*.

| KNM-ER | M ¹ | | M ² | | M ³ | |
|----------------|----------------|----------------|----------------|----------------|----------------|------|
| | Specimen | L | W | L | W | L |
| 5923 | 2.18 | 1.45 | 1.41 | 1.40 | — | — |
| 5924 | 2.10 | 1.47 | — | — | — | — |
| 5925 | 2.13 | 1.45 | — | — | — | — |
| 5927 | 2.10 | 1.43 | — | — | — | — |
| 5928 | 2.13 | 1.43 | — | — | — | — |
| 5929 | 2.30 | 1.36 | — | — | — | — |
| 5930 | 2.14 | 1.33 | — | — | — | — |
| 5931 | — | — | 1.60 | 1.34 | — | — |
| 5932 | — | — | 1.69 | 1.31 | — | — |
| 5933 | — | — | — | — | 1.09 | 1.15 |
| M ₁ | | M ₂ | | M ₃ | | |
| L | W | L | W | L | W | |
| 2392 | 2.13 | 1.22 | 1.35 | 1.24 | — | — |
| 2393 | — | 1.07 | 1.22 | 1.10 | 0.81 | 0.85 |
| 5912 | 2.00 | 1.23 | 1.40 | 1.22 | 0.85 | 0.96 |
| 5913 | 2.11 | 1.20 | 1.50 | 1.25 | 1.10 | 0.95 |
| 5914 | 2.10 | 1.25 | 1.40 | 1.25 | 1.07 | 0.97 |
| 5915 | 2.13 | 1.15 | — | — | — | — |
| 5916 | — | — | 1.40 | 1.24 | — | — |
| 5917 | — | — | 1.45 | 1.14 | — | — |
| 5918 | — | — | 1.48 | 1.25 | — | — |
| 5919 | — | — | 1.45 | 1.35 | — | — |
| 5920 | — | — | 1.40 | 1.15 | — | — |
| 5921 | — | — | — | — | 1.13 | 1.00 |
| 5922 | — | — | — | — | 1.10 | 1.00 |

morphology to those of Recent *Thallomys paedulcus* from Zimbabwe to those of *Thallomys quadrilobatus* from Bed I of Olduvai figured by Jaeger (1976). The cheek teeth are slightly broader and perhaps larger overall than those of *T. paedulcus*.

On M¹, T1 and T4 are set distal to T3 and T6 with a short crest passing from the base of T3 towards T6. The stephanodont crests from T4 to T8 and from T6 to T9 are distinct but low. The cusp T9 is perhaps larger in the Turkana species than in the living species and there is a faint indication of posterior cingular Z, a structure not present in the living forms. The M² is strongly stephanodont with well-developed crests from T4 to T8 and T6 to T9. The T1 is a strong columnar cusp not flattened transversely as in the living species. Also, T9 is a much stronger cusp than that on M² of *T. paedulcus* and there is a small but distinct posterior cingular Z present on the Turkana M²s. M³ has a strong T1 and a distinct but transversely flattened T3. On the central crest T4, T5, and T6 are distinct with T5 displaced towards the anteroexternal corner of the crown. As the one M³ in this collection is relatively unworn, both T8 and T9 are discernible in the posterior loph, which is distinctly separated from the T4–T5–T6 loph by narrow valleys.

The first lower molar is essentially indistinguishable from M₁ of *T. paedulcus*, the only difference being the presence of a very low, faint Sm ridge between Sv and S1 and a slightly broader posterior shelf between the End and Td cusps in the fossil. The buccal cingulum is continuous from the posterior border of Sv to the rear of Td. There appears to be a Cv5 cusp on the cingulum. There are anteroposterior crests which unite S1, Sv, Epd, and Eod along the midline of the tooth and also a short, anteriorly directed midline crest for End and Td. The four principal cusps on M₂ unite with short anteriorly directed crests in the midline. Both Sv and C₃ cusps are present as is a strong Z cusp. On M₃ a small Sv is present. On the posterior loph the End cusp is large and transversely expanded, with only a very small Td component to this loph.

DISCUSSION. The specimens here assigned to *Thallomys quadrilobatus* are essentially identical to those described by Jaeger (1976) from Bed I at Olduvai. Jaeger considered *T. quadrilobatus* to be directly ancestral to the modern species of *Thallomys* and we agree. A reduction in size of T9 and decrease in size or loss of the posterior cingulum (Z) on M¹ and M², together with reduction of Sm on M₁ are all that separate the fossil from the modern species.

Measurements of molars of *Thallomys quadrilobatus* are given in Table 6.

Genus *Mus* Linnaeus, 1758

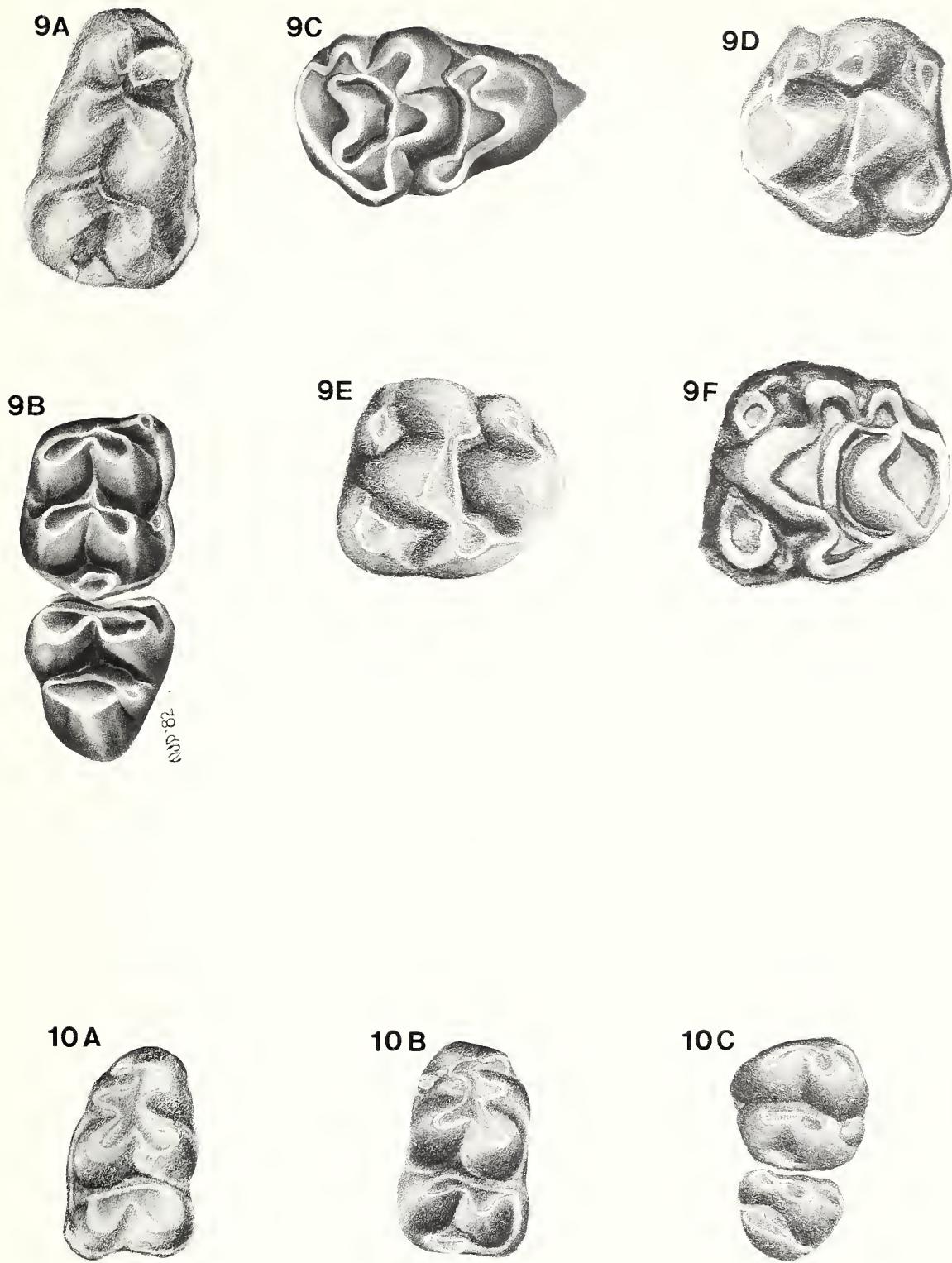
Mus sp.

Figure 10

REFERRED MATERIAL. 5934–5937, M₁; 5938, RM₂–M₃.

LOCALITY. 130-A.

DESCRIPTION. Only lower molars of this small species of *Mus* have been recovered. M₁ has a short crest directed



Figures 9 and 10. *Thallomys quadrilobatus* and *Mus* sp. **9.** *Thallomys quadrilobatus*. (A) KNM-ER 5904, RM₁; (B) KNM-ER 5906, RM₂₋₃; (C) KNM-ER 5900, RM¹; (D) KNM-ER 5903, RM²; (E) KNM-ER 5902, LM²; (F) KNM-ER 2398, LM², ×20. **10.** *Mus* sp. (A) KNM-ER 5935, LM₁; (B) KNM-ER 5936, RM₁; (C) KNM-ER 5938, RM₂₋₃, ×20.

Table 6. Measurements in mm of molars of *Thallomys quadrilotatus*.

| KNM-ER Specimen | | L | W |
|--------------------|----------------|------|------|
| 5900 | M ¹ | 2.45 | 1.68 |
| 5901 | M ¹ | 2.44 | 1.66 |
| 2398 | M ² | 1.61 | 1.57 |
| 5902 | M ² | 1.69 | 1.59 |
| 5903 | M ² | 1.60 | 1.60 |
| 5908 | M ² | 1.64 | 1.72 |
| 5909 | M ³ | 1.64 | 1.46 |
| 5904 | M ₁ | 2.21 | 1.32 |
| 5905 | M ₁ | 2.27 | 1.45 |
| 5907 | M ₂ | 1.75 | 1.49 |
| 5906 | M ₂ | 1.76 | 1.49 |
| | M ₃ | 1.49 | 1.41 |

internally from the anterointernal corner of S1. There is no anterior Sm cusp, although on KNM-ER 5935, the anterior crest is somewhat swollen. S1 is anterolingual on all the first molars. The buccal cingulum is continuous from Sv to the posterior border of M₁ and Cv5 is present on KNM-5936, while on the other M₁s it is absent. A small Z ridge or ledge is present. Sv and Sv5 are small on M₂ and on M₃ only a narrow Sv is present. M₃ is not greatly reduced.

DISCUSSION. The specimens here referred to as *Mus* are the smallest of the Turkana murids and are just slightly larger than the teeth of *Mus petteri* from Olduvai Bed I (Jaeger, 1976). However, in the absence of any upper first molars, reference to any specific species of *Mus* is not possible. The Turkana species differs from *Mus petteri* in possessing the anterior crest from Sv and a somewhat more prominent buccal cingulum on M₁. A distinct species of *Mus* may have been present at Turkana but more material is needed to characterize it.

Measurements of molars of *Mus* sp. are given in Table 7.

CONCLUSIONS

1. The assemblage from locality 130-A at Turkana, while somewhat younger than those from the Omo Members F and G Olduvai Bed I, most closely resembles those local faunas.

Table 7. Measurements in mm of molars of *Mus* sp.

| KNM-ER Specimen | | L | W |
|--------------------|----------------|------|------|
| 5934 | M ₁ | 1.68 | 0.96 |
| 5935 | M ₁ | 1.66 | 1.00 |
| 5936 | M ₁ | 1.69 | 1.09 |
| 5937 | M ₁ | 1.64 | 1.00 |
| 5938 | M ₂ | 1.08 | 1.00 |
| 5938 | M ₃ | 0.71 | 0.75 |

2. The Turkana rodents strongly suggest an arid environment with intermittent stream drainages bordered by sparse riverine forest and *Acacia* scrub.

3. Some 720 man-days of fieldwork produced only 80 specimens of rodents, bats, and insectivores. Suitable depositional environments for preservation of small mammals thus, appear to be quite rare in the Koobi Fora Formation.

ACKNOWLEDGMENTS

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THREE NEW LUMINESCENT OSTRACODES OF THE GENUS
VARGULA (MYODOCOPIDA, CYPRIDINIDAE)
FROM THE SAN BLAS REGION OF PANAMA

Anne C. Cohen and James G. Morin



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

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THREE NEW LUMINESCENT OSTRACODES OF THE GENUS *VARGULA* (MYODOCOPIDA, CYPRIDINIDAE) FROM THE SAN BLAS REGION OF PANAMA

Anne C. Cohen¹ and James G. Morin²

ABSTRACT. Three new species of luminescent myodocopid ostracodes, *Vargula graminicola*, *V. shulmanae*, and *V. contragula* from the San Blas Islands, Panama are described. *V. graminicola* and *V. shulmanae* are sibling species differing in few morphological characters but distinctive in diet, habitat, and bioluminescent patterns. They are compared to *Vargula parasitica* (Wilson, 1913), a morphologically similar Jamaican ostracode. *V. contragula* is morphologically a very distinct species. All three new species produce distinctive bioluminescent patterns in the water column at night. *V. graminicola* occurs within and above shallow marine seagrass beds, *V. shulmanae* occurs primarily within and over steep slopes and walls of deeper coral reefs, and *V. contragula* is found mainly on gorgonian dominated shallow low profile coral reefs and slopes.

RESUMEN. Se describen tres nuevas especies de ostrácodos mio-docopidos luminiscentes, *Vargula graminicola*, *V. shulmanae* y *V. contragula* de las islas de San Blas, Panamá. *V. graminicola* y *V. shulmanae* son especies gemelas que difieren en pocos caracteres morfológicos pero que se diferencian claramente en su dieta, hábitat y patrones de bioluminiscencia. Estas especies son comparadas con *Vargula parasitica* (Wilson, 1913), un ostráculo de Jamaica de similar morfología. *V. contragula* es una especie morfológicamente muy diferente. Las tres nuevas especies producen patrones de bioluminiscencia distintos en la columna de agua durante la noche. *V. graminicola* se encuentra en el interior y por encima de lechos de praderas de yerbas marinas de poca profundidad, *V. shulmanae* está principalmente en el interior y sobre pendientes pronunciadas y murallas de arrecifes de coral más profundos, en tanto que *V. contragula* habita principalmente en arrecifes y pendientes de poca profundidad dominados por corales gorgónicos.

INTRODUCTION

Many species within the ostracode genus *Vargula* Poulsen, 1962, are known to be luminescent. Luminescent nocturnal displays, presumably for purposes of sexual communication, have been shown to occur within the genus in the U.S. Virgin Islands (Morin and Bermingham, 1980). During nocturnal surveys of the reefs and surrounding habitats of the San Blas Islands, Panama, the junior author discovered a wide variety of distinctive luminescent display patterns produced by os-

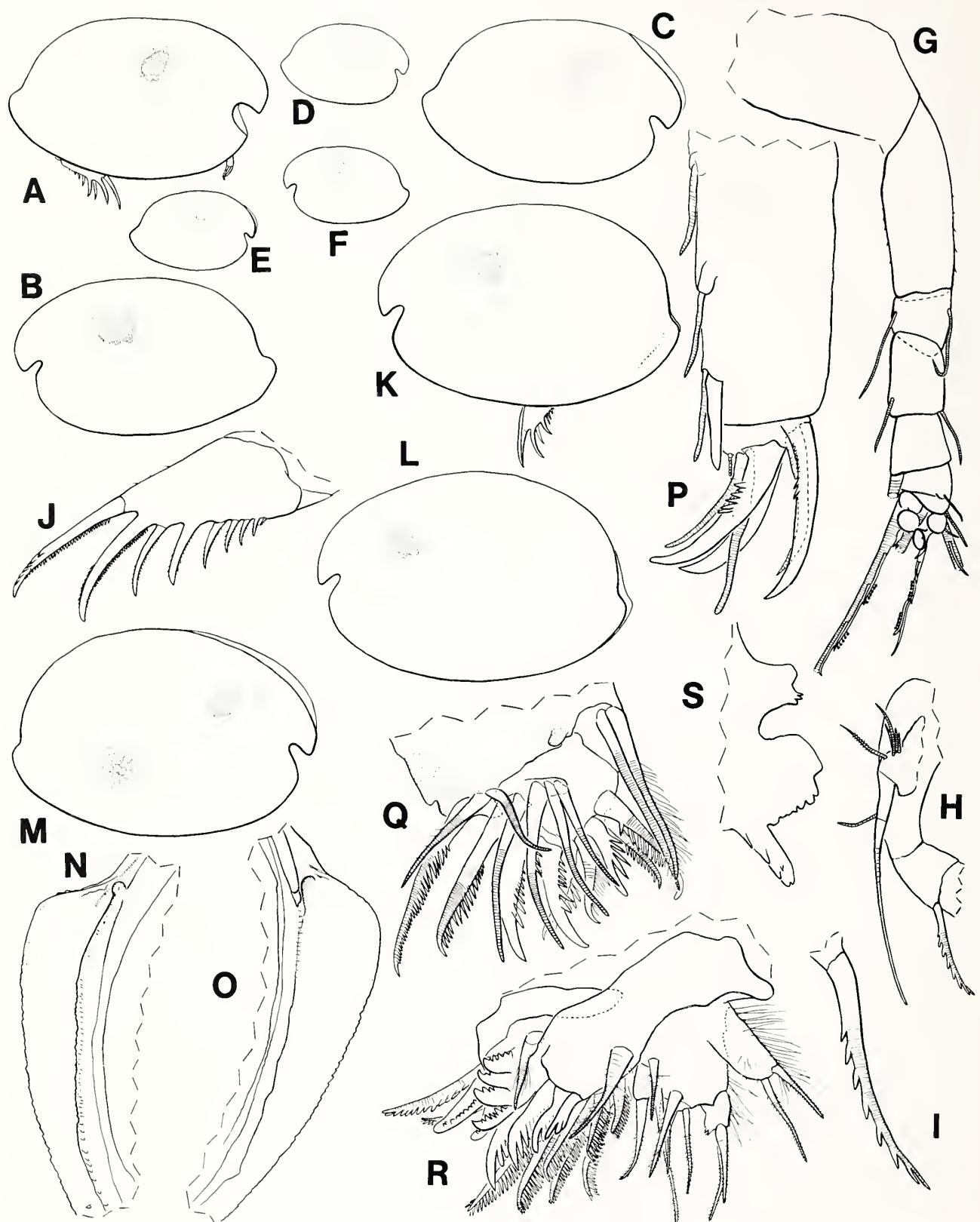
tracodes that were closely associated with particular habitats. From our collections, it has become clear that each luminescent pattern is produced by a distinctly different species and that each species is associated with a particular habitat; thus there is a great deal of resource partitioning among these ostracodes. Furthermore, it appears that all of these species are undescribed. This paper is the first of several in which we describe these species and aspects of their biology. Papers dealing with their population biology, activity patterns, and bioluminescent displays are in preparation. Three obvious and abundant luminescent *Vargula* species in the shallow Caribbean waters of Panama are described here.

MATERIALS AND METHODS

Specimens were collected using a variety of methods but all were caught at night when they are most active in the water column and along the substrate surfaces. Specimens were caught in the water column 1) indiscriminately using a diver-pushed double plankton net ($\frac{1}{3}$ m diameter, 0.5-mm mesh) or, more often, by sweeps through the luminescent displays. Diver-collected sweeps were done either 2) repeatedly using a 20-cm diameter, 0.5-mm mesh net through the displays or 3) individually using a 'discrete trap.' A discrete trap consisted of a double-walled triangular net (24 cm on a side and 0.5-mm mesh) sealed together on two sides and with Velcro across the top so that it could be sealed or opened into a cone. After passing the cone through a discrete luminescent display the contents could be trapped inside by pressing the Velcro together. In both sweep collection methods the luminescent display type observed consistently correlated with the expected species actually caught (see general biology sec-

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tions). Epibenthic collections were made by attracting ostracodes to 4) fish carcasses enclosed in plastic window screen (to keep out most of the isopods and other larger organisms) [=fish trap] or 5) 'cone traps.' These cone traps were baited with dead fish and made from weighted plastic freezer containers ($8 \times 8 \times 6$ cm) with four 2-cm holes cut through on the sides. Each hole was covered by window screen (1.7-mm mesh) on the outside (to let in ostracodes but keep out isopods) and a cone of 0.5-mm mesh plankton netting with a 2-mm inner orifice on the inside.

Details of the luminescent displays were obtained by direct observations, timed analysis of underwater tape recordings of divers comments, and laboratory observations. Details of all these methods will be presented elsewhere (Morin, in preparation). Ostracodes were usually preserved by 1) placing them for 10–15 min in a mixture of 50% seawater and 50% 0.36 M MgCl₂ (isotonic to seawater) [this mixture acted as an anesthetic to relax but not kill the ostracodes], 2) transferring them to buffered 4% formaldehyde for 10–20 min for fixation, and then 3) placing them in 70% ethanol (usually they were transferred to a second 70% ethanol solution later). Using a dissecting microscope, overall body measurements were made to the nearest 0.02 mm on both living and preserved ostracodes (both were equal). All other measurements were made using a compound microscope.

Holotypes and some paratypes are deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. The remaining paratypes are deposited in the USNM and in the Natural History Museum of Los Angeles County (LACM).

SYSTEMATICS

Vargula graminicola, new species

Figures 1, 2, 3A, 3B, 4A

HOLOTYPE

USNM 193214 adult male, length 1.71, height 1.06 mm; in alcohol. **Sample 19.** 6 Sept. 1983 of about 1930 hr, $\frac{1}{4}$ –2 m above bottom at 5-m depth over grass bed just west of T-Bar

Reef, San Blas, Panama; taken by sweep net; Diana Pilson, col.

ALLOTYPE

USNM 193215 gravid adult female, length 2.01, height 1.33 mm; in alcohol. **Bottle 10** (data below).

PARATYPES

Sample 32. 8 Sept. 1983 at 2010–2020 hr, 1–2 m above turtle grass at 5-m water depth ca. 10–15 m west of T-Bar Reef, San Blas, Panama; sweep nets of lower part of 20 luminescent displays; J.G. Morin, col.; 1 male (JM3-A, on slide and in alcohol), 3 males (JM3-K, with choniostomatid copepods), 91 males (JM3-C-E, J, L), 4 A–2 males (JM3-F, N) (LACM). **Sample 19.** 6 Sept. 1983 at about 1930 hr, $\frac{1}{4}$ –2 m above bottom at 5-m depth over grass bed just west of T-Bar Reef, San Blas, Panama; taken by sweep net—part of haul; Diana Pilson, col.; 112 males, 1 juv. (USNM 193218, 193219, 193220, 193221). **Bottle 10.** 31 Aug. 1983 at 1900–2000 hr, ca. 4 m east of T-Bar Reef, San Blas, Panama, about 5-m depth; "fish trap" in sand blowout; J.G. Morin, col.; 1 female (JM10-10-T-X, with choniostomatid copepod), 1 female, 1 male (JM10-10-T-W), 10 females (JM10-10-T), 1 female, 1 ?A–2 ovigerous female (JM10-10-T-Y) (LACM). **Bottle 9.** 31 Aug. 1983 at 1900–2000 hr, on east side of T-Bar Reef, San Blas, Panama, about 3-m depth, "fish trap" among corals on reef; J.G. Morin, col.; 1 male, 1 female (USNM 193216, 193217). **Bottle 18.** 6 Sept. 1983 at 2000 hr on east side of T-Bar Reef, San Blas, Panama, "fish trap" on grass bed; J.G. Morin, col.; 1 male, on SEM stub and in alcohol, 1 male on SEM stub, and 1 female on SEM stub (LACM). **JM Box 1#24.** 12–13 Dec. 1983 between 2400 and 0200 hr (combined from 1 collection each night), sweep nets $\frac{1}{4}$ –2 m above turtle grass at 5-m depth ca. 100–200 m west of Vieja Reef, San Blas, Panama; J.G. Morin, col.; 1 female (B, on slide and in alcohol), 1 male (A) (LACM). **JM Box 2#14-A.** 12–13 Dec. 1983, data same as JM BOX 1#24; 1 male (on slide and in alcohol) (LACM). **Sample 1210.1a.** 12 Oct. 1984 at 1900–1915 hr, on grass beds northwest side of Reef 26 (Macaroon), San Blas, Panama, about 4-m water depth; bait-

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Figure 1. *Vargula graminicola*. A. JM3-A, male, valve length 1.75 mm: right lateral view of complete specimen showing valve, lateral eye, and tips of right mandible and furca. B, C. USNM 193216, male, length 1.71 mm, lateral views of complete specimen showing valve and lateral eye: B. Left valve; C. Right valve. D. USNM 193219, male, length 1.71 mm, lateral view of complete specimen showing valve and lateral eye. E. Holotype, USNM 193214, length 1.71 mm, left lateral view of complete specimen showing valve and lateral eye. F. USNM 193219, male, length 1.71 mm, lateral view of complete specimen showing valve and lateral eye. G. 2310.3-A, male, length 1.67 mm, medial view of left 1st antenna (d–e-bristles and distal parts of sensory, c–f, g-bristles not shown). H, I. JM3-A, male, length 1.75 mm, 2nd antenna: H. Medial view of endopodite and first 2 joints of exopodite; I. Bristle of 2nd exopodite joint. J. USNM 193216, male, left lamella of furca. K. JM Box 1-24B, female, length 2.01 mm, left lateral view of complete specimen, showing valve, lateral and medial eyes, furca, and caudal list (dotted line). L, M. USNM 193217, female, length 2.01 mm, lateral views of complete specimen: L. Left valve and lateral eye; M. Right valve, lateral eye, and eggs (dotted lines). N–S. JM Box 1-24B, female: N. Inside view of caudal process of left valve; O. Inside view of caudal process of right valve; P. Tip of left mandible, medial view, showing 3rd and distal 2nd joints of endopodite; Q. Tip of right maxilla, lateral view, showing 2nd and distal 1st joints of endopodite; R. Exopodite of right 5th limb, posterior view; S. Anterior of body and upper lip.

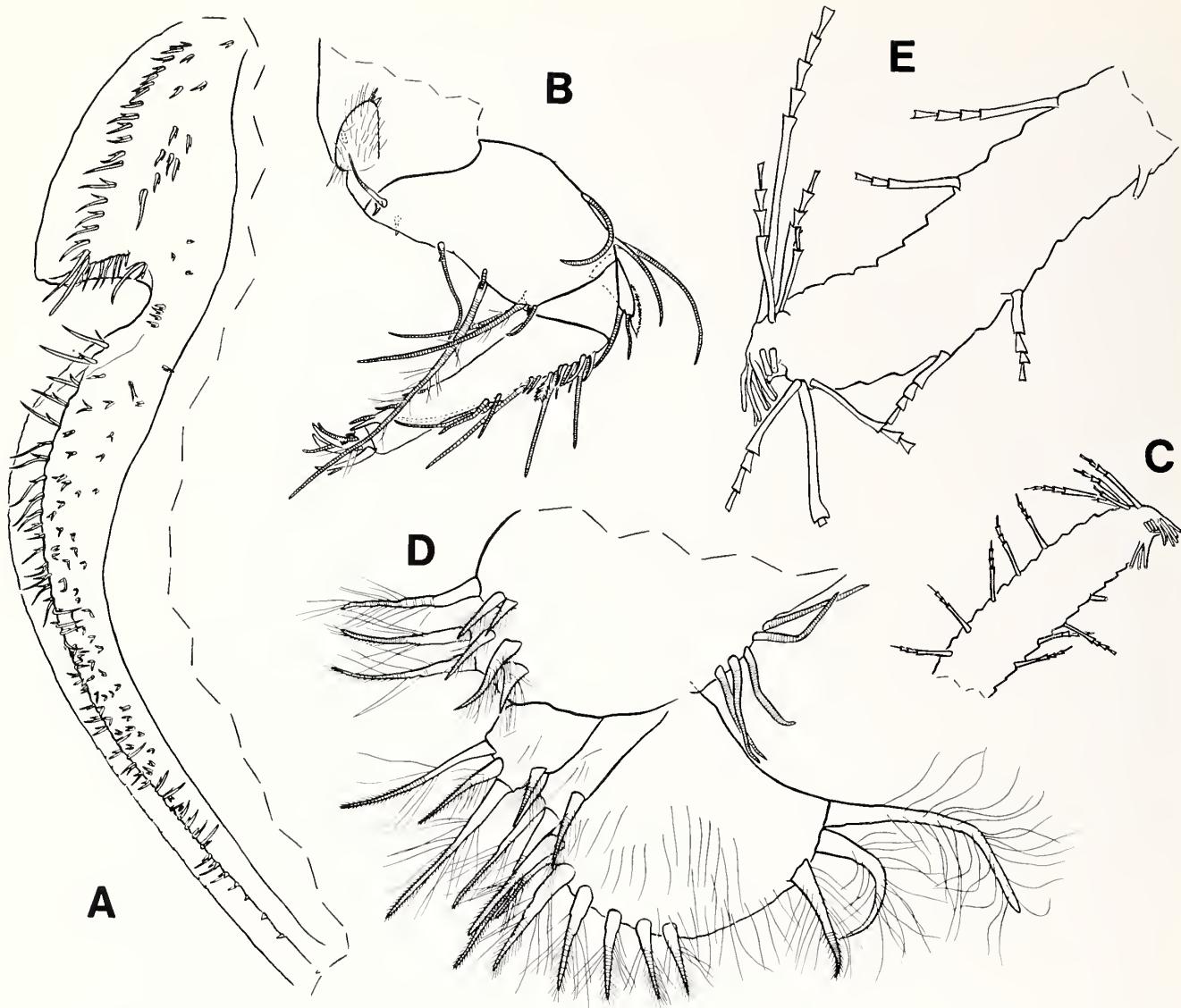


Figure 2. *Vargula graminicola*. A-C. JM Box 1-24B, female, length 2.01 mm: A. Inside view of anterior end of right valve; B. Left mandible, medial view; C. Tip of 7th limb. D, E. JM3-A, male, length 1.75 mm: D. 6th limb; E. 7th limb.

ed multiple cone trap; J.G. Morin, col.; 3 females (A-C) (LACM). **Sample 2310.3.** 23 Oct. 1984 at 1830–1910 hr, on grass beds ca. 40 m west of Reef 26, San Blas, Panama, about 5-m water depth; baited multiple cone trap; J.G. Morin, col.; 1 male (A), 5 males (B) (LACM).

DIAGNOSIS. Caudal process low (below incisur), and shaped as triangular curved point. Female carapace length 1.80–2.25 mm; male 1.52–1.85 mm. Furca: 9 pairs of claws; claws 2 and 4 fused to lamella; claw 4 broader than, but not longer than claw 3. Second antenna: Bristle on 2nd endopodial joint with 6–8 (usually 7–8) stout ventral spines. Mandible: No terminal bristles with bulbous base. Maxilla: 2 alpha-, 3 beta-bristles, 4 a-, 3 b-, and 3 c-bristles. Fifth limb: 4th and 5th exopodial joints separated by suture; 4 bristles

on 4th joint, 2 bristles on 5th joint. Infold: Rostrum with row of 19–33 bristles parallel to outer margin plus 0–2 bristles anterior to and 4–12 bristles posterior to row; anteroventral infold with row of 38–53 bristles plus 20–69 bristles posterior to row. Seventh limb: Longest of 7 long teeth in comb lateral, not central; with peg opposite comb; without dorsal jaw. Lip: Tusks unbranched, with terminal and distal short hairs (sparser in females).

ETYMOLOGY. *Vargula graminicola* is derived from the Latin *graminis* which means “of or pertaining to grass” and the Latin *-icola* which means “an inhabitant.” This species inhabits seagrass bed habitats.

DESCRIPTION OF ADULT MALE. Carapace (Figs. 1A–F, 3A, 4A). Similar to that of adult female, only about 90% as long but more elongate, with short but larger, more pointed

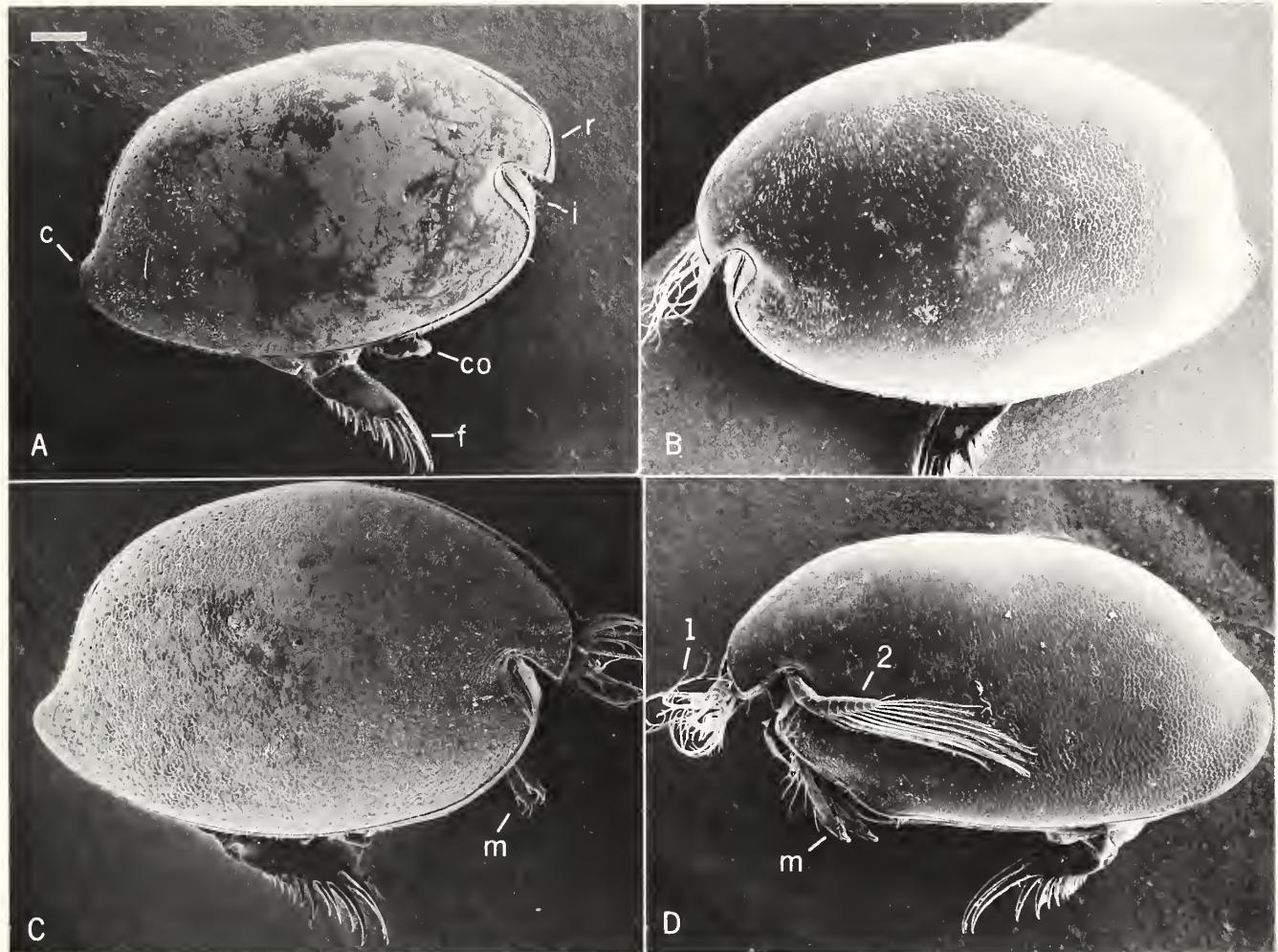


Figure 3. *Vargula graminicola*, *V. shulmanae*, and *V. contragula*. **A, B.** *Vargula graminicola*. **A.** Bottle 18; 6 Sept. 1983, SEM-1A-179 specimen #3, male, right lateral view showing valve, furcae, and copulatory organ. **B.** Bottle 18; 6 Sept. 1983, SEM-1B-168 specimen #2, female, left lateral view showing valve, proximal furcae, and distal setae of first antennae. **C.** *Vargula shulmanae*, 2111.6-SEM-1C-237 specimen #6, male, right lateral view showing valve, furcae, and distal 1st antennae and mandibles. **D.** *Vargula contragula*, 2310.1a-SEM-3a-197 specimen #2, male, left lateral view showing valve, furcae, distal 1st and 2nd antennae, and mandibles. Scale bar = 200 μm . **r** = rostrum; **i** = incisur; **c** = caudal process; **1** = 1st antenna; **2** = 2nd antenna; **m** = mandible; **co** = copulatory organ; **f** = furca.

(shaped as triangular curved point), caudal process, and straighter dorsal margin.

Infold. Infold of rostrum with about 22–33 double bristles forming row parallel to rostral margin and continuing posteriorly along incisur margin (about 3–8 along incisur margin), 0–2 double bristles anterior to row, about 4–12 double bristles posterior to row, 1–2 double bristles near dorsal edge of incisur and 1–3 tiny double bristles dorsal to inner edge of incisur. Anteroventral infold with row of 4–5 double bristles near inner edge of incisur, 1–2 short double bristles near posterior edge of incisur infold, about 38–53 double bristles paralleling margin and continuing onto ventral infold (including 2–5 bristles on anteroventral incisur margin), about 20–69 double bristles posterior to row, row followed posteriorly on left valve by 3–8 widely spaced single bristles; list becoming broader in vicinity of caudal process with posterior

fringe (fringe usually with minute pointed processes), list with 10–38 tiny bristles (unclear, about 38 in left valve), possibly with 1 tiny bristle posteroventral to list, about 10–12 tiny bristles or projections (unclear in left valve) forming row paralleling posterior edge of caudal process. Left valve with caudal list ending dorsally in knob. Right valve similar to that of female.

Selvage. Selvage with lamellar prolongation with smooth edge and striations present along ventral and anterior margins of valves; lamellar prolongation along ventral margin of incisur broader and with striations more visible than elsewhere.

Size. USNM 193214 length 1.71, height 1.06 mm (holotype). Range ($n = 113$) for all specimens measured: length 1.52–1.85 mm, height 0.91–1.10 mm.

First antenna (Fig. 1G). First joint bare; 2nd joint with

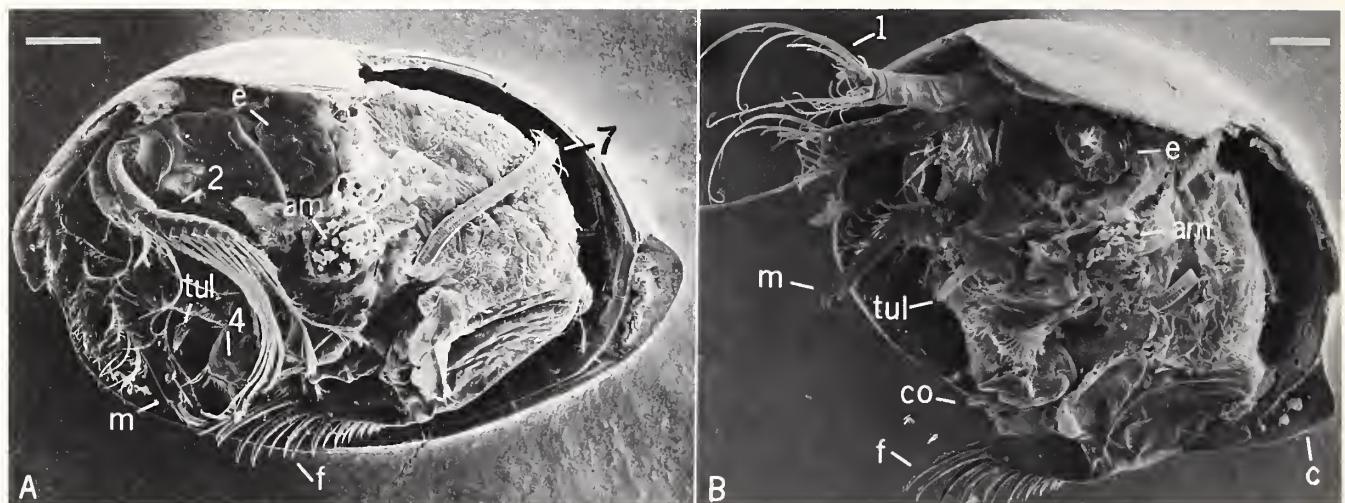


Figure 4. *Vargula graminicola* and *V. shulmanae*. A. *Vargula graminicola*, Bottle 18; 6 Sept. 1983, SEM-2B-252 specimen #1, male, inside view; left valve, 1st antenna and 5th limb removed. B. *Vargula shulmanae*, 2111.6-SEM-2C-233 specimen #1, male, inside view; left valve, 2nd antenna, mandible, maxilla, 5th and 6th limbs removed. Scale bars = 200 μm . c = caudal process; 1 = 1st antenna; 2 = 2nd antenna; m = mandible; 4 = 4th limb (maxilla); 7 = 7th limb; co = copulatory organ; f = furca; e = lateral eye; tul = tusk of upper lip; am = severed ends of central adductor muscles.

spines forming medial rows and on dorsal margin. Third joint short, ventral margin half or less than half length of dorsal margin, with medial spines forming row, 1 dorsal spinous bristle just proximal to middle and 1 long spinous terminal medial ventral bristle; 4th joint with 1 spinous terminal or subterminal dorsal bristle and 1 spinous distal or terminal ventral medial bristle. Sensory bristle of 5th joint with 10 long proximal filaments, 2 more slender distal filaments and bifurcate tip, bifurcate tip and last filament with narrowed tips. Sixth joint with short spinous medial bristle near distal margin. Seventh joint: a-bristle spinous, longer than bristle of 6th joint; b-bristle with stout proximal filament with bulbous base followed by large sucker, short filament with narrowed tip, and small distal process ending in narrowed pointed tip, 2 distal slender filaments each bearing 5–6 small suckers (distal filament not extending beyond tip of bristle); c-bristle similar to b-bristle but about twice as long, and with larger basal filament and sucker; bristle with 2 distal filaments with 4–5 small suckers, about 7 long slender bare distal filaments, and bifurcate tip. Eighth joints: d- and e-bristles bare, filamentous, about same length as b-bristle, tips blunt or with minute process; f-bristle with 8–9 slender filaments increasing in length distally, some with 1–3 spines; g-bristle with 10 slender filaments increasing in length distally and with 1 spine each (except last filament), bifurcate tip; c-, f-, and g-bristles long (g-bristle longest), longer than sensory bristle of 5th joint.

Second antenna (Figs. 1H, I, 4A). Protopodite with short spinous distal medial bristle. Endopodite 3-jointed: 1st joint with 4 proximal bristles (1 short, 3 very short) and 1 short distal spinous bristle; 2nd joint elongate with 1 short terminal bristle (missing on 1 limb examined), 3rd joint about $\frac{1}{2}$ – $\frac{1}{3}$ length of 2nd joint with long terminal filament (Fig. 1H). Exopodite: 1st joint with spines on dorsal margin; 2nd joint

with rows of medial and lateral spines crossing ventral margin, bristle not reaching or almost reaching end of 9th joint, with 6–7 stout ventral spines (Fig. 1H, I); joints 3–8 with basal spines becoming longer distally and with bristles with natatory hairs; lateral spine of 9th joint slightly larger than spine of 8th joint; 9th joint with 4 bristles (2 longest with natatory hairs, 1 not as long with natatory hairs and short spines, 1 shorter with short spines).

Mandible (Fig. 4A). Coxale endite spinous, with bristle near base. Basale: Ventral margin with 1 short and 1 long spinous a-bristle with bases on medial side, 1 short b-bristle with base on lateral side (close to a-bristles), 1 long spinous and 1 short c-bristle near middle of margin, and 2 distal d-bristles, both some distance from c-bristles (1 shorter with short spines and 1 very long with long proximal and short distal spines); dorsal margin with 1 long spinous distal bristle with short spines and 2 long unequal subterminal bristles with short spines. Exopodite with medial hirsute dorsal process extending to pointed tip and 2 long ventral bristles with short spines (distal shorter). First endopodial joint with 4 ventral bristles (1 long with long proximal and short distal spines, 1 long with short spines, 2 short with short spines). Second endopodial joint: Medial and lateral rows of spines or hairs, dorsal margin with 16–18 bristles (5–6 long spinous bristles, 5 shorter bristles with short spines or hairs, 4–6 short hirsute medial bristles, 2 short stout medial bristles with stout spines or possibly hairs); ventral margin with 2 single distal bristles (bristles with bases together on 1 limb of 1 specimen) and 1 subterminal bristle equal in length to and with base on lateral side of base of stout finger-like subterminal unringed process (probably modified bristle) [tips either bifurcate or hollow and middle bristle extending beyond base of subterminal bristle]; process not touching 3rd joint and with slender rounded point usually extending beyond or to end of

3rd joint. End joint with 3 long claws with proximal spines and 4 bristles, none with bulbous base and none longer than claws (1 dorsolateral bare and slightly ringed claw-like bristle extending almost to end of dorsal claw, 1 prominent short bare ventral bristle, 1 long [$\frac{3}{4}$ claw length] spinous ventral medial bristle with bifurcate tip, 1 long stout, but not bulbous, spinous lateral bristle extending to tip of claws).

Maxilla. Endite I with 12 stout spinous claw-like bristles; endite II with 4 spinous bristles (3 long stout), endite III with 4–5 spinous bristles (4 stout, long). Coxale with stout dorsal bristle proximally hirsute and with short distal spines. Basale with 1 long spinous lateral bristle, 1 long spinous medial bristle on or near ventral margin and base of exopodite and 1 spinous terminal medial bristle (may be on 1st endopodal joint). Exopodite with 1 long proximal bristle with long proximal hairs and short distal spines and 2 long terminal bristles (1 with long proximal hairs and short distal spines, 1 with short spines only). First endopodial joint with rows of medial hairs, 2 alpha-bristles (outer bristle longer with long hairs, inner bristle with short spines), 3 beta-bristles (outer longest and pectinate, inner 2 with short spines); cutting tooth large and prominent, bifid (proximal projection with rounded point, distal projection more than twice as large with rounded squarish shape); additional short rounded tooth on terminal lateral margin near ventral margin. Second endopodial joint with 4 long distally ringed a-bristles (2 longest with proximal short spines); 3 long, stout, very pectinate claw-like b-bristles (1 unringed, 2 ringed); 3 distally ringed c-bristles (2 very pectinate, 1 short); 3 stout, very pectinate d-bristles (1 ringed).

Fifth limb. Epipod with 42–48 bristles. Protopodite with large distal undulate anterior tooth and 1 long anterior bristle with long proximal and short distal spines. Endite I with 7 stout unequal bristles (6 with long spines, 1 short with shorter spines); endite II with 5–6 bristles (5 stout with long spines including 2 distally pectinate); endite III with 7 unequal bristles (most stout with long spines, 5 distally pectinate). First exopodial joint with 6 pectinate teeth and 1 proximal peg (smooth except for tiny spines on tip), 1 large spinous bristle near peg, row of 4 anterior bristles with long proximal spines or hairs (1 of 2 short proximal bristles may be on protopodite, 2 distal bristles longer, stouter); 2nd exopodial joint with 10–11 long stout pectinate claw-like end bristles arranged somewhat into 3 rows (4 bristles unringed, claw-like), and 1 posterior bristle with long proximal hairs and long distal spines. Inner lobe of 3rd exopodial joint hirsute, with 3 bristles (1 proximal posterior with long proximal hairs and short distal spines and 2 terminal with short spines); outer lobe hirsute with 2 terminal bristles with short spines (1 with long proximal hairs or spines). Fourth and 5th joints hirsute, separated by faint but distinct suture, 4th joint with 4 subterminal bristles with short spines, 5th joint with 2 terminal bristles with short spines and terminal group of spines (5th joint with 2 lobes, each with 1 bristle in JM2-C, but only 1 lobe in JM3-A).

Sixth limb (Fig. 2D). Hirsute laterally, 5 bare bristles in place of epipod. Endite I with 3 bristles (2 short with long hairs, 1 long with longer hairs); endite II with 5 bristles (3 short with long hairs, 2 long with long proximal hairs and

short distal spines); endite III with 4 bristles with long proximal hairs and short distal spines (2–3 long, 1–2 short); endite IV with 3 bristles with long proximal hairs (2 long with short distal spines, 1 short). End joint spinous, with 6–7 spinous bristles decreasing in length posteriorly, each with long stout distal spine-like hairs (1 more medial with shorter proximal spines), followed by space and 3 hirsute posterior bristles increasing in length posteriorly (anterior of these with stout distal spines). Limb with suture separating end joint from proximal part of limb, partial suture at base of endites III and IV (sometimes II).

Seventh limb (Figs. 2E, 4A). Comb side with 1–2 distal and 3–4 terminal bristles, each with 2–4 bells; peg side with 3 distal and 3 terminal bristles, each with 2–3 bells. Comb consisting of 7 long spinous teeth with widened tips (2 lateral and 1 middle teeth shortest) and 4 short blunt teeth (2 on each side) with long basal spines and possibly with bumpy tips. Single procumbent short peg (slightly shorter than short comb teeth) with hook-like inner basal protuberance and terminal wreath of about 8 tiny teeth; terminal surface between comb and peg possibly ridged at base of comb.

Furca (Figs. 1J, 3A, 4A). Each lamella with 9 claws; claws 2 and 4 fused to lamella, remaining claws separated from lamella by suture; claw 3 more slender than but about same length as claw 4; claws 1 and 2 with long row of posterolateral (a few proximal teeth longer on claw 2) and distal row of medial teeth; all remaining claws with long row of posterolateral teeth and at least claws 3–5 with medial teeth.

Bellonci organ. Short, cylindrical, rounded.

Eyes. Medial eye small, pigmented (sometimes restricted to band). Lateral eye about twice size of medial eye, pigmented, with about 12 ommatidia. Lateral eye length ranges in size from 0.23 to 0.30 mm and pigmented area from 0.20 to 0.25 mm ($n = 113$). Eye pigment brown in reflected light; maroon or maroon-brown in transmitted light.

Upper lip. Anterior undivided part with numerous glandular processes with unpigmented lobular tips and proximal bands of maroon pigment; middle part with 2 long tusks, 1 on each side; each tusk with short distal and terminal hairs and with glandular processes (1 terminal and 3–6 posterior; processes sometimes appearing to have pointed tips); part posterior to tusks, rounded, hirsute (proximal hairs bunched).

Anterior of body. Rounded projection dorsal to 2–3 shorter usually pointed projections.

Posterior of body. Smooth.

Copulatory organ (Fig. 3A). Anterior lobe rather conical, longer than short posterior lobe, which has at least 1 group of about 3 bristles.

DESCRIPTION OF ADULT FEMALE. Carapace (Figs. 1K–M, 3B). Oval with deep incisur and protruding caudal process; anteroventral, posteroventral, posterodorsal, and anterodorsal margins broadly rounded. Greatest height near middle; not markedly higher in posterior half. Caudal process small (slightly larger in right valve than in left), dorsal margin rather straight, forming obtuse angle with rather truncate posterior margin of valve, dorsal edge of process slightly shorter than dorsal edge of incisur; both incisur and dorsal

edge of process at about midheight of valve. Dorsal edge of incisur slightly overlapping ventral edge at inner end; faint line on outer surface of valve curving from inner dorsal edge of incisur to anterior margin of valve ventral to incisur. Tip of rostrum with few nodes. Outer surface smooth but with faint pattern resembling overlapping scales, visible at 100 \times ; scale-like pattern producing minute points on anteroventral and posteroventral margin. Surface with rather regularly distributed small pores, some with minute bristles.

Infold (Figs. 1N, O, 2A). Similar to that of adult male except rostrum (Fig. 2A) with about 7–10 double bristles posterior to main row of 19–30 double bristles, 0–1 bristle anterior to row; anteroventral infold with row of about 38–51 double bristles parallel to margin (including about 2–4 on anteroventral margin of incisur) about 34–64 double bristles posterior to row; 0–3 bristles posteroventral to list near beginning of caudal process, list of caudal process in left valve (Fig. 1N) with numerous tiny bristles and projections forming irregular row and posterior margin with tiny ripples, caudal list straight except for slight bend in dorsal half, caudal list of left valve terminating dorsally with round knob and possibly with a rounded dorsally directed process with posterior groove, dorsal and posterior to knob; caudal list of right valve (Fig. 1O) with more than 50 tiny bristles, sometimes with minute pointed processes or fringe on ventral posterior edge, caudal list rather straight, ending in raised dorsally directed bar; small pocket formed in infold posterior to dorsal end of caudal list, pocket may be half socket (open ventrally) receiving knob from left valve.

Selvage. Similar to male.

Adductor muscle scars. About 13 irregular scars, some divided.

Size. USNM 193215 length 2.01, height 1.33 mm (allotype). Range ($n = 24$) for all specimens measured: length 1.80–2.25 mm, height 1.18–1.43 mm.

First antenna. Similar to male except b-bristle of 7th joint about $\frac{1}{3}$ – $\frac{1}{2}$ longer than a-bristle, with 2 short proximal filaments; c-bristle with about 8 filaments (with teeth or spines) becoming longer distally, about 6 times length of b-bristle; 8th joint with distal filament of f- and g-bristles much longer than others, small round knob at medial dorsal base of f-bristle.

Second antenna. Similar to male except exopodite with bristle of 2nd joint not reaching 9th joint, with 7–8 spines and with narrowed ringed tip.

Mandible (Figs. 1P, 2B). Similar to male except bristle apparent on coxale endite of 1 limb but not other limb of specimen examined; 2nd endopodite joint with 15–16 dorsal bristles, only 1 short medial bristle bearing stout spines; ventral margin of 2nd joint (Fig. 1P) with 2 single distal bristles and 1 subterminal bristle together with subterminal unringed finger-like sclerotized process sometimes extending beyond 3rd joint; 3rd endopodite joint with 1 of 4 bristles (stout ventral lateral) extending just beyond claws (Fig. 1P).

Maxilla (Fig. 1Q). Similar to adult male.

Fifth limb (Fig. 1R). Similar to adult male except proximal protopodite (coxale?) with pair of small sclerotized teeth bearing minute teeth or spines; both exopodite joints 1 and

2 appearing to arise independently from protopodite of specimen examined; joint 1 has a more medial base and could be considered an endopodite; joint 3 arises from joint 2 and joints 2–5 could be considered joints 1–4 of an exopodite.

Sixth limb. Similar to adult male.

Seventh limb (Fig. 2C). Similar to adult male except comb side with 4–5 distal and 5 terminal bristles, peg side with 4–5 distal and 3 terminal bristles. Comb consisting of 7 long teeth (similar to those in male) and 6 short blunt teeth (3 on each side). Peg similar to that of male but about same length as short comb teeth.

Furca. Similar to that of adult male.

Bellonci organ. Similar to that of adult male but with blunt end.

Eyes. Similar to those of adult male but lateral eye about 1½ times as large as medial eye. Overall size and ommatidia size of lateral eye smaller than in male. Length ranged from 0.21 to 0.26 mm and pigmented area from 0.16 to 0.21 mm ($n = 24$).

Upper lip. Lip similar to that of adult male except tusk with very faint short hairs (Fig. 1S).

Anterior of body. Anterior of body with rounded projection dorsal to 3–5 shorter usually pointed projections (Fig. 1S).

Posterior of body. With a few short hairs.

Genitalia. Sclerotized ring with attached spermatophores.

Eggs. JM10-10T-Z with 20 eggs in ovary; the largest egg was 0.22 mm. 1210.1a, 3 females with 15–18 eggs in ovary. Other females had smaller eggs.

Ovigerous juvenile. One small ovigerous female (JM10-10-T-1) bears about 18 eggs/ovary (eggs = 0.023–0.027 mm). It has the diagnostic characters shared by *V. graminicola* and *V. shulmanae* (valve shape; furcal claws; distal bristles of mandible, maxilla, and 5th limb; 7th limb comb). It has the specific diagnostic characters of *V. graminicola*: 6 (lowest adult number) stout spines on the 2nd exopodite bristle of the 2nd antenna and rostral infold with 4–6 bristles posterior to row of 21–22 bristles. We identify this female as a juvenile, probably an A-1 instar, because it has these juvenile characters: length only 1.22 mm, height 0.80 mm; 7th limb with only 2 bristles, both terminal, strongly tapered and with only 1 bell; furca with only 7 claws; anteroventral infold with only 14–16 bristles (this high number also shows affinity with *V. graminicola*) posterior to row of 27–30 bristles.

GENERAL BIOLOGY. Geographical distribution. Caribbean; known from the vicinity of the western San Blas Islands, Panama (9°33'14"N, 78°55'23"W).

Habitat. *Vargula graminicola* is abundant in shallow (3–10 m) sea grass (*Thalassia testudinum* and *Syringodium filiforme*) beds with good water circulation and away from coral reefs and sand ‘blowouts’.

Ecology, behavior, and bioluminescence. *Vargula graminicola* is a benthic species that in Panama lives in current-swept sea grass beds within the turf, rubble, and top few mm of the sand. Individuals are infaunal by day and epibenthic and demersal by night. Sex ratios appear to be about 1:1 below the level of the top of the sea grass (ca. 15 cm) and in the substrate, but above the sea grass highly skewed at night

toward males. Males become demersal zooplankters above the sea grass at night if a bright moon is not present; females are only occasionally found up in the water column. The males appear in the water column in large numbers about 45 min after sunset and remain there most of the night as long as there is no moonlight. Much of the time they are found at the level of the sea grass, but, periodically, they rise obliquely or vertically upward (ca. 50–90°) in linear clusters, each time producing a species specific group luminescent display. They swim at a rate of about 11.1 ± 1.4 (sd) cm s⁻¹ ($n = 31$ laboratory trials of individuals). Each group may contain from 2 to 40 males. The light occurs as a train of short duration extracellular secretions left behind by each rapidly swimming male. Each light pulse, which appears as a discrete point source, has a duration of 0.28 ± 0.08 s ($n = 109$). Each cluster of pulses is spaced about 15 to 25 cm from the next; the spacing is even for a given train. There are usually 8 to 12 pulse clusters per train, each train takes about 18 s to produce and is about 1.5 to 2 m in total length. Trains are repeated at about 60-s intervals. There is loose synchrony of different trains within a large area of the sea grass (>50 m²) and clusters of displaying males are horizontally separated by 15 cm to about 1 m or more. These luminescent displays apparently act as calling signals by the upwardly swimming males to the sexually receptive epibenthic females who then swim up into the water column. Presumably the females copulate with at least one of the males. Details of mating are unknown. The females are capable of luminescing, but apparently do not do so during these nocturnal displays. The displays continue for most of the night until about an hour before dawn. The frequency of the displays, however, is most intense during the first hour or two.

It is not known what *V. graminicola* feeds on naturally, but they are the only *Vargula* species in the San Blas strongly attracted to fish or crustacean carrion. Along with about equal numbers of *Skogsbergia lernerii* as many as 10,000 *V. graminicola* (males, females, and juveniles) have been captured from a single fish carcass in less than 1 hr at night. They have been observed to be preyed upon by demersal fishes (including *Holocentrus rufus*) and a cerianthid (?*Arachnanthus nocturnus*) and an actiniarian (?*Aiptasia tagetes*) anthozoan; all cases of predation initiated a long-lasting (>20 s) luminescent glow from the ostracode. Papers detailing the luminescent display patterns (Morin, in press) and the population biology of *V. graminicola* are in preparation.

Color of live ostracodes. Males are similar in color to females and are mostly transparent except for the eyes (see above), the region of the luminescent organs (=light organs) and the abdomen. The light organ is a yellow-brown rectangular region in the upper lip below the eye. The abdomen is an orangish-brown to tan color. This color may be affected by diet since they become paler in captivity when fed solely on white muscle from fish.

Parasites. Four ostracodes contained copepod parasites belonging to the Choniostomatidae (identification verified by T. Bowman). One female (JM10-10-T-X) with 20 eggs in its ovary had 1 female choniostomatid loosely attached to the exterior posterodorsal part of the body within the mar-

supium area of the valves. Three males (JM3-K) each bore a male choniostomatid loose within the anterior part of the valve near the base of the 1st and 2nd antennae. One or 2 of these also had a female attached to the dorsal body just posterior to the heart. Choniostomatid parasites have been reported previously in cypridinid ostracodes including a species of *Vargula* (Kornicker, 1975; Bradford, 1975).

Vargula shulmanae, new species

Figures 3C, 4B, 5, 6

HOLOTYPE

USNM 193222 adult male, length 1.94, height 1.25 mm; in alcohol. **Sample 1212.12.** 12 Dec. 1984 at 1840–1940 hr, about 12–14-m depth on reef wall, Sail Rock, San Blas, Panama; discrete traps of displays; J.G. Morin, col.

ALLOTYPE

USNM 193223 adult female, length 2.35, height 1.65 mm; in alcohol. **Sample 2111.5** (data below).

PARATYPES

Sample 2510.3. 25 Oct. 1984 at 1845–1905 hr, about 4-m depth on reef wall, Sail Rock, San Blas, Panama; sweep nets of displays; J.G. Morin, col.; 1 male (A, on slide and in alcohol), 46 males (C–T) (LACM). **Sample 2510.1a.** Data as in Sample 2510.3; J.G. Morin, col.; 1 female (C, on slide and in alcohol) (LACM). **Sample 2011.2.** 20 Nov. 1984 at 1840–1910 hr, about 6–9-m depth on reef slope, Korbiski Reef, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 2 males (A, B) (LACM). **Sample 2111.2.** 21 Nov. 1984 at 1838–1902 hr, about 11–15-m depth on reef wall, Sail Rock, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 52 males (A–F) (USNM 193224, 193225, 193226, 193227, 193228, 193229), 3 juv. (G) (USNM 193233). **Sample 2111.3.** Data as in Sample 2111.2; J.G. Morin, col.; 1 female (LACM). **Sample 2111.5.** Data as in Sample 2111.2; J.G. Morin, col.; 2 juv. (B), 1 ?A–1 ovigerous female (C) (LACM). **Sample 2111.6.** Data as in Sample 2111.2; J.G. Morin, col.; 1 male, on SEM stub and in alcohol, and 1 male on SEM stub (LACM). **Sample 2311.5.** 23 Nov. 1984 at 1842–1920 hr, about 8–10 m depth on reef slope, Korbiski Reef, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 2 males (A, B), 1 juv. (LACM). **Sample 2311.8.** Data as in Sample 2311.5; J.G. Morin, col.; 2 males (A, B, with choniostomatid copepods), 2 males (C, D) (LACM). **Sample 1212.9.** 12 Dec. 1984 at 1840–1940 hr, about 12–14 m depth on reef wall, Sail Rock, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 2 males (LACM). **Sample 1212.12.** Data as in Sample 1212.9; J.G. Morin, col.; 1 male (C), 1 female (A, lost?) (LACM). **Sample 1312.1.** 13 Dec. 1984 at 1843–1910 hr, about 4-m depth on low reef, Reef 26 (Macaroon), San Blas, Panama; discrete trap of display; J.G. Morin, col.; 1 male (B) (LACM).

DIAGNOSIS. Caudal process low (below incisur) and shaped as triangular curved point. Female carapace length

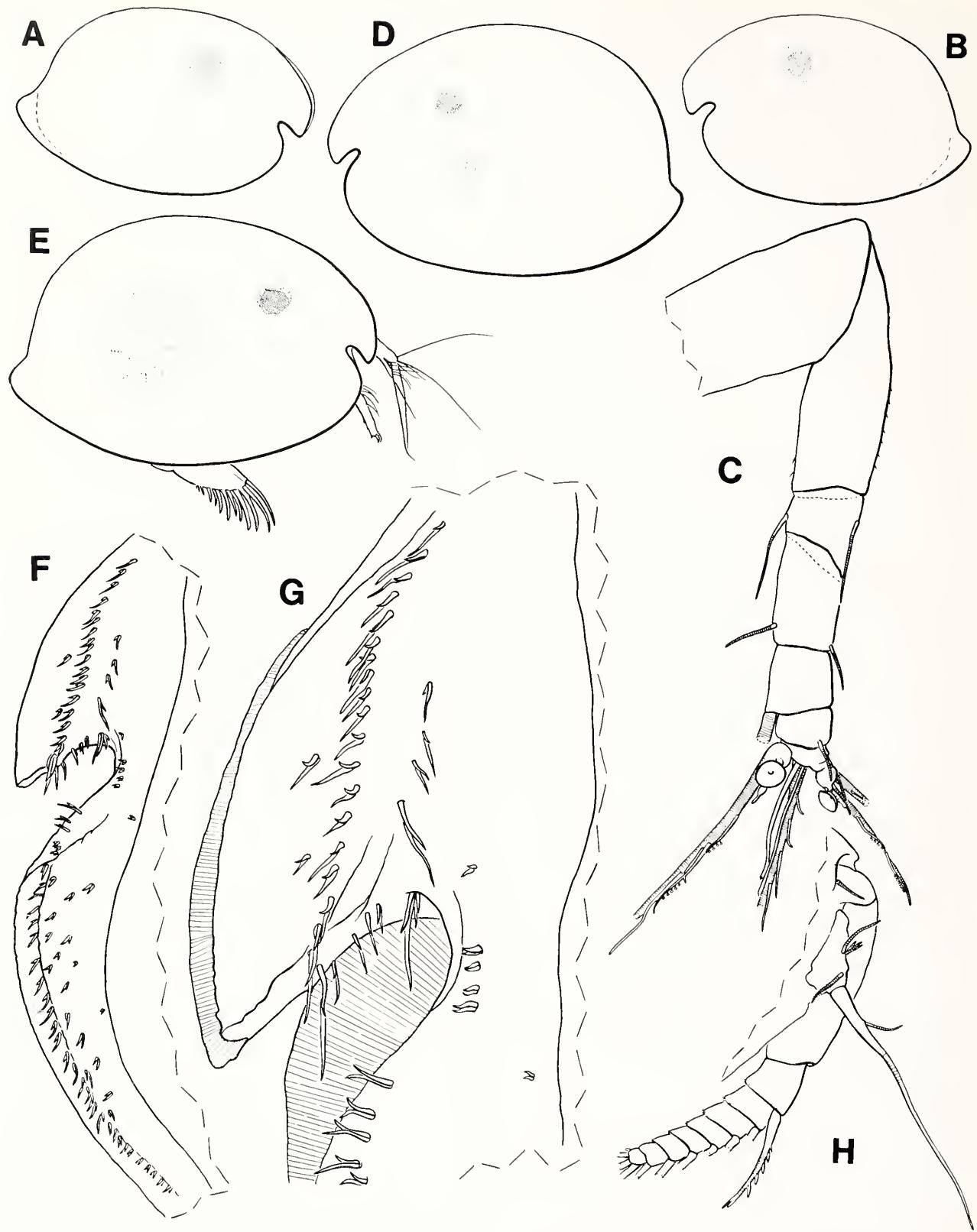


Figure 5. *Vargula shulmanae*. A, B. Holotype, USNM 193222, male, length 1.94 mm, right and left lateral views of whole specimen showing valves, lateral eyes, and caudal infold (dashed line). C. 1312.1-B, male, length 1.94 mm, left 1st antenna, medial view (distal parts of sensory, c-, f-, g-bristles not shown). D. USNM 193223, female (allotype), length 2.35 mm, left view of whole specimen showing valve, lateral eye.

2.33–2.55 mm; male 1.79–2.01 mm. Furca: 8–9 pairs of claws; claws 2 and 4 fused to lamella; claw 4 broader than, but not longer than claw 3. Second antenna: Bristle on 2nd exopodite joint with only 4–6 proximal and 1 subterminal stout ventral spines. Mandible: No terminal bristles with bulbous base. Maxilla: 2 alpha-, 3 beta-, 4 a-, 3 b-, and 3 c-bristles. Fifth limb: 4th and 5th joints separated by suture; 4 bristles on 4th joint, 2 bristles on 5th joint. Infold: Rostrum with row of 20–33 bristles parallel to margin plus 0–2 bristles anterior to and 1–6 bristles posterior to row; anteroventral infold with row of 32–43 bristles plus 0–1 bristle anterior and 0–17 bristles posterior to row. Seventh limb: Males with only 1–3 proximal bristles on comb side, total of 10–16 bristles on limb; females with 3–4 proximal bristles on comb side, total of 13–18 bristles; longest of 7 long teeth in comb lateral, not central; with peg opposite comb; without dorsal jaw. Lip: Tusks unbranched; with short distal and terminal hairs.

ETYMOLOGY. *Vargula shulmanae* is named after Dr. Myra J. Shulman who, along with one of us (J.G.M.), first collected the species.

DESCRIPTION OF ADULT MALE. Carapace (Figs. 3C, 4B, 5A, B). Oval with deep incisur and protruding caudal process; anteroventral, posteroventral, posterodorsal, and anterodorsal margins broadly rounded. Greatest height near middle; not markedly higher in posterior half. Caudal process short, below midheight of valve, but projecting to rounded point, process slightly larger in right valve than in left, dorsal margin rather straight, forming obtuse angle with rather truncate posterior margin of valve, dorsal edge of process slightly shorter than dorsal edge of incisur; both incisur and dorsal edge of process at about midheight of valve. Dorsal edge of incisur slightly overlapping ventral edge at inner end; faint line on outer surface of valve curving from inner dorsal edge of incisur to anterior margin of valve ventral to incisur. Tip of rostrum with few nodes. Outer surface smooth but with faint pattern resembling overlapping scales, visible at 100×; scale-like pattern producing minute points on anteroventral and posteroventral margin. Surface with rather regularly distributed small pores, some with minute bristles.

Infold. Infold of rostrum with about 20–31 double bristles forming row parallel to rostral margin and continuing posteriorly along incisur margin (about 5 bristles along incisur margin), 0–1 bristle anterior to row, 1–4 double bristles posterior to row, 2 double bristles near inner edge of incisur. Anteroventral infold with 3 short bristles near inner edge of incisur; about 20–31 double bristles forming row parallel to margin (about 3–4 of these anteroventral to incisur), 0–1 double bristle anterior to and 1–4 double bristles posterior to row; about 7 widely spaced bristles on ventral margin. List becoming broader in vicinity of caudal process with posterior fringe of minute processes, bristles or pores (right

valve with posterior fringe of irregular minute triangular spine-like processes); ventral ⅓ of left list broader, with 0–1 bristle anteroventral to list, list ending in dorsal knob; right list ending in dorsal bar.

Selvage. Typical for genus.

Size. USNM 193222 length 1.94, height 1.25 mm (holotype). Range (n = 131) for all specimens measured: length 1.79–2.01 mm, height 1.14–1.28 mm.

First antenna (Figs. 4B, 5C). First joint bare; 2nd joint with medial spines forming rows and spines on ventral and dorsal margins. Third joint short, ventral margin half or more than half length of dorsal margin, with medial spines forming row and 1 dorsal spinous bristle just proximal to middle and 1 long spinous ventral bristle near middle of joint; 4th joint with 1 spinous terminal dorsal bristle and 1 spinous distal ventral medial bristle. Sensory bristle of 5th joint with 10 long proximal filaments (some with minute filaments or spines), 2 more slender distal filaments and bifurcate tip, bifurcate tip and last filament with narrowed tips. Sixth joint with short spinous medial bristle near dorsal distal margin. Seventh joint: a-bristle spinous, slightly longer than bristle of 6th joint; b-bristle with stout proximal filament with bulbous base followed by large sucker and a small distal process ending in a narrowed pointed tip, 2 distal slender filaments each bearing 5 small suckers (distal filament not extending beyond tip of bristle); c-bristle similar to b-bristle but about 2 times as long, basal filament and sucker larger, 2 distal filaments with 4 small suckers, with about 5–6 long slender bare distal filaments, bifurcate tip. Eighth joint: d- and e-bristles bare, filamentous, almost as long as b-bristle, tips blunt or with narrowed process; f-bristle with about 7 slender filaments increasing in length distally, some perhaps with 1–3 spines; c-, f-, and g-bristles long (g-bristle longest), longer than sensory bristle of 5th joint; g-bristle with 9 slender filaments increasing in length distally and with 1 spine each (except last filament) and process on bifurcate tip.

Second antenna. Protopodite with short spinous distal medial bristle. Endopodite 3-jointed: 1st joint with 4 proximal bristles (1 short, 3 very short) and 1 short distal spinous bristle; 2nd joint elongate with 1 short spinous subterminal bristle, 3rd joint about ½–⅓ length of 2nd joint with long terminal filament. Exopodite: 1st joint with spines on dorsal margin; 2nd joint with rows of medial and lateral spines crossing ventral margin, bristle reaching 6th or 7th joint, with 4 proximal and 1 subterminal stout ventral spine and narrowed tip; joints 3–8 with basal spines becoming longer distally and with bristles with natatory hairs; lateral spine of 9th joint about same length as spine of 8th joint and about twice length of 9th joint; 9th joint with 4 bristles (3 long with natatory hairs, 1 shorter apparently bare).

Mandible (Figs. 3C, 4B). Coxale endite spinous, with bristle near base. Basale: Ventral margin with 1 short and 1 long

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and muscle scars. E–H. 2510.1a–C, female, length 2.39 mm: E. Right view of whole specimen showing valve, lateral eye, eggs (dashed lines), tip of 1st antenna, mandible, and furca; F. Inside view of anterior end of right valve; G. Inside view of rostrum of right valve; H. 2nd antenna, medial view of endopodite, exopodite, and distal protopodite (only bases of bristles on exopodial joints 3–9 shown).

spinous a-bristle with bases on medial side, 1 short b-bristle with base on lateral side (close to a-bristles), 1 long spinous and 1 short c-bristle near middle of margin, and 2 distal d-bristles, both some distance from c-bristles (1 shorter with short spines and 1 very long with groups of long proximal spines and short distal spines); dorsal margin with 1 long spinous distal bristle with short spines and 2 long unequal subterminal bristles with short spines. Exopodite with medial hirsute dorsal process extending to pointed tip and 2 long ventral bristles with short spines (distal shorter). First endopodial joint with 4 ventral bristles (1 long with long proximal and short distal spines, 1 long with short spines, 1 short with short spines and 1 minute bare). Second endopodial joint: Medial and lateral rows of spines or hairs, dorsal margin with 17 bristles (5 long spinous bristles, 5 shorter hirsute bristles, 6 short hirsute medial bristles, 1 short stout medial bristle with stout spines or possibly hairs); ventral margin with 2 medium length single distal bristles (bristles with bases together on 1 specimen) [tips either bifurcate or hollow and middle bristle usually extending beyond base of subterminal bristle and finger-like process] and 1 subterminal bristle equal in length to and with base on lateral side of base of stout finger-like subterminal unringed process (probably modified bristle); process not touching 3rd joint and with slender rounded point extending almost to end of 3rd joint. End joint with 3 long claws (1 with proximal spines) and 4 bristles, none with a bulbous base but stoutest reaching just beyond claws (1 dorsal lateral bare and slightly ringed claw-like bristle extending $\frac{3}{4}$ – $\frac{3}{4}$ length of dorsal claw, 1 prominent short bare ventral bristle, 1 long [$\frac{3}{4}$ claw length] spinous ventral medial bristle, 1 long stout, but not bulbous, spinous lateral bristle extending just beyond tip of claws).

Maxilla. Endite I with 11 stout bristles with long spines; endite II with 5 bristles with long spines (4 long stout), endite III with 5 spinous bristles (4 stout, long with long spines, 1 proximal short slender with short spines). Coxale with stout dorsal bristle proximally hirsute and distally with short spines. Basale with 1 long spinous lateral bristle, 1 long spinous medial bristle on or near ventral margin and base of exopodite and 1 spinous terminal medial bristle. Exopodite with 1 long proximal bristle with long proximal hairs and short distal spines and 2 long terminal bristles (1 with long proximal hairs and short distal spines, 1 with short spines only). First endopodial joint with rows of medial hairs, 2 alpha-bristles (outer bristle longer with long hairs, inner bristle with short spines), 3 beta-bristles (outer longest and pectinate, 1 of inner 2 with short spines); cutting tooth rather large and prominent, bifid (short slender proximal projection with rounded point, distal square molar-like projection more than twice as large with 2 points); possibly with 2 additional short rounded teeth on terminal lateral margin (1 near ventral margin, 1 near base of beta-bristles). Second endopodial joint with 4 long distally ringed a-bristles (1 with proximal short spines); 3 long, stout, very pectinate claw-like b-bristles (2 ringed, 1 slightly ringed); 3 distally ringed c-bristles (2 very pectinate, 1 short); 3 stout, very pectinate d-bristles (2 ringed).

Fifth limb. Epipod with at least 36 bristles. Protopodite with large distal undulate anterior tooth and 1 long anterior

bristle with long proximal and short distal spines. Endite I with 6 stout unequal bristles with long spines; endite II with 5 stout bristles with long spines (1 distally pectinate); endite III with 6 unequal bristles (most stout with long spines, 4 distally pectinate). First exopodial joint with 6 pectinate teeth and 1 proximal peg (smooth except for tiny spines on tip), 1 large pectinate bristle (with proximal spines) near peg, row of 3 anterior bristles with long proximal spines or hairs (2 long stout distally pectinate, 1 short); 2nd exopodial joint with 11 long stout pectinate claw-like end bristles arranged somewhat into 3 rows of 4 (4 bristles unringed, claw-like); 1 posterior bristle with long hairs. Inner lobe of 3rd exopodial joint hirsute, with 3 bristles (1 proximal posterior with long proximal hairs and short distal spines and 2 terminal with short spines); outer lobe hirsute with 2 terminal bristles with short spines (1 with long proximal hairs or spines). Fourth and 5th joints hirsute, separated by faint but distinct suture, 4th joint with 4 subterminal and terminal bristles with short spines, 5th joint with 2 terminal bristles with short spines and terminal group of spines.

Sixth limb (Fig. 6G). Hirsute laterally, 5 bare bristles in place of epipod. Endite I with 3 bristles (2 short with long spines or hairs, 1 long with longer spines); endite II with 5 bristles (3 short with long hairs, 2 long with long proximal and short distal spines); endite III with 4 bristles with long proximal spines or hairs and short distal spines (3 long, 1 short); endite IV with 3 bristles with long proximal hairs or spines (2 long with short distal spines, 1 short). End joint spinous, with 7–8 spinous bristles decreasing in length posteriorly, each with long stout proximal spines and medium-long distal spines (1 more medial and slender with shorter proximal spines), followed by space and 3 hirsute posterior bristles increasing in length posteriorly (anteriormost of these with stout distal spines). Limb with suture separating end joint from proximal part of limb, partial suture at base of endite III.

Seventh limb. Comb side with 1–2 distal and 4–5 terminal bristles, each with 2–4 bells; peg side with 2–3 distal and 3–4 terminal bristles, each with 2–4 bells. Comb consisting of 7 long spinous teeth with widened tips (2 lateral and 1 middle teeth shortest) and 4 short blunt teeth (2 on each side) with long basal spines and possibly with bumpy tips. Single procumbent long peg (slightly longer than short comb teeth) with distal and terminal tiny teeth.

Furca (Figs. 3C, 4B). Each lamella with 8–9 claws; claws 2 and 4 fused to lamella, remaining claws separated from lamella by suture; claw 3 more slender than but slightly longer than claw 4; claws 1–5 or 6 with long row of stout and approximately equal posterolateral teeth and distal row of anterior spines.

Bellonci organ. Short, cylindrical, with conical tip.

Eyes (Fig. 4B). Medial eye small, pigmented (sometimes restricted to band). Lateral eye about twice size of medial eye, pigmented and about 14 ommatidia. Lateral eye length ranged from 0.29 to 0.34 mm and pigmented area from 0.20 to 0.28 mm ($n = 131$). Eye pigment brown in reflected light; maroon or maroon-brown in transmitted light.

Upper lip (Fig. 4B). Anterior undivided part with numer-

ous glandular processes with unpigmented lobular tips and proximal bands of maroon pigment; middle with 2 long tusks, 1 on each side; each tusk with short distal and terminal hairs and with glandular processes; part posterior to tusks, rounded, hirsute.

Anterior of body. Rounded projection dorsal to 2–3 smaller usually pointed projections.

Posterior of body. Mostly smooth; small group of short hairs sometimes visible midposteriorly.

Copulatory organ (Fig. 4B). Anterior lobe rather conical, longer than short posterior lobe which has at least 1 group of about 3 bristles.

DESCRIPTION OF ADULT FEMALE. **Carapace** (Fig. 5D, E). Oval with deep incisur and protruding caudal process; anteroventral, posteroventral, posterodorsal, and anterodorsal margins broadly rounded. Greatest height near middle (at or just posterior to middle, not markedly higher in posterior half). Caudal process small (slightly larger in right valve than in left), dorsal margin rather straight, forming obtuse angle with rather truncate posterior margin of valve, dorsal edge of process about same length as dorsal edge of incisur; both incisur and dorsal edge of process at about midheight of valve. Dorsal edge of incisur slightly overlapping ventral edge at inner end; faint line on outer surface of valve curving from inner dorsal edge of incisur to anterior margin of valve ventral to incisur. Tip of rostrum with few nodes. Outer surface smooth but with faint pattern resembling overlapping scales, visible at 100 \times ; scale-like pattern producing minute points on anteroventral and posteroventral margin. Surface with rather regularly distributed small pores.

Infold (Fig. 5F, G). Similar to that of adult male except rostrum (Fig. 5G) with about 3–5 double bristles posterior to main row of 24–33 double bristles, 0–2 bristles anterior to row; anteroventral infold (Fig. 5F) with row of about 35–43 double bristles parallel to margin (about 4 of these ventral to incisur margin), about 0–17 double bristles posterior to row; list of caudal process in left valve with numerous tiny bristles and projections forming irregular row and posterior margin with tiny ripples, caudal list straight except for slight bend in dorsal half, caudal list of left valve terminating dorsally with round knob, with 0–2 bristles anteroventral to list; caudal list of right valve with minute pointed processes or fringe on ventral posterior edge, caudal list rather straight, ending in raised dorsally directed bar.

Selvage. Similar to male.

Size. 2510.1a-c length 2.39, height 1.63 mm; 2211.3 length 2.33, height 1.68 mm; USNM 193223 length 2.35, height 1.65 mm (allotype); 1212.12-A length 2.55, height 1.70 mm. Only 4 females (and 1 A-1 ovigerous female) have been collected.

First antenna. Similar to male except b-bristle of 7th joint about $\frac{1}{3}$ – $\frac{1}{2}$ longer than a-bristle, with 2 short proximal filaments and process on tip; c-bristle with about 8 filaments (with teeth or spines) becoming longer distally, about 5 times length of b-bristle, with process on tips of filaments and bristle; 8th joint with distal filament off-f- and g-bristles much longer than others, small round knob at medial dorsal base of f-bristle.

Second antenna (Fig. 5H). Similar to male except exopodite with shortest bristle of 9th joint, bearing few spines; bristle of 2nd joint reaching 7th–9th joint, with 5–6 spines.

Mandible (Fig. 6A). Similar to male except coxale endite with stout partly annulate spine on tip; 2nd endopodite joint with 15 dorsal bristles (only 4 short hirsute medial bristles); ventral margin of 2nd joint with 2 single distal bristles and 1 subterminal bristle together with subterminal unringed finger-like sclerotized process. Third endopodite joint with 1 of 4 bristles (stout ventral lateral) extending just beyond claws.

Maxilla (Fig. 6B). Similar to adult male except 2nd endopodial joint with 2 longer (of 4) a-bristles bearing a few stout proximal spines, 2 of 3 b-bristles distally ringed.

Fifth limb (Fig. 6C). Similar to adult male except epipodial appendage with about 46 bristles; proximal part of protopodite (coxale?) with pair of small sclerotized teeth bearing minute stout spines; exopodite joint 1 with 1–2 bare bristles near base of peg.

Sixth limb. Similar to adult male except end joint with 6–8 instead of 7–8 anterior bristles.

Seventh limb (Fig. 6D). Similar to adult male except comb side with 3–4 distal and 3–5 terminal bristles, peg side with 4–5 distal and 3–4 terminal bristles. Comb consisting of 7 long teeth (similar to those in male) and 4–5 short blunt teeth (2–3 on each side).

Furca (Fig. 6E). Similar to that of adult male except 3rd claw both shorter and more slender than 4th claw.

Bellonci organ (Fig. 6F). Similar to that of adult male but with blunt tip.

Eyes (Fig. 6F). Similar to those of adult male but lateral eye less than 1½ times as large as medial eye. Overall size and ommatidia size of lateral eye smaller than in male. Length of lateral eye ranged from 0.23 to 0.29 mm and pigmented area from 0.18 to 0.23 mm.

Upper lip (Fig. 6F). Lip similar to that of adult male except tusk with short distal as well as terminal short hair.

Anterior of body (Fig. 6F). With rounded projections dorsal to 2–5 smaller, usually pointed projections.

Posterior of body. With a few short hairs.

Genitalia. Sclerotized ring (possibly with small ventral projections) with attached spermatophores.

Eggs. 2510.1a-c with 26 eggs in ovary; the largest egg is 0.22 mm; 1212.12A with 32 eggs in ovary, 0.23–0.25 mm; 2111.5-A with 24 eggs in ovary, 0.058–0.077 mm.

Ovigerous juvenile. One small ovigerous female (2111.5C) bears about 13 eggs/ovary (eggs = 0.058 mm). It has the diagnostic characters shared by *V. graminicola* and *V. shulmanae*. It has the specific diagnostic characters of *V. shulmanae*: 5 (lowest adult number) stout spines on the 2nd exopodite bristle of the 2nd antenna; rostral infold with 1–2 bristles posterior to row of 19–23 bristles; anteroventral infold with 0–1 bristle posterior to row of 31–33 bristles (lowest adult number). We identify this female as an A-1 instar because it has these juvenile characters: length only 1.88 mm, height 1.28 mm; 7th limb with 14–15 bristles (lowest adult number), all strongly tapered and with only 1–2 bells; furca with only 8 claws (lowest adult number).

GENERAL BIOLOGY. Geographical distribution. Known

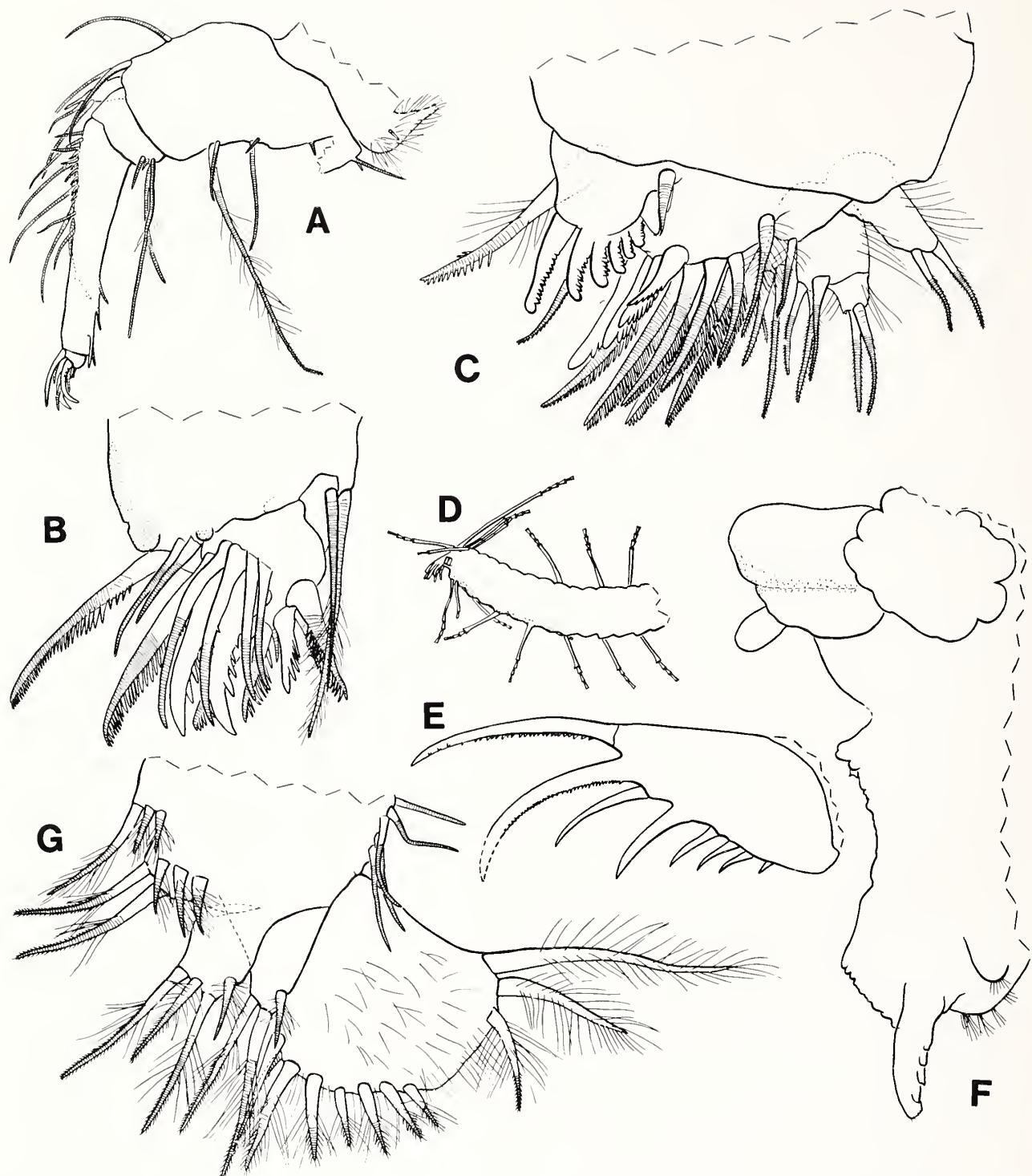


Figure 6. *Vargula shulmanae*. A-D. 2510.1a-C, female, length 2.34 mm; A. Right mandible, medial view; B. Tip of right maxilla, lateral view, showing 2nd and distal part of 1st endopodial joints; C. Tip of right fifth limb, posterior view, showing exopodite; D. Tip of 7th limb. E, F. USNM 193223, female (allotype), length 2.35 mm: E. Left lamella of furca, lateral view; F. Left view of anterior of body showing lateral and medial eye, bellonci organ, upper lip. G. 2510.3-A, male, length 2.01 mm, 6th limb.

only from the vicinity of the type-locality of the western San Blas Islands, Panama ($9^{\circ}33'14''N$, $78^{\circ}55'23''W$).

Habitat. This species is most abundant on slopes and walls of coral reefs with good water circulation. Most occur at depths of 4 to >20 m. Individuals generally occur in areas with dense coral cover and high coral diversity. Almost always there is a well-developed canopy of large gorgonians above an understory of massive and foliaceous scleractinian corals, all on steep slopes.

Ecology, behavior, and bioluminescence. *Vargula shulmanae* is a benthic species of steep coral slopes. On dark nights males become demersal zooplankters and range up to 5 m above the reef (but above and among the gorgonians). They appear in the water column about 55 min after sunset for about one to two hours. On only 4 occasions have females been caught in plankton nets. During the period that they are planktonic, males repeatedly emit specific downward trains of luminescent signals. For each train, the light is a vertical sequence of widely spaced extracellular secretions emitted by one male swimming rapidly downward at about 8.1 ± 1.3 cm s $^{-1}$ ($n = 22$ laboratory trials). Each signaling male is accompanied by as many as 12 nonsignaling males or subadult males. Each luminescent pulse has a duration of about 7.2 s (from 10 estimates) and a diameter of about 1–2 mm. Each train contains about 5–8 pulses and the total train length is about 1.5–2 m and lasts about 30–40 s. The interpulse distance between the first two pulses is about 30–50 cm; subsequent interpulse distances become much closer (the last pair is about 5 cm apart). Each train is followed by a 30–40 s nonluminescent dark period before the sequence is repeated nearby. There is a loose synchrony of displays over the reef face. Displays are usually spaced at least 1 m apart. Presumably these displays act as mating signals by the swimming males to the sexually receptive benthic females. Copulation probably occurs in the water column when the female swims to the signaling male. Females are capable of luminescing but have not been observed to produce any mating signals. We do not know what they feed on; they are not attracted to fish or crustacean carrion. A paper discussing their luminescent displays is in preparation (Morin, in press).

Color of live ostracode. Males are similar in color to females and are mostly transparent except for the eyes (see above), the light organ, and the abdomen. Both the light organ and the abdomen are distinctly brownish in color.

Parasites. Female no. 2111.5-A with eggs in ovary has 2 choniostomatid copepod parasites: 1 female attached to dorsum of ostracode and 1 male on anterior of ostracode, dorsal to 1st joint of left 1st antenna and medioanterior to left lateral eye.

DISCUSSION. *Vargula graminicola* and *V. shulmanae* are so similar morphologically that they may be regarded as sibling species. The two species have almost identical valves with a low, short, rather pointed triangular caudal process (Fig. 3A, C). *V. shulmanae* is larger, slightly rounder (less elongate), and has a slightly more triangular caudal process

than *V. graminicola*. The two species apparently do not overlap in size, but do overlap in ratio of valve length to height (see below). They differ very little except in the number of bristles on the infold and the number of stout spines on the bristle of the 2nd joint of the exopodite of the 2nd antenna. But the two species live in distinctly different habitats, produce different luminescent displays and have different diets (*V. shulmanae* will not eat carrion while *V. graminicola* will). Both *V. graminicola* and *V. shulmanae* have limbs which are almost identical to those of *V. parasitica* (Wilson, 1913), described from Jamaica. *V. parasitica* has a much smaller (very inconspicuous) and more rounded caudal process than *V. graminicola* and *V. shulmanae*. These three species are the only Caribbean species of *Vargula* with a small caudal process except for two undescribed species from Belize (Cohen, manuscript) and *V. harveyi*, another Jamaican species, of which only the female is known (Kornicker and King, 1965). All six of these species share some morphological limb characters (discussed below), but *V. harveyi* is distinguished by a distal jaw on the 7th limb.

Wilson's original description of *V. parasitica* is brief and does not describe all of the limb characters. Harding (1966) expanded the description based upon specimens collected by Wilson from the same host as the holotype. Kornicker (1984) further expanded the description based upon examination of the holotype (determining that it is an adult female) and other Jamaican specimens. The senior author of this paper has also examined the holotype of *V. parasitica* and four paratypes including specimens upon which Harding (1966) based his redescription (males A, C, female B, USNM 43586, 112672), and two females (USNM 78656) used by Kornicker (1984) in his supplementary description.

The following is a comparison of *Vargula parasitica*, *V. graminicola*, and *V. shulmanae*:

Caudal process: Larger, lower, more protruding, more pointed in *V. graminicola* and *V. shulmanae* (particularly females) than in *V. parasitica*. In *V. graminicola* and *V. shulmanae* the dorsal margin of the process diverges from the posterior margin of the valve at a distinct angle, producing a triangular shaped caudal process below midvalve height in both sexes. In *V. parasitica* the caudal process is more broadly rounded, shorter and not triangular, and shows more sexual dimorphism. In females (Wilson, 1913:pl. 33, fig. 30; Harding, 1966:fig. 2; Kornicker, 1984:fig. 12a) the process is high, above midvalve height and very short, forming almost a continuous curve with the posterior valve margin. In males (Harding, 1966:fig. 1) the process is low (confined to the lower half of the valve) and slightly longer than in the female).

Valve size: In Wilson's figure (pl. 53, fig. 303) the greatest height of the valve of *V. parasitica* is distinctly posterior to the middle. In Harding's and Kornicker's specimens of *V. parasitica* and also in *V. graminicola* and *V. shulmanae* it is near the middle. *V. parasitica* is intermediate in size between the smaller *V. graminicola* and larger *V. shulmanae*,

its length overlapping slightly with males and females of *V. graminicola* and overlapping more with males of *V. shulmanae*. Wilson reported that the (female) holotype of *V. parasitica* is 1.8 mm long and 1.15 mm high. The senior author remeasured the holotype and found it to be 2.05 mm long and 1.47 mm high. The range of valve length for females of *V. parasitica* is 2.01–2.17 mm (Kornicker, 1984). Females are 2.43–2.55 mm in *V. shulmanae* and 1.80–2.01 mm in *V. graminicola*. In *V. parasitica*, Harding's and Kornicker's males range from 1.75 to 1.9 mm long. Males of *V. graminicola* are 1.52–1.75 mm long, while males of *V. shulmanae* are 1.82–2.01 mm long. The ratio of male length to height is 1.65 ± 0.04 (mean \pm s.d.) [range = 1.58–1.76] ($n = 55$) in *V. graminicola* and 1.59 ± 0.03 (mean \pm s.d.) [range = 1.52–1.65] ($n = 60$) in *V. shulmanae*.

Infold: The six specimens of *V. parasitica* (including four paratypes) examined by the senior author and the specimens of *V. shulmanae* examined all have fewer bristles on the infold than *V. graminicola*. However all the specimens of *V. parasitica* were collected before 1924 and their infolds appear to have deteriorated more (with some bristles broken off) than the infolds of specimens of *V. graminicola* and *V. shulmanae* which were collected in 1983–1984. The rostrums of *V. parasitica* specimens bear 4–9 (male) and 6–13 (female) bristles in a row parallel to the rostrum compared to *V. shulmanae* with 20–31 (10 males) and 24–33 (four females) and *V. graminicola* with 22–33 (10 males) and 19–30 (four females). The specimens of *V. parasitica* have 0–2 anterior and 0–3 posterior to the row (this area unclear in some) compared to 0–2 anterior and 1–6 posterior in 15 *V. shulmanae* and 0–2 anterior and 4–12 posterior bristles in 10 *V. graminicola*.

The anteroventral infold of the specimens of *V. parasitica* is unclear in some specimens and has a row of 30–31 (male), 25–34 (female, possibly more on 1 specimen) bristles compared to 32–43 in 19 *V. shulmanae* and 38–53 in 14 *V. graminicola*. In *V. parasitica* there are 0–5 bristles posterior to the anteroventral row compared to 0–4 (19 males) and 0–17 (4 females) in *V. shulmanae* and 20–69 (10 males) and 34–64 (4 females) in *V. graminicola*.

The caudal infold of these three species of *Vargula* is similar and bears very minute papillae or bristles, difficult to count.

In order to make more accurate comparisons between the infolds of *V. parasitica* and the two new Panamanian species, fresher specimens of *V. parasitica* with well-preserved infolds are needed.

Second antenna: The number of stout spines on the bristle of the 2nd exopodite joint is 6–7 (male), 7–9 (female) in *V. parasitica*; 7–8 (rarely 6) in *V. graminicola*; 5–6 (rarely 7) in *V. shulmanae*.

Sixth limb: The holotype of *V. parasitica* has 2 posterior end bristles; Harding's specimens of *V. parasitica* and the two Panamanian species have 3 posterior end bristles.

Seventh limb: All three species have a terminal comb in which the central tooth of the 7 long teeth is shorter than the adjacent long teeth, apparently a unique character among the Cypridinidae. Wilson's description and figure (pl. 53, fig. 311)

of *V. parasitica* show about 23 proximal and 2 terminal bristles, but the 7th limb on the holotype slide has about 7 proximal and more than 2 terminal bristles. Harding reports 14 bristles on the 7th limb of *V. parasitica* and Kornicker reports that females have 3 proximal and 5 terminal bristles on the comb side and 4 proximal and 3 terminal bristles on the peg side; males have 2 proximal and 4 terminal comb side bristles and 4 proximal and 3 terminal peg side bristles. In *V. graminicola* females have 4–5 proximal and 5 terminal comb side bristles and 4–5 proximal and 3 terminal peg side bristles; males have 1–2 proximal and 3–4 terminal comb side bristles and 3 proximal and 3 terminal peg side bristles. In *V. shulmanae* females have 3–4 proximal and 3–5 terminal comb side bristles and 4–5 proximal and 3–4 terminal peg side bristles. Kornicker's specimens of *V. parasitica* have a comb with 7–8 long teeth and 4 short teeth on each side. The two Panamanian species have 7 long teeth and 3 short teeth on each side.

Furca: In all three species both the 2nd and 4th claws are united to the lamella. Wilson reported 14 claws; the senior author found 9 pairs on the holotype. Harding's and Kornicker's specimens of *V. parasitica* and also the two Panamanian species have 8–9 pairs.

Eyes: More pigmented in specimens of the two Panamanian species than in Kornicker's specimens of *V. parasitica*. This could be an artifact of preservation differences.

Ovigerous juveniles: Ovigerous but apparently A–1 juvenile females have been found in both *V. graminicola* and *V. shulmanae*. While these bear small ovarian eggs, they do not fall within the adult size range and may be discriminated from adults by their 7th limbs, which bear few and strongly tapered bristles with only 1–2 bells.

Vargula parasitica, *V. graminicola*, and *V. shulmanae* are distinct species but are united by many shared characters. In all three species (plus two undescribed species from Belize) the 4th and 5th joints of the 5th limb are separated by a suture (not fused) and bear 4 bristles on the 4th joint (right limb of 2510.1a-C female *V. shulmanae* has only 3 bristles [Fig. 4C]), 2 on the 5th joint. Both fused and unfused 4th and 5th joints are present in other species of *Vargula* and other members of the tribe Cypridinini. The 4th and 5th joints are separated in the tribe Gigantocypridinini and in *Codonocera* and *Pterocypridina* (assigned to separate groups within the Cypridinini by Kornicker, 1983). In all three species (plus *V. harveyi* and the two species from Belize) the maxilla bears 2 alpha-, 3 beta-, and 4 a-bristles. Some other species of Cypridinini share these characters. The presence of 4 a-bristles is also shared with *Codonocera*, *Pterocypridina*, and *Monopia* (also assigned to a group within the Cypridinini by Kornicker, 1983). None of the three species bears a terminal bristle with a bulbous base on the mandible; this bulbed bristle is apparently unique, probably derived in some species of *Vargula*. All three species share an apparently unique probably derived character, a 7th limb with a comb in which the central tooth is shorter than those adjacent to it. The phylogenetic polarity of the many characters shared by these three species is still either undetermined or not fully determined, but it is likely that the three species are closely related.

A comparison of the figures illustrating the limbs shows that not only do the species have the same number of bristles on each joint of each limb, but that the bristles are similar in length, width and ornamentation, with the very few exceptions noted above.

Vargula contragula, new species

Figures 3D, 7, 8

HOLOTYPE

USNM 193230 adult male, length 1.88, height 1.03 mm; in alcohol. **Sample 2310.1a.** 23 Oct. 1984 at 1835–1850 hr, at 4-m depth and about 1–2 m above low coral reef on Reef 26 (Macaroon), San Blas, Panama; sweep nets of displays; J.G. Morin, col.

PARATYPES

Sample 39. 12 Sept. 1983 at ca. 0415 hr, about 8-m depth and 1 m above sand-coral slope on east side of Ukkup-Tupo, San Blas, Panama; 31 net sweeps of luminescent displays; J.G. Morin, col.; 1 male (JM2-B, on slide and in alcohol), 2 males (JM2-L, lost) (LACM). **Sample 38.** 9 Sept. 1983 at 1920–1930 hr, ½–2 m above coral-sand slope on east side of Ukkup-Tupo, San Blas, Panama; 50 net sweeps of displays, partial sample; J.G. Morin, col.; 1 male (JM5-B) (LACM). **Sample 1110.2a.** 11 Oct. 1984 at 1845–1924 hr, 5-m depth, above coral-sand slope on east side of Ukkup-Tupo, San Blas, Panama; sweep net of displays, partial sample; J.G. Morin, col.; 3 males (LACM). **Sample 1810.1.** 18 Oct. 1984 at 1915–1930 hr, at 5-m depth and about 1–2 m above coral-sand slope on southeast side of Taiantupo, San Blas, Panama; sweep net of displays; J.G. Morin, col.; 2 males (LACM). **Sample 2310.1a.** 23 Oct. 1984 at 1835–1850 hr, at 4-m depth and about 1–2 m above low coral reef on Reef 26 (Macaroon), San Blas, Panama; sweep nets of displays, partial sample; J.G. Morin, col.; 1 male (A, on slide and in alcohol) (C–F) 22 males, and 1 male on SEM stub (LACM). **Sample 2011.3.** 20 Nov. 1984 at 1840–1910 hr, about 5–8 m depth and about 1–2 m above coral (with some sand) slope on southeast side of Korbiski Reef, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 8 males (USNM 193231). **Sample 2311.2.** 23 Nov. 1984 at 1840–1920 hr, at 7–10 m depth and about ½–2 m above coral-sand slope on southeast side of Korbiski Reef, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 5 males (USNM 193232). **Sample 1312.1.** 13 Dec. 1984 at 1845–1915 hr, at 4-m depth and about 1–2 m above low coral reef on Reef 26, San Blas, Panama; discrete traps of displays; J.G. Morin, col.; 1 male (A, on slide and in alcohol), 12 males (C–E) (LACM).

DIAGNOSIS. Anteroventral corner of valve not evenly curved but with rounded projecting bulge; caudal process large, about half height of valve. Females unknown; male carapace length 1.71–2.00 mm. Furca: 7–9 pairs of claws; claw 2 fused to lamella. Mandible: 2nd joint of endopodite with only 2 ventral bristles (1 proximal, 1 distal and lateral to sclerotized finger-like projection); 3rd joint with 1 terminal bristle with bulbous base. Maxilla: 1st joint of endopodite with 1 alpha- and 1 beta-bristle and large bifid cutting tooth;

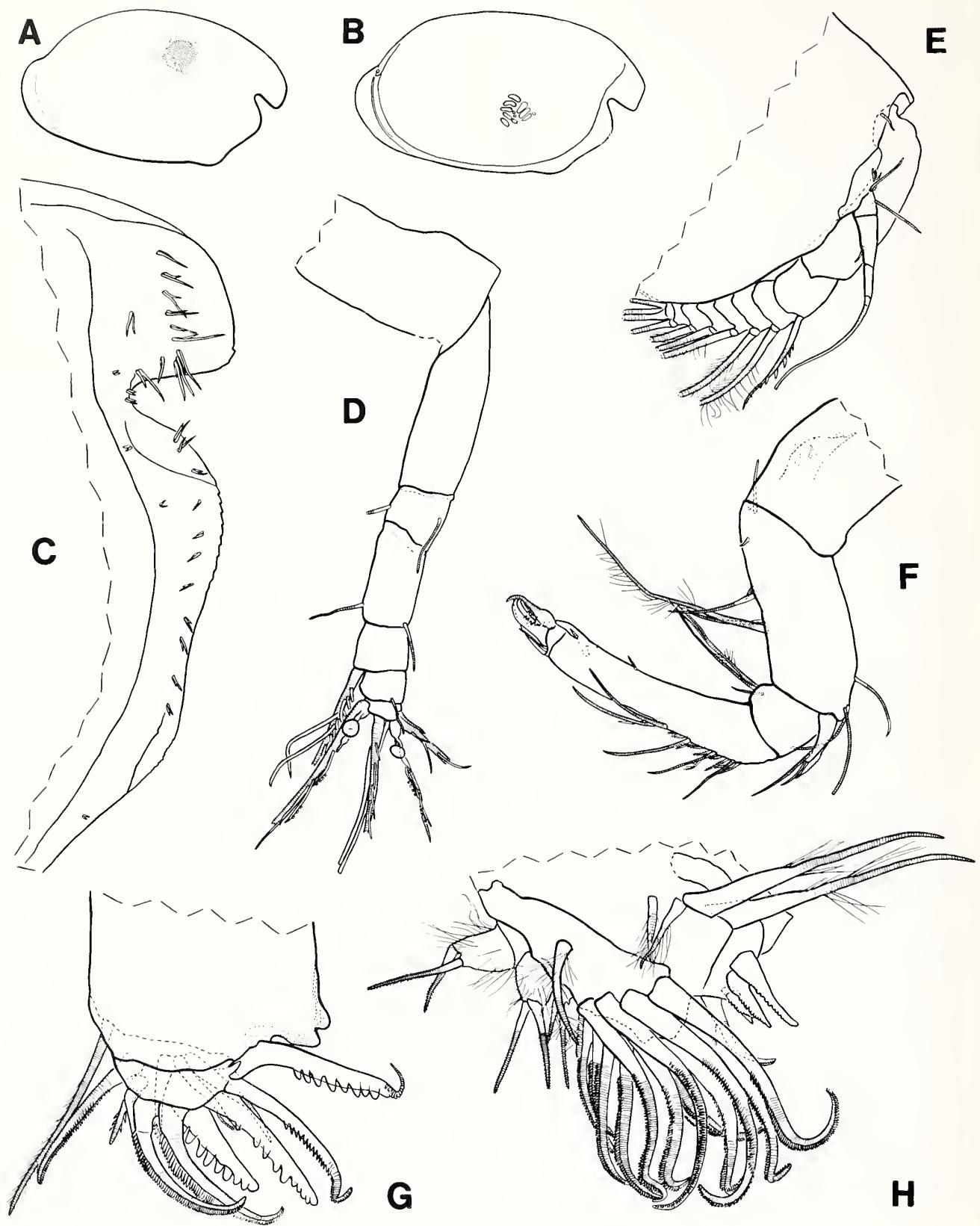
2nd joint with only 3 a-, 2 b-, and 3 c-bristles, 3 distal bristles (1 beta-, 2 d-bristles) long, stout with conspicuously large rounded teeth; 2 distal bristles (1 beta- and the 3rd d-bristle) attenuated distally. Fifth limb: 1st exopodial joint with only 3 pectinate teeth and 1 peg; 4th and 5th joints fused with only 2 bristles. Sixth limb: End joint with 4–5 anterior bristles and 3–4 hirsute posterior bristles. Seventh limb: Comb consisting of 7 long and 4–6 short teeth (2–4 short teeth/side) opposite peg; no dorsal jaw. Lip: Tusks unbranched, hirsute distally.

ETYMOLOGY. *Vargula contragula* is derived from the Latin *condensatio* which means “condensation” and the Latin *tragula* which means “trail.” High-flying jet aircraft often leave behind them a visible ‘condensation trail’ of moisture; the contracted name for this commonly observed pattern is ‘contrail.’ Similarly *contragula* is the contraction of the same Latin words and refers to the closely spaced, lateral trail of luminescent pulses left behind nocturnally swimming males of this species.

DESCRIPTION OF ADULT MALE. Carapace (Figs. 3D, 7A, B). Oval with deep incisur, large protruding caudal process, and small protruding process at anteroventral corner; posteroventral, posterodorsal, anterodorsal, ventral, and dorsal margins broadly rounded. Caudal process slightly larger in right valve than in left, margin broadly curved forming obtuse angle with curved posterior margin of valve; dorsal edge of process shorter than dorsal edge of incisur and above midheight of valve; inner end of incisur above midheight of valve. Dorsal edge of incisur slightly overlapping ventral edge at inner end; faint line on outer surface of valve curving from inner dorsal edge of incisur to anterior margin of valve ventral to incisur. Valve surface smooth but with faint pattern resembling overlapping scales, visible at 100 \times ; scale-like pattern producing minute points on tip of rostrum and on anteroventral margin of valve. Numerous minute pores scattered rather regularly over valve surface, some with minute bristles.

Infold (Fig. 7C). Infold posterior to rostrum with row of about 9–11 long double bristles (members of each pair unequal in length and very unequal in 2–3 bristles dorsal to incisur), 1 bristle posterior to these, 1 long and 0–1 shorter bristle on dorsal inner edge of incisur, 1 tiny bristle posterior and dorsal to inner edge of incisur. Anteroventral infold with 1–3 short bristles near inner corner of incisur, 1 tiny bristle posterior to inner corner of incisur, row of about 7–13 long double bristles on anterior margin (including 3 ventral to incisur), 0–1 bristles posterior to row; 0–6 (fewer in right valve) shorter bristles on ventral margin; list becoming broader in vicinity of caudal process with numerous minute processes, crenulations or ripples (including at least 15 tiny bristles in left valve); 0–5 bristles ventral to left list; list ending dorsally in knob (left valve) or bar (right valve); about 10 minute bristles forming widely spaced row on posterior edge of caudal process of both valves.

Selvage. Selvage with lamellar prolongation with smooth edge and faint striations present along ventral and anterior margins; lamellar prolongation along ventral margin of incisur broader and with more visible striations than elsewhere.



Size. USNM 193230 length 1.88, height 1.03 mm (holotype). Range ($n = 129$) for all specimens measured: length 1.71–2.00 mm, height 0.98–1.13 mm.

First antenna (Figs. 3D, 7D). First joint bare. Third joint short with medial spines, 1 medium long spinous dorsal bristle just proximal to middle and 1 medium long spinous ventral bristle with base near middle or terminal. Fourth joint with 2 medium long spinous bristles (1 terminal dorsal, 1 distal ventral). Sensory bristle of 5th joint with 10 long proximal filaments, 2 more slender distal filaments, and bifurcate tip. Sixth joint with medium long spinous medial bristle near dorsal margin. Seventh joint: a-bristle spinous, about same length as bristle of 6th joint; b-bristle with stout proximal filament with bulbous base followed by large distal sucker and distal process, and 2 slender distal filaments each bearing 2–5 (usually 3–4) smaller suckers, filaments not extending beyond bristle tip, b-bristle about 2–3 times length of a-bristle; e-bristle with stout proximal filament with bulbous base (slightly larger than that of b-bristle) followed by large distal sucker and distal process, 2 proximal slender filaments with small suckers (each with 3–4), about 4–6 longer, slender bare distal filaments with spine-like tips, and bifurcate tip. Eighth joint: d- and e-bristles bare and filamentous, d-bristle longer than e-bristle, e-bristle longer than b-bristle; f- and g-bristles with 9–10 slender filaments increasing in length distally and bearing a few spines, and bifurcate tip; c-, f-, and g-bristles stouter and much longer than remaining bristles.

Second antenna (Figs. 3D, 7E). Protopodite with very short distal medial bristle. Endopodite 3-jointed: 1st joint with 4 proximal bristles (1 short, 3 very short) and 1 short distal bristle with short spines; 2nd joint elongate with 1 very short distal bristle with short spines; 3rd joint short (about $\frac{1}{2}$ length of 2nd joint) with long terminal filament. Exopodite: 1st joint with minute terminal process; bristle of 2nd joint reaching to end of 6th, 7th, 8th or 9th joint, with 6–12 stout more proximal, mostly ventral spines, and about 0–5 minute spines on narrower distal portion; joints 3–8 with natatory hairs only; joints 2–8 with increasingly stouter ventral spines; lateral spine of 9th joint slightly shorter than ventral spine of 8th joint; 9th joint with 4 unequal bristles (3 longest with natatory hairs).

Mandible (Figs. 3D, 7F). Coxale endite spinous, with bristle near base and stout terminal spine with some annulations. Basale: Ventral margin with 2 a-bristles (1 long spinous, 1 short) with bases on medial side, 1 short lateral b-bristle (close to a-bristles), 1 long spinous (short spines) and 1 short

c-bristle near middle of margin, and 2 long distal d-bristles, separated by space from c-bristles (1 with short spines, 1 very long and stout with long proximal hairs or spines and short distal spines); dorsal margin with 1 long distal bristle and 2 long subterminal bristles, all with short spines. Exopodite with medial hirsute dorsal process extending to pointed tip and 2 spinous bristles. First endopodial joint with 4 ventral bristles (1 longest with few longer and more short spines, 1 long with short spines, 1 not as long with short spines, 1 minute; minute bristle missing and longest bristle distally bifurcate on illustrated limb of 1312.1-A). Second endopodial joint: Dorsal margin with 12–17 bristles (5 long bristles with short spines, 6–10 short hirsute medial bristles, 1 short stout medial bristle with stout spines, 1 short to medium length medial bristle with short spines); ventral margin with 1 short distal bristle and 1 shorter subterminal bristle with base on lateral side of stout finger-like subterminal unringed process (process almost as long and broad as claws on 3rd joint). End joint with 3 long claws (2 ventral claws stouter than dorsal claw and with very stout bases and stout proximal teeth) and 4 bristles (1 dorsal bristle about half claw length, 1 short slender ventral bristle, 1 slender ventral bristle almost as long as claws, 1 ventral bristle with large bulbous base and extending beyond claws).

Maxilla (Fig. 7G). Endite I with about 12 long stout distally ringed bristles with many long slender spines; endite II with about 6 mostly stout long distally ringed bristles with long spines; endite III with about 5 mostly longer bristles with long proximal and short distal spines and rings. Coxale with stout hirsute dorsal bristle. Basale with 1–2 long medial bristles and 1 lateral hirsute bristle at base of exopodite. Exopodite hirsute with 1 long hirsute proximal bristle and 2 long terminal bristles (1 stouter hirsute, both with distal short spines). First endopodial joint with long slender alpha-bristle with short hairs and long, stout, claw-like, pectinate beta-bristle with 8–9 very large stout rounded proximal teeth (distal $\frac{1}{4}$ – $\frac{1}{5}$ of bristle narrow, ringed flexible with about 22 minute teeth); cutting tooth prominent, usually bifid (usually composed of 2 rather pointed triangular parts); [1 limb of 1312.1-A with trifid tooth, no beta-bristle, 3 long pectinate c-bristles, 1 long unringed pectinate d-bristle with 8 large teeth and 2 long pectinate d-bristles with slender ringed tips]. Second endopodial joint with 3 medium-short ringed pectinate a-bristles (shorter than all but 2 end bristles), 2 pectinate b-bristles (1 long, 1 short, both ringed), 1 short slender ringed and 2 long stout ringed pectinate c-bristles, and 3 long stout pectinate d-bristles (2 very stout bare, claw-like with

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Figure 7. *Vargula contragula*, males. A. JM2-B, length 1.76 mm, right lateral view of whole specimen showing valve, lateral eye, and caudal infold (dashed line). B, C. 1312.1-C, length 1.86 mm: B. Inside of left valve showing valve, infold, and muscle scars; C. Inside view of anterior part of left valve. D. USNM 193232-A, length 1.86 mm, left 1st antenna, medial view (distal parts of sensory, c-, f-, g-bristles not shown). E. 2310.1a-A, length 1.98 mm, left second antenna, medial view, showing endopodite, exopodite, and distal part of protopodite (only bases of bristles on exopodial joints 3–9 shown). F. 1312.1-A, length 1.94 mm, right mandible, lateral view. G, H. 2310.1a-A: G. Tip of right maxilla, medial view, showing 2nd and distal part of 1st endopodial joints; H. Tip of right 5th limb, anterior view, showing exopodite.

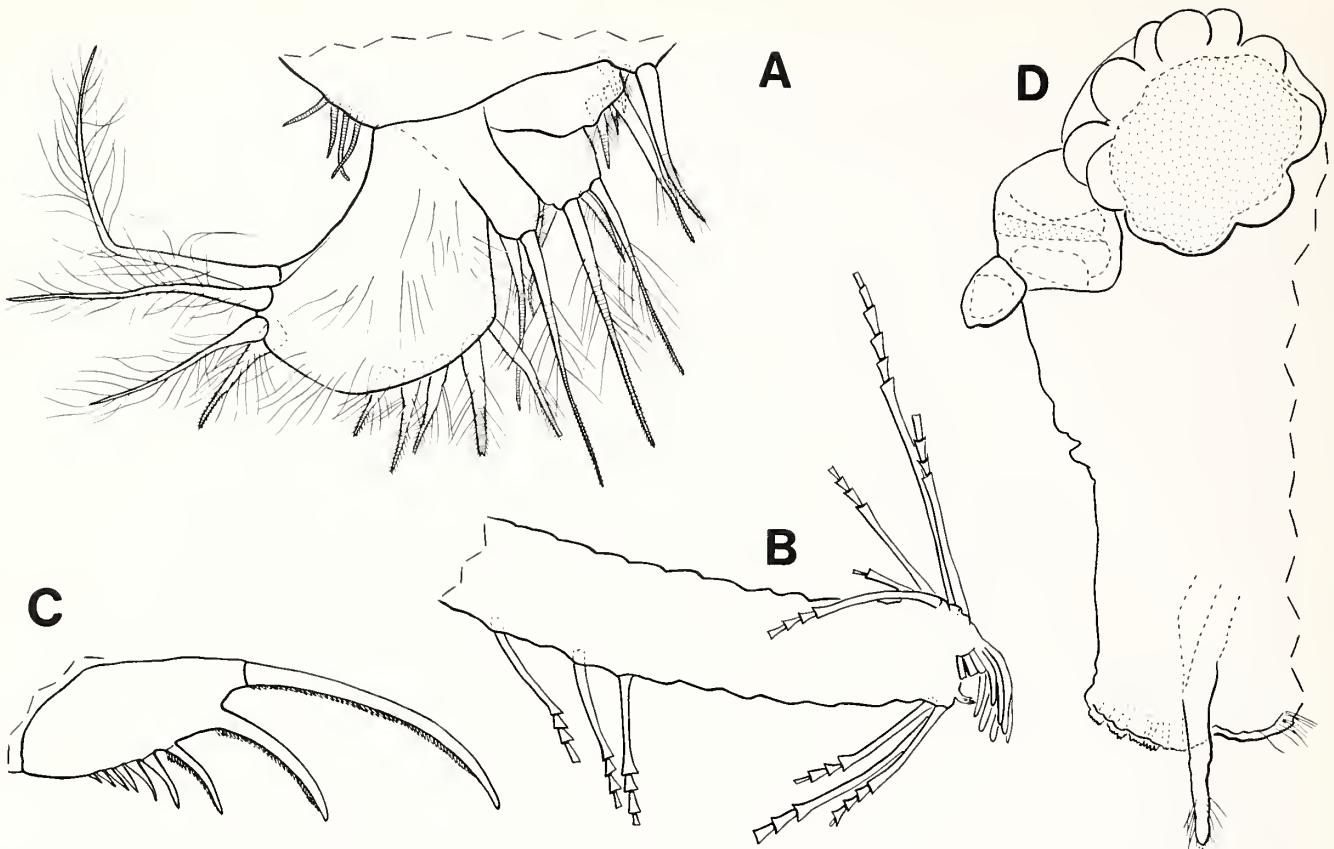


Figure 8. *Vargula contragula*, males. A. JM2-B, length 1.76 mm, 6th limb. B. 2310.1a-A, length 1.98 mm, tip of 7th limb. C. JM5-B, length 1.71 mm, right lamella of furca, lateral view. D. USNM 193231-A, length 1.75 mm, left view of anterior of body showing lateral and medial eyes, bellonci organ, and upper lip.

about 8–10 very large rounded teeth, and 1 longer with about 15 small teeth and slender ringed flexible tip with minute teeth [similar to beta-bristle].

Fifth limb (Fig. 7H). Epipod with about 45 bristles. Protopode with 1 hirsute bristle (may be in row on 1st joint of exopodite). Three endites with about 17 bristles, all with long spines or stout hairs and some also with short spines. Endite I with 1–2 long and 5 short bristles with long spines; endite II with 4–6 rather short bristles; endite III with 3 short and 4 medium-length bristles (2 unringed, 2 pectinate). First exopodial joint with only 3 pectinate teeth and 1 pointed proximal peg (slightly longer than shortest tooth); long pectinate bristle with proximal long hairs or spines present near peg; anterior side with 3(–4) bristles forming row near inner margin (all with long proximal hairs, 2 very long with distal short spines). Second exopodial joint with 13–14 very long slender flexible pectinate bristles (all ringed), 1 proximal hirsute anterior bristle and 1 proximal posterior bristle (proximally hirsute with distal short spines). Inner lobe of 3rd exopodial joint with 2 bristles with long proximal hairs and short distal spines; outer lobe hirsute with 2 terminal bristles (with short spines). Fourth and 5th exopodial joints fused, hirsute, with 2 bristles (with short spines) [minute partially sclerotized process present terminally between bristles of 1312.1-A].

Sixth limb (Fig. 8A). Three to four bare bristles in place of epipod. Endite I and II each with 3 bristles (1 long with long distal spines, 2 short with long hairs); endite III with 4 bristles (2 long with long mid and short distal spines, 2 short proximally hirsute); endite IV with 2 long bristles (longest bristle with long mid and short distal spines, other bristle proximally hirsute). End joint hirsute with 4–5 anterior bristles (decreasing in size to short posteriorly) with long proximal hairs or spines and short distal spines, followed by space and 3–4 increasingly longer hirsute bristles (shortest with distal short spines).

Seventh limb (Fig. 8B). Comb side with 0 distal and 4–5 terminal bristles, each with 1–4 bells; peg side with 3 distal and 3 terminal bristles, each with 2–5 bells. Comb consisting of 7 long spinous teeth (alate at tip and longest tooth in middle) and 4–6 short blunt teeth (2–4 on each side). Single stout short erect curved peg with comb of terminal and lateral teeth, present opposite long comb.

Furca (Figs. 3D, 8C). Each lamella with 7–9 claws; claw 2 fused to lamella, remaining claws separated from lamella by suture; claw 1 much longer than claw 2; claw 3 distinctly longer than claw 4; teeth present on all claws, claws 1–3 with rather regular teeth on anterior margin and on lateral and medial posterior margin.

Bellonci organ (Fig. 8D). Short, cylindrical, distal half conical, narrowing to narrow, blunt tip.

Eyes (Fig. 8D). Medial eye unpigmented. Lateral eye larger than medial eye, with dark brown or maroon pigment and about 16 ommatidia. Lateral eye length ranged in size from 0.25 to 0.33 mm and pigmented area from 0.18 to 0.28 mm ($n = 129$).

Upper lip (Fig. 8D). Anterior undivided part unpigmented, with numerous small pointed or rounded glandular processes; middle with 2 long tusks, 1 on each side; distal third of each tusk with long hairs and few minute processes; part posterior to tusks, rounded, hirsute.

Anterior of body (Fig. 8D). With rounded projection dorsal to smaller rounded projection.

Posterior of body. Bare.

Copulatory organ. Posterior lobe helmet-shaped with bristles near tip, and possibly base, lobe curving over distal part of narrower anterior lobe; rounded posterior part of organ with many small lobes or teeth.

GENERAL BIOLOGY. Geographical distribution. Known only from the vicinity of the type-locality of the western San Blas Islands, Panama ($9^{\circ}33'14''N$, $78^{\circ}55'23''W$).

Habitat. *V. contragula* is mostly found at depths less than 9 m in association with gorgonian covered reefs, either low profile patch reefs or shallow sloping reefs, that have substantial open and rubble areas between the corals and gorgonians.

Ecology, behavior, and bioluminescence. *Vargula contragula* is a benthic species that lives in low profile patch reefs and reef slopes with extensive gorgonian populations. Males become planktonic about 1–3 m above the reefs, but usually among the gorgonians, for about 1 hour at night. They appear quickly about 50 min after sunset. No females have been caught. While they are planktonic *V. contragula* males produce distinctive luminescent displays. These displays are a series of extracellular light pulses left behind a male as it swims rapidly (about 9 cm s^{-1}) and obliquely upward at an angle of 30° to 50° . It may be accompanied by up to six nonluminescing males. Each pulse has a duration of about 4 s. The first two pulses are spaced about 15 cm apart, the second and third about 8 cm, the third and fourth about 5 cm, and subsequent interpulse intervals are about 2 cm apart. Many dozens of these closely spaced pulses may be produced during a single display and cover a distance of several meters. While they are being produced by the male at one end of the train, they are fading away slowly at the other end (a distance of about 30 cm and containing about 15 visible pulses at any one time). The effect is like a miniature glowing contrail from a jet aircraft, moving through the water at a low angle to the bottom. The paths of the trains are either linear or slightly curved. Often several males will commence their displays near one another and then radiate outward. Thus there is loose synchrony among males. The displays cease rather abruptly, within about 10 min, approximately an hour after they begin. As with the two species described above, it is assumed that these displays are mating signals from planktonic males to sexually receptive benthic females. It is not known what they feed on; they are not attracted to fish or

crustacean carrion. No predation upon them has been observed.

Color of live ostracode. The body is mostly transparent except for the eyes, light organ, and abdomen. The light organ is an orange-brown color while the abdomen is a distinctly orangish color.

DISCUSSION. *Vargula contragula* shows the diagnostic characters of the genus *Vargula* (Kornicker, 1975). Polarity of characters within the genus is uncertain. *V. contragula* possesses some apparently unique characters (autapomorphies) and shares others with some congeners. *V. contragula* is the only species of *Vargula* with a 5th limb with a 1st exopodite joint bearing only 3 teeth plus a peg. Only one other species of Cypridinidae, *Pterocypridina sex* Kornicker, 1983 (*Pterocypridina* group), has 3–4 teeth and a peg (Kornicker, personal communication). Almost all species of Cypridinidae have 6 teeth plus a peg. Reductions have also occurred in *V. dentata* Kornicker, 1975 (5 teeth plus a peg) and other *Cypridina* group species: *Codonocera suensonii* Poulsen, 1962 (4 teeth plus a peg), *C. goniacantha* Müller, 1906, *C. polygonia* Müller, 1906, *C. weberi* Müller, 1906, and *Rugosidoloria serrata* Kornicker, 1975 (all with 5 teeth plus a peg).

Only one other species of *Vargula*, *V. spinulosa*, has a valve with a bulge on the anteroventral corner similar to that of *V. contragula*. *V. spinulosa* also has a furca with the 2nd claw united to the lamella, but has a 7th limb with a dorsal jaw and differs from *V. contragula* in many other respects including those noted below.

Vargula contragula has some apparently uniquely shaped distal bristles on the maxilla: 1 beta- and 2 d-bristles are stout and claw-like with prominently large rounded teeth, but the beta- and one of these d-bristles also have unusual very slender ringed minutely toothed distal portions.

Vargula contragula and *V. hilgendorfii* are the only known species of *Vargula* with a mandible with the ventral margin of the 2nd endopodite joint with only 1 single distal bristle proximal to the usual subterminal bristle paired with a sclerotized finger-like projection. But a few specimens of some other species of *Vargula* occasionally have an aberrant limb with a reduced number of bristles on this joint.

Vargula contragula shares some characters almost exclusively with a few Caribbean species of *Vargula*. Of the 22 described species of *Vargula* (including the three described herein) six are from the Caribbean Sea. There are 8–10 additional Caribbean species which we will describe in future papers (4–5 from San Blas, Panama and 3–4 from Carrie Bow Cay, Belize). The 14–16 Caribbean species fall mainly into three groups of species sharing concordant morphological characters: 1) *Vargula contragula*, *V. bullae* Poulsen, 1962, 3–4 undescribed species from San Blas and 1–2 undescribed species from Belize; 2) *V. harveyi* Kornicker and King, 1965, and 1 undescribed species from San Blas; and 3) *Vargula parasitica*, *V. graminicola*, *V. shulmanae*, and two undescribed species from Belize.

Group 1. The species in the first group (containing *V. contragula*) share the following characters, most of which occur in few other species of *Vargula*: high, usually prominent

caudal process, mandible with a bulb-based end bristle; 5th limb with fused 4th and 5th joints bearing a total of only 2 bristles; maxilla with 1 alpha-, 1 beta-, 3 a-, and a total of 5 b- and c-bristles (except *V. bullae* has 2 beta-bristles); furca with only the 2nd claw united to the lamella (except *V. bullae* and 1–2 undescribed species from San Blas with both the 2nd and 4th claws united to the lamella); 7th limb with comb of 7 long teeth (longest in center) and adjacent short teeth.

Apparently the Caribbean species of *Vargula* are the only species of the Cypridinidae possessing a mandible with a bulb-based end bristle except for *V. tsujii* Kornicker and Baker, 1977, from California, NE Pacific Ocean, *V. hilgendorfii* (Müller, 1890) from the west Pacific, and *V. plicata* Poulsen, 1962, from the Celebes Sea.

The reduction in number of bristles on the maxilla and on the fused 4th and 5th joints of the 5th limb occurs in some other members of Cypridinidae (although 1 alpha-bristle occurs only in some members of the *Cypridina* genera group), but in *Vargula* occurs in only 3 of the 16 presently known non-Caribbean species: *V. tsujii* (shares all of the listed characters of the first Caribbean group except the high caudal process and the 7 long teeth in the comb of the 7th limb), *V. hilgendorfii* (shares with the first Caribbean group only the bulb bristle, 2nd claw only of furca fused, high caudal process, and 1 alpha-bristle), and *V. magna* Kornicker 1984, from North Carolina and west Florida (shares with the first Caribbean group only the reduction of maxilla bristles).

Only four non-Caribbean species of *Vargula* have only the 2nd claw fused to the lamella: *V. tsujii*, *V. hilgendorfii*, *V. spinulosa* Poulsen, 1962, from Korea (shares with the first Caribbean group only the high caudal process and fused 2nd claw of the furca), and *V. spinosa* Poulsen, 1962, from Japan (shares only the fused 2nd claw of the furca).

Group 2. The species in the second group share the following characters: low and short caudal process; mandible with end bristles without or with slightly bulbous base; 5th limb with unfused or partially fused 4th and 5th joints with 4–5 bristles; maxilla bristles and furca as described in group 3; 7th limb with comb as described in group 1.

Group 3. The species of the third group share the following characters: low and usually short caudal process; mandible without bulb-based end bristle; 5th limb with unfused 4th and 5th joints bearing a total of 6 bristles; maxilla with 2 alpha-, 3 beta-, 4 a-, 3 b-, and 3 c-bristles (number of b- and c-bristles unclear and possibly different in *V. parasitica*); furca with 2nd and 4th claws fused to lamella; 7th limb with comb having 7 long teeth (with the longest teeth adjacent to the center tooth) and short lateral teeth.

Only four other non-Caribbean species of *Vargula* are also known to have a 7th limb with a comb with 7 long teeth and in all of them the central tooth is longest: *V. norvegica* (Baird, 1860) from the eastern North Atlantic Ocean; and, in the Pacific Ocean, *V. plicata*, *V. lusca* Kornicker, 1975, from south of Tasmania, and *V. ascensus* Kornicker, 1979, from New Zealand.

The geographically concordant suites of characters suggest that some Caribbean species of *Vargula* are closely related to each other and that the taxon may be a promising subject

for cladistic analysis. However, the high number of new species which we have found proportional to those presently described suggests that many more species may still be undescribed throughout the world. An analysis also will require better determination of the polarity of the character state transformations based upon further study of the relationship of *Vargula* to other genera in the Cypridinini and their character states. Study of the possibly undescribed species of choniostomatid copepods parasitic on some of these species also might be useful in determining phylogenetic relationships.

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Number 374
15 May 1986

CONTRIBUTIONS IN SCIENCE

LATE MIocene AND HOLOCENE MAMMALS, EXCLUSIVE
OF THE NOTOUNGULATA, OF THE RÍO ACRE
REGION, WESTERN AMAZONIA

Carl D. Frailey



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

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**LATE MIOCENE AND HOLOCENE MAMMALS, EXCLUSIVE
OF THE NOTOUNGULATA, OF THE RÍO ACRE
REGION, WESTERN AMAZONIA**

Carl D. Frailey

**Contributions in Science, Number 374
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**Natural History Museum of Los Angeles County
900 Exposition Boulevard
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LATE MIocene AND HOLOCENE MAMMALS, EXCLUSIVE OF THE NOTOUNGULATA, OF THE RÍO ACRE REGION, WESTERN AMAZONIA

Carl D. Frailey¹

ABSTRACT. Although the Cenozoic fossil record of South America is relatively good, major fossil-bearing strata are found primarily in temperate South America and the South American land mammal ages are established on the faunal sequence found in those deposits. Studies of vertebrate fossils in other parts of South America, including those in this paper, tend to confirm the universality of these faunal ages.

The discovery of a diverse Late Miocene (Huayquerian) local fauna along the Río Acre on the border between Peru and Brazil provides the first opportunity to examine a wide representation of the Late Tertiary fauna of the Amazon. Several taxa are recorded as fossils in the Amazon Basin for the first time: Dasypodidae (Pampatheriinae), Proterotheriidae, Macrauchenidae, Erethizontidae, Dasyprotidae, Dinomyidae (*Potamarchus murinus*, *Telicomys amazonensis* n. sp., *Tetrastylus* sp.), Neoepiblemidae, Hydrochoeridae (*Kiyutherium orientalis*), Caviidae (Cardiomysinae), Echimyidae (Heteropsomyinae), and Sirenia (Trichechidae). The affinities of this local fauna with the Late Miocene savanna fauna of Argentina suggest that a widespread savanna community extended into the Amazon Basin. However, a new genus of Mylodontidae and what may be a new family of Marsupialia underscore major differences between tropical and temperate faunas of South America during the Cenozoic.

One Holocene taxon is discussed on the basis of new material. The discovery of the ground sloth *Nothropus priscus* in deposits along the Río Acre conclusively supports the placement of *Nothropus* in the Nothrotheriinae as a close relative of *Nothrotheriops*, a genus that preferred a dry habitat. This relationship, and the discovery of the specimen at the base of a thick formation that has a maximum radioisotopic date of 11,000 years, indicates that major climatic and environmental changes occurred in the western margin of the Amazon Basin during the Holocene.

RESUMEN. Aunque el registro de fósiles del Cenozoico en Sudamérica es bastante amplio, los estratos de fósiles más importantes se encuentran primariamente en la zona templada de Sudamérica, y las Edades Mamíferas de Sudamérica están establecidas por la secuencia de fauna en esos depósitos. Estudios de fósiles de vertebrados en otras partes de Sudamérica, incluyendo lo expuesto en este estudio, tienden a confirmar la universalidad de estas edades faunísticas.

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El descubrimiento de una diversa fauna local en la última fase del Mioceno (Huayqueriense) en el Río Acre cerca de la frontera entre el Perú y el Brasil, provee la primera oportunidad de examinar una muestra amplia de la fauna Amazónica de la última fase del Terciario. Varios taxa han sido registrados de fósiles en la Cuenca del Amazonas por la primera vez: Dasypodidae (Pampatheriinae), Proterotheriidae, Macrauchenidae, Erethizontidae, Dasyprotidae, Dinomyidae (*Potamarchus murinus*, *Telicomys amazonensis* n. esp., *Tetrastylus* sp.), Neoepiblemidae, Hydrochoeridae (*Kiyutherium orientalis*), Caviidae (Cardiomysinae), Echimyidae (Heteropsomyinae) y Sirenia (Trichechidae). Las afinidades de esta fauna local con la fauna de la sabana de la Argentina durante la última fase del Miocene, sugiere que una comunidad de sabana ampliamente distribuida se extendía hasta la Cuenca Amazónica. Sin embargo, un nuevo género de Mylodontidae y lo que pudiera resultar una nueva familia de Marsupialia hacen notar mayores diferencias entre las faunas tropicales y templadas de Sudamérica durante el Cenozoico.

Un taxón Holoceno se comenta en base del nuevo material. El descubrimiento del perezoso terrestre *Nothropus priscus* en los depósitos a lo largo del Río Acre definitivamente sostiene la ubicación de *Nothropus* en los Nothrotheriinae como una relación cercana de *Nothrotheriops*, un género que mostraba una preferencia por una habitación seca. Esta relación, y el descubrimiento del espécimen a la base de una formación gruesa que tiene una máxima fecha radioisotópica de 11,000 años, indica que los mayores cambios climáticos y ambientales ocurrieron en el margen del oeste de la Cuenca Amazónica durante el Holoceno.

INTRODUCTION

The present knowledge of South American faunal history rests on a fossil record that is largely preserved in Argentina (Fig. 1). The concentration of major Cenozoic vertebrate localities in Argentina and their relative paucity elsewhere in South America has created a situation in which the fossil record of Argentina has been used to typify conditions

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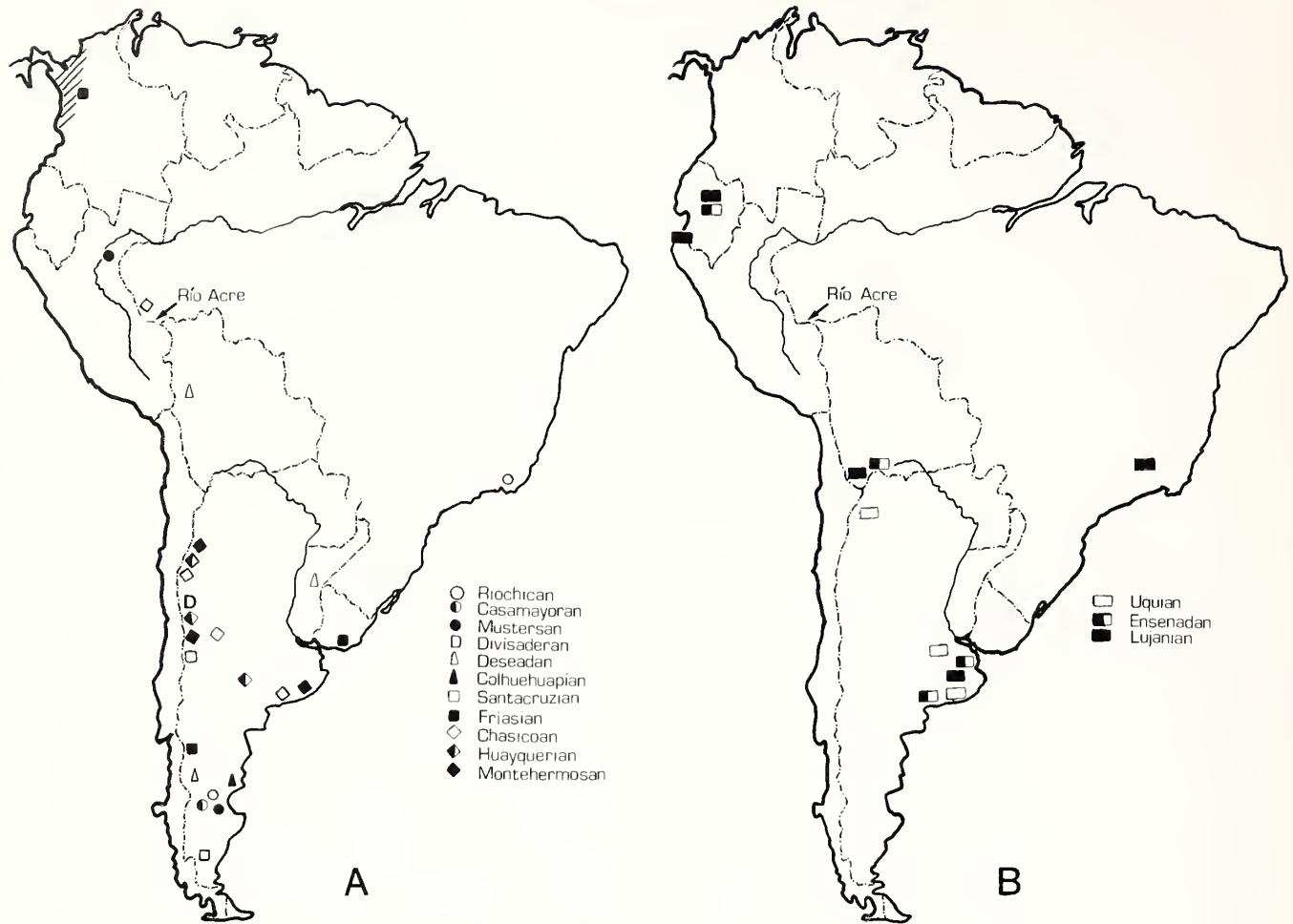


Figure 1. Maps of South America with distributions of major vertebrate localities and the location of the Río Acre. A, Tertiary localities; B, Pleistocene localities (modified from Patterson and Pascual, 1972).

throughout South America. The Cenozoic faunas of Argentina comprise the types for all but one (the Friasian) of the South American land mammal ages and smaller faunas found elsewhere in South America are naturally compared to the established land mammal ages. However, the extent of zoogeographic differences between faunas of South America is largely unknown and cannot even now be treated in discussions of the development of the South American fauna.

The lack of information regarding Cenozoic mammals is nowhere more acutely felt than when discussing the Amazon Basin. The small number of localities and known taxa are shown in Figure 1 and Table 1. Additionally, the fossils that were found in previous years were often highly fragmented and abraded beyond recognition. Stratigraphic placement or correlation could seldom be determined. Nonetheless, these fossils have served as holotypes for numerous new genera and species which are known only from the Amazon Basin and frequently only from the holotype specimens. The taxa listed in Table 1 are assuredly a heterochronous grouping, but, for the most part, the genera listed in Table 1 are found in

Pleistocene deposits in other areas of South America. *Griphodon peruvianus* is the oldest fossil mammal from the Amazon and is dated as probably Mustersan in age (Middle Eocene) by Patterson (1942). An astrapothere, *Synastratherium*, is dated morphologically as Oligocene (Paula Couto, 1976). In this paper, on stratigraphic grounds, I question that age assignment and suggest a Late Miocene age. The three endemic toxodontida and the rodents are with more certainty of Late Tertiary age although again they do not necessarily form a single fauna.

Other than incidental recovery of isolated specimens such as those described by Roxo (1921) and Anthony (1924), only three more extensive vertebrate fossil collections have been made in this region. Two of these collections, described by Spillman (1949) and Willard (1966), were the direct result of exploration for petroleum in eastern Peru. The extensive Bassler Collection of Peruvian fossils (collected between 1921 and 1931 but only described much later by Willard, 1966) is of interest in that it was assembled from several of the major rivers in eastern Peru (Willard, 1966, fig. 8). Vertebrate

Table 1. Faunal list of Cenozoic mammalian taxa previously reported from the Amazon Basin.

| |
|---|
| Marsupalia |
| ? <i>Abderites</i> , in Willard, 1966 |
| Edentata |
| Cingulata |
| Glytodontidae |
| <i>Panochthus</i> , in Paula Couto, 1956 |
| cf. <i>Hoplophorus</i> , in Willard, 1966 |
| Glyptodontidae, indet., in Spillman, 1949 |
| Dasyopodidae, indet., in Spillman, 1949 |
| Pilosa |
| <i>Eremotherium</i> , in Paula Couto, 1956 |
| <i>Lestodon armatus</i> , in Paula Couto, 1956 |
| <i>Scelidotherium</i> , in Paula Couto, 1956 |
| Megalonychidae, indet., in Paula Couto, 1956 |
| Rodentia |
| Dinomyidae |
| * <i>Phoberomys bordasai</i> Patterson, 1942 |
| Echimyidae |
| ** <i>Palaeoechimys peruvianus</i> Spillman, 1949 |
| Hydrochoeridae |
| * <i>Protohydrochoerus schirasakae</i> Spillman, 1941 (in Spillman, 1949) |
| * <i>Protohydrochoerus tahuamanii</i> Spillman, 1949 |
| Notoungulata |
| Toxodontidae |
| ** <i>Trigodonops lopesi</i> (Roxo) 1921 |
| ** <i>Abothrododon pricei</i> Paula Couto, 1944 |
| ** <i>Neotrigodon utoquineae</i> Spillman, 1949 |
| <i>Toxodon</i> cf. <i>platensis</i> , in Paula Couto, 1956 |
| <i>Toxodon</i> , in Willard, 1966 |
| Astrapotheria |
| ** <i>Synastrapotherium amazonense</i> Paula Couto, 1976 |
| indet., in Willard, 1966 |
| Pyrotheria |
| ** <i>Griphodon peruvianus</i> Anthony, 1924 |
| Proboscidea |
| Mastodontidae |
| <i>Haplomastodon waringi</i> , in Paula Couto, 1956 |
| <i>Cordillerion</i> , in Willard, 1966 |
| Sirenia |
| <i>Trichechus</i> , in Paula Couto, 1956 |
| Cetacea |
| ** <i>Plicodontinia mourai</i> Miranda-Ribeiro, 1938 (in Paula Couto, 1956) |
| Perissodactyla |
| Tapiridae |
| <i>Tapirus</i> , in Willard, 1966 |
| Artiodactyla |
| Tayassuidae |
| *Dicotyles traunmüllerri Spillman, 1949 |
| <i>Dicotyles</i> , in Willard, 1966 |

fossils, if only as fragments, appear to be widely distributed in the strata along the eastern margin of the Andes.

Recent years have seen two paleontological expeditions to the Río Juruá of Brazil (1956 and 1962, in Paula Couto, 1978) and preliminary papers on the fossils collected (Paula Couto, 1976, 1978). However, as in earlier collections, well-preserved fossils and a single major assemblage, a true local fauna, eluded discovery.

In September, 1977, and July, 1979, Dr. Kenneth E. Campbell of the Los Angeles County Museum and I collected vertebrate fossils at several localities along the Río Acre west of Iñapari, Peru (Fig. 2) on the northern border of Madre de Dios Province. Subsequent short trips to the Río Acre below Iñapari were conducted by Dr. Campbell alone. The trips were initially planned following discoveries by local inhabitants of several large fossil turtles in strata that are exposed along the river. Reports of these fossils reached Dr. Campbell in 1974 while he was making an ornithological collection in the nearby town of Iberia. Two of the turtles (*Podocnemis* sp.) were eventually recovered; one is now at the University of Kansas Museum of Natural History (KUVP 49492) and a second is at the Museo Nacional, "Javier Prado," in Lima. In addition, and of greater significance, was the identification of two formations, one Late Miocene and one Holocene, each with mammalian fossils (Table 2). This paper describes the mammalian fossils, other than the notoungulates, that were discovered along the Río Acre. The remainder of the fossils are still under study. These new fossils provide greater insight into the Cenozoic faunal history of tropical South America than was ever before possible. At the same time, the numerous single or fragmentary specimens that cannot be identified below high taxonomic levels yet seem unlike known genera and specimens indicate that much of the Cenozoic diversity of the Amazon Basin remains undiscovered.

MEASUREMENTS, ABBREVIATIONS, AND LOCALITIES

All measurements used in this paper are in millimeters unless otherwise indicated. Teeth measurements, length × width, were taken at the occlusal surface unless stated otherwise. Parentheses around a measurement indicate an approximate measurement. Rodent dental nomenclature follows Patterson and Wood (1982) unless otherwise noted. Skeletal measurements are standardized following DeBlase and Martin (1974) and Driesch (1976). In the illustrations, arrows indicate the anterior and labial directions from a tooth. Abbreviations used are KUVP, University of Kansas, Museum of Natural History; GB, Servicio Geológico de Bolivia (GEO-BOL), La Paz, Bolivia; LACM, Natural History Museum of Los Angeles County; b.p., before present.

Miocene and Holocene localities along the Río Acre are on record with the Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County. Several local-

* Species known only from the Amazon Basin.

** Genus and species known only from the Amazon Basin.

Generalized Geologic Section of Río Acre, Peru

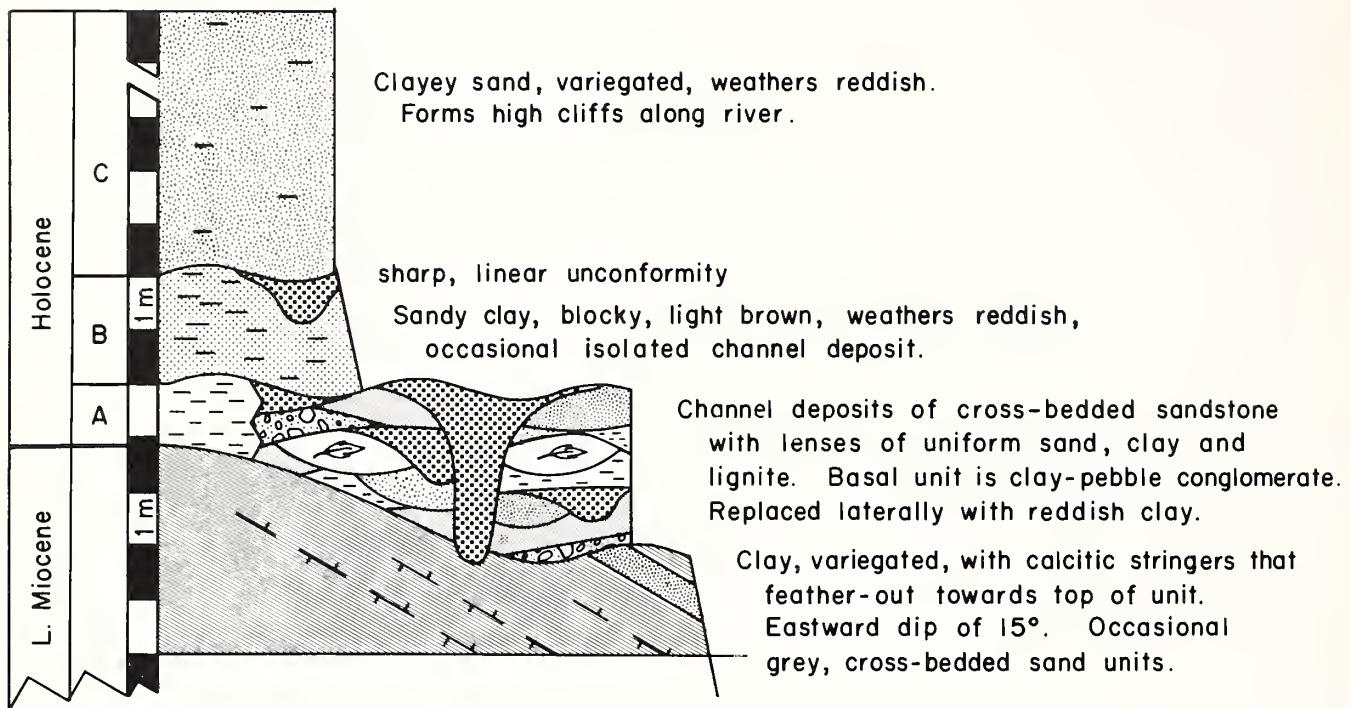


Figure 2. Generalized geologic section along the Río Acre (reprinted with permission from Campbell and Frailey, 1984). The Acre Conglomerate Member was named later (Campbell et al., 1985). Here it is the lowest conglomeratic lense of Member A.

ties, those that produced the fossils discussed in this paper, are marked on Figure 3.

GEOLOGY

The surface geology of the northern part of Madre de Dios Province has recently been mapped by the Oficina Nacional de Evaluación de Recursos Naturales (ONERN) of the Republic of Peru (ONERN, 1977). Only one formation, the Iñapari Formation of presumed Pliocene–Pleistocene age, is shown to outcrop along the Río Acre. Later work indicates that at least two formations are present (Fig. 2, from Campbell and Frailey, 1984). The upper formation is composed of four units and represents most of the exposed section along the Río Acre. It is this formation that best matches the description of the Iñapari Formation (ONERN, 1977) and our usage of this name was restricted to it. The age of the Iñapari Formation, however, is Holocene rather than either Pliocene or Pleistocene (Campbell and Frailey, 1984). The underlying formation is hence unnamed and was referred to as the Tertiary red beds by Campbell and Frailey (1984) based on a presumed correlation to some part of the undifferentiated Tertiary Red Beds of Singewald (1927, 1928) and Oppenheim (1937).

TERTIARY RED BEDS

This formation is principally composed of variegated clays (green, red, and tan) with calcitic stringers that follow the bedding planes. At Belgica (Fig. 3), gray, cross-bedded well-sorted sand units replace the variegated clay. In these units are found fossil pelomedusid turtles in what are apparently channel deposits. The site at LACM 4418 may also represent a lensing channel sequence, but at all other places along the river the lithology is uniform. The red beds have a north-south strike and an approximate 15° dip to the east (see Fig. 3). The top of the formation is blocky clay, weathering reddish, in which the irregularly shaped calcitic stringers and the visible bedding planes feather-out near the undulating contact with the overlying Holocene Iñapari Formation. This evidently represents a weathering surface, perhaps the B level of soil formation. The top of the weathered zone forms a bench in many exposures. The contact between this and the overlying unit is also the site of a perched water table that causes numerous small springs to form at this level. The perched water table indicates that a significant lithologic difference exists between the two formations which is not obvious in field examination. The red beds are not visible at every bank exposure along the Río Acre.

Table 2. Faunal list of the Río Acre region.

| Río Acre Local Fauna |
|---|
| Tertiary |
| Chondrichthyes ¹ |
| Batoidea |
| Potamotrygonidae |
| Osteichthyes ¹ |
| Osteoglossidae |
| Doradidae |
| Pimelodidae |
| Characidae |
| <i>Colossoma</i> |
| Callichthyidae |
| Reptilia ¹ |
| Chelonia |
| Pelomedusidae |
| Testudinidae |
| Crocodilia |
| Gavialidae |
| <i>?Gavialosuchus</i> |
| Alligatoridae |
| <i>?Caiman</i> |
| <i>?Brachygnathosuchus</i> |
| Aves ¹ |
| Mammalia |
| Marsupialia |
| Edentata |
| Mylodontidae |
| <i>Stenodon campbelli</i> n. gen. and sp. |
| Megalonychidae |
| Dasyopidae |
| Pampatheriinae |
| Rodentia |
| Erethizontidae |
| Dinomyidae |
| <i>Potamarchus murinus</i> |
| <i>Telicomys amazonensis</i> n. sp. |
| <i>Tetrastylus</i> |
| Hydrochoeridae |
| <i>Kiyutherium orientalis</i> |
| Caviidae |
| Cardiomysinae |
| Genus A |
| Genus B |
| Neopiblemidae |
| Dasyproctidae |
| Echimyidae |
| Heteropsomyinae |
| Litopterna |
| Proterotheriidae |
| Macrauchenidae, new genus |
| Notoungulata ¹ |

Table 2. Continued.

| |
|---|
| Astrapotheria |
| <i>?Synstrapotherium</i> |
| Sirenia |
| Trichechiidae |
| <i>?Ribodon</i> |
| Iñapari Member A Local Fauna |
| Holocene |
| Reptilia ¹ |
| Chelonia |
| Pelomedusidae |
| cf. <i>Peltocephalus</i> sp. ² |
| Mammalia |
| Edentata |
| Megalonychidae |
| <i>Nothropus priscus</i> |

¹ Not discussed in this paper.² Identified by Dr. Eugene Gaffney, pers. comm., 1982.

Fossils are rare in the red beds. They were found in only two localities, LACM 4418 and 4606. The site stratigraphy at LACM 4418 is complex and may represent stream deposition at the top of the red beds. An explanation for the general rarity of fossils in the red beds is that the fossils are in fact not derived from the red beds but rather come from channels which are incised into the red beds and hence are younger. The stratigraphy at LACM 4418 could be such a channel sequence in this interpretation. Support for this suggestion comes from the observation near LACM 4418 of a thick, incised channel sandstone deposited at the top of the red beds and itself truncated by the unconformity between the red beds and the Iñapari Formation. This channel deposit may be younger than any part of the red beds. If channels such as this are the source of the Huayquerian fossils rather than the red beds, then the red beds are older and may not even be of Huayquerian age.

For the present, the red beds are considered to be the source of the Huayquerian fossils in that LACM 4606 produced fossils (*Potamarchus*) which were also found in Unit A of the Iñapari Formation in LACM 4611. There are no visible channel-fill deposits in LACM 4606 and the locality appears to be in the red beds. The fossils found in the red beds and those re-worked from this formation and re-deposited in the Iñapari Formation are designated the Río Acre Local Fauna.

IÑAPARI FORMATION

The Holocene Iñapari Formation is composed of four members that were designated the Acre Conglomerate Member, Member A, Member B, and Member C by Campbell and Frailey (1984) and Campbell et al. (1985). Each will be discussed separately.

ACRE CONGLOMERATE MEMBER. A clay-pebble conglomerate is frequently present and readily identifiable at



Figure 3. The Río Acre and the location of five sites discussed in the text. LACM locality numbers and equivalent field numbers are listed. Strike-dip symbols refer only to the Tertiary red beds.

the base of the Iñapari Formation. Average pebble size is 1 cm with an occasional cobble up to 20 cm in diameter. The matrix is gray or brown, well-sorted, unconsolidated sand. Calcitic inclusions appear to have been derived from the underlying red beds. Fossils of small animals and broken pieces of larger animals and fossil wood are common in this unit although the majority of fossils, all the mammals thus far known, are evidently re-worked from the red beds. Many of the fossils are rounded by abrasion but delicate fossils, such as small fish spines and minute rodent teeth, are also preserved intact. The Miocene fossils found at LACM 4611 were in this conglomerate.

MEMBER A. Above the Acre Conglomerate Member is a complex series of channel deposits composed of cross-bedded brown to buff sandstones with lenses of pure buff sandstones, variegated clays, and lignites. Fragments of fossil vertebrates are found throughout this lensing sequence. Some are probably re-worked from the red beds although their fragmentary nature prevents positive assertion of this. The ground sloth, *Nothropus priscus*, was discovered in a channel-sand deposit near the base of this unit at LACM 4609. Fossil vertebrates found in this member are referred to as the Iñapari Member A Local Fauna. Large pieces of fossil wood and well-preserved leaves are abundant in the lignite lenses. These channel deposits (see Fig. 2) may be replaced laterally by a variegated, blocky clay that is red in outcrop. This facies is

less extensive than the channel lenses and produced no fossils.

The thickness of Member A varies between 1 and 5 meters with the least thickness observed where the channel deposits are absent and replaced by the uniform clay.

MEMBER B. Member B is separated from Member A by an undulating contact. Member B is blocky, light brown, sandy clay that weathers reddish. Occasional isolated channel cuts are present in this unit. Member B is usually horizontally bedded with rare instances of structural slump. Its thickness is approximately 5 meters. No fossils were found in Member B.

MEMBER C. The uppermost member of the visible section forms high, inaccessible cliffs along the river. Member C is separated from Member B by a sharp, conspicuous, linear contact. Member C is composed of a clayey sand, variegated in color (tan, red, and green) that weathers reddish. Thickness is approximately 30 meters. No fossils were recovered from Member C.

GEOLOGICAL CORRELATION AND PREVIOUS WORK

The geology of the western margin of the Amazon Basin is not well described in the literature and correlation based on

published descriptions is far from certain. The first description of the geology along the Río Acre (ONERN, 1977) is brief as are descriptions of the geology to the south of the Río Acre in Madre de Dios Province, Peru (Oppenheim, 1946, 1975; ONERN, 1972) or to the north of the Río Acre in the state of Acre, Brazil (Oppenheim, 1937; Paula Couto, 1978). The descriptions of geology are all similar and may represent the same sequence.

Oppenheim (1946) named the Madre de Dios Formation for a thick succession of clays and sandstones that are exposed in high river banks along the Madre de Dios River from the Bolivian border to the Inambari River and along the lower part of the Inambari River basin. This is evidently the formation that is called the "Montaña Formation" in the geologic map included in the same paper. ONERN (1972) calls most of this surface stratum simply "Quaternary alluvials" but does use the term Madre de Dios Formation for exposures along the upper Madre de Dios and Inambari rivers. Following Oppenheim (1946), these are given a later Tertiary age designation without elucidation. Either part of the Madre de Dios Formation of Oppenheim (1946) is now called Quaternary alluvium by ONERN (1972) or Oppenheim (1946) did not include or overlooked the Quaternary alluvium when he described the geologic section and ONERN included it as the uppermost, most surficial deposit on their geologic map. Oppenheim (1975) continued to use the Madre de Dios Formation for exposures in the lower part of the Madre de Dios River after his original usage. From the descriptions of both Oppenheim (1946) and ONERN (1972), the Madre de Dios Formation could include both the Iñapari Formation (in its restricted usage) and the Tertiary red beds. If this proves to be the case, the name Madre de Dios has priority over the name Iñapari Formation and should be used over all of Madre de Dios Province, Peru, and perhaps into Acre, Brazil. In this paper, as in Campbell and Frailey (1984), the identification of separate Madre de Dios and Iñapari formations by ONERN (1972, 1977) is followed and the uppermost strata along the Río Acre are referred to the Iñapari Formation.

Little has been written of the Tertiary geology north of the Río Acre. Oppenheim (1937) described riverbank outcrops of light-to-dark red clays and sandstones with light, greenish bands of limestones or calcareous clays along the Río Juruá in Acre, Brazil, as the Cruzeiro Red Beds. The description is similar to the appearance of the Iñapari Formation along the Río Acre and could be the same formation. On the basis of the fossils found in a localized overlying deposit, Oppenheim (1937) placed the Cruzeiro Red Beds as pre-Pliocene in age and correlative in part to the Red Beds of Singewald (1927) and the Formación de Puca of Steinmann (1929). Singewald's Red Beds were described from along the Ucayali drainage and produced a new genus of pyrothere, *Griphodon peruvianus* (Anthony), 1924, which Patterson (1942) placed as equal to or slightly later than Mustersan (Middle Eocene). This is much older than the fossils found in the Tertiary red beds of the Río Acre and if correct means that the Iñapari Formation is much younger than the Red Beds of Singewald (1927, 1928), the Puca Formation of Steinmann (1929), or the Cruzeiro Red Beds of Oppenheim (1937).

Paula Couto (1978) includes a field sketch of the upper Juruá River that was made by G.G. Simpson in 1956. This section is very similar to the Río Acre section (Campbell and Frailey, 1984). A conspicuous element in Simpson's section is a "heavy conglomerate" at the position of the Acre Conglomerate Member in the Río Acre section. Above the "heavy conglomerate," Paula Couto places two units, yellow-greenish clays and silts that are overlain by fine, buff sands. Below the conglomerate is a "Puca type" stratum that easily corresponds to the red beds of the Río Acre. The use of the phrase "Puca type" is not explained by Paula Couto but evidently refers to the thick Puca Formation of Steinmann (1929) which Steinmann thought was the same as Singewald's Red Beds and which Oppenheim (1937) furthermore thought was correlative with the Cruzeiro Red Beds. If this is a true correlation, these beds are of Mustersan age (at least in part) on the basis of the included pyrothere.

Either similar deposits were formed over an extensive time period of Middle Eocene to Late Miocene or the "Puca type" stratum of Paula Couto (1978) is not correlative with any of the Puca Formation (and Singewald's Red Beds) but is instead much younger than either. On the other hand, perhaps the *Griphodon* was actually found in much older deposits that were mistaken for red beds, and the Red Beds of the Ucayali River, the Puca (or part of it), and "Puca type" beds are in fact correlative after all. A third possibility, that *Griphodon* is not Mustersan and the correlation of red beds is accurate, depends on the unlikely possibility that a primitive pyrothere survived in the Amazon Basin long after the Oligocene extinction of this group elsewhere in South America.

The Red Beds and the Cruzeiro Red Beds are not the uppermost strata listed in the sections of Singewald (1928) and Oppenheim (1937). Above the Red Beds of Singewald are the unfossiliferous Brown Beds and above the Cruzeiro Red Beds of Oppenheim is the localized Aquidabam deposit that he thought was probably Pliocene in age. Patterson (1942) gave a probable correlation of these with each other and with the Paraná deposits of Argentina. The correlation with the Paraná is based on Tertiary invertebrates in the Aquidabam deposit, structural folding in the Brown Beds (hence deposited prior to and folded by the Andean uplift), and fossil vertebrates in the Paraná. This correlation was initially uncertain and made even more so with recent opinions on mixed taxa in the Paraná fauna (Pascual and Bondesio, 1968).

All of these formations would presumably fall into the thick and rather broadly defined Late Tertiary Grupo Chiriacó of Williams (1949). ONERN (1977) places this group in the vicinity of the Río Acre although not actually exposed along the river.

The angular unconformity that occurs near the low-water line of the Río Acre marks the boundary between the Tertiary red beds and the sediments of the Holocene Iñapari Formation. This boundary has been noted in numerous publications on Amazonian geology in the vicinity of the Río Acre (Kummel, 1948; Rüegg and Rosenweig, 1949; Mousinho de Meis, 1971; Paula Couto, 1978; RADAMBRASIL, 1976, 1977) although the identities and ages of the formations involved could not be confidently established. Recent publi-

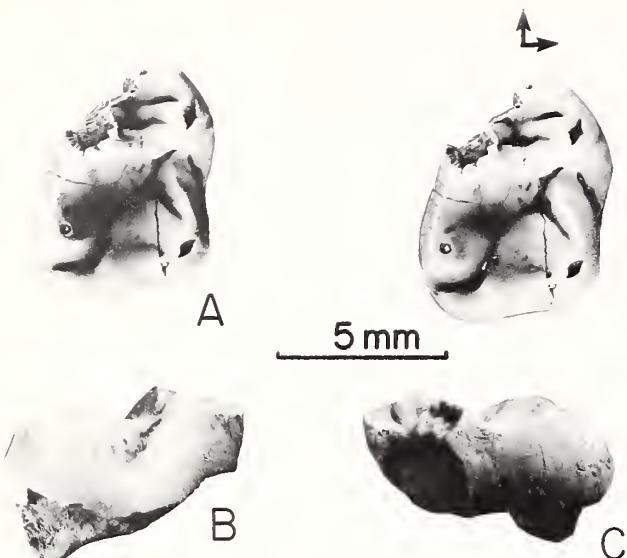


Figure 4. Marsupialia, LACM 117501, right lower tooth. A, stereoscopic occlusal view; B, labial view; C, lingual view.

cations (Campbell and Frailey, 1984; Campbell et al., 1985) indicate that the formation relationships are consistent over a sizeable portion of the western margin of the Amazon Basin and regional correlation, at least, is not hopeless despite the present stratigraphic confusion that is outlined here.

SYSTEMATICS

Río Acre Local Fauna
Late Miocene

Order Marsupialia Illiger, 1811

Family Indeterminate

Figure 4

MATERIAL. LACM 117501, lower tooth.

LOCALITY. LACM 4611.

DESCRIPTION. This lower tooth is flat and wide with a small trigonid and a large, broadly basined talonid. All the cusps are low and rounded. The cusps of the trigonid are united by a narrow U-shaped crest that encompasses a shallow trigonid basin that is partially filled by a crest that runs lingually from the protoconid. The metaconid is slightly higher than the protoconid (the paraconid is missing due to breakage). The entoconid and hypoconid are of equal height. The hypoconulid is a widened portion of the posterior crest of the talonid basin and is situated immediately posteromedially from the entoconid.

DISCUSSION. The presence of the Marsupialia is indicated by a single tooth that is not referable to known marsupials. This tooth has characteristic marsupial features in that the trigonid is compressed anteroposteriorly and the hypoconulid lies near the entoconid. However, unlike all



Figure 5. *Stenodon campbelli* n. gen. and sp., LACM 117502, skull, holotype, ventral view (photograph).

previously described marsupial teeth, this specimen has low, rounded cusps and a broadly basined talonid which are altogether very procyonid-like in appearance. This tooth may represent the existence of a marsupial family that was ecologically equivalent to the Procyonidae in South America. Their fate upon the entry of true procyonids in South America in the Huayquerian is as unknown as their history prior to their inclusion in the Río Acre Local Fauna. However, in some aspects such as crown height and degree of trituberculy, this tooth is similar to molars of the Prepidolopidae from the Argentinian Eocene (Pascual, 1981). The little that is known of the Prepidolopidae or this marsupial group from the Miocene of the Amazon Basin unfortunately precludes more than tentative considerations of relatedness.

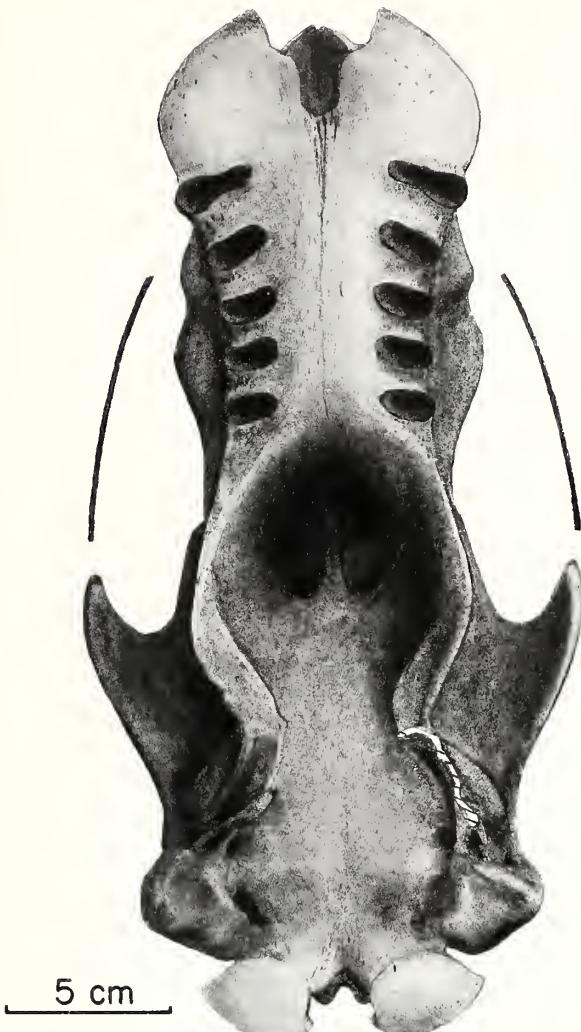


Figure 6. *Stenodon campbelli* n. gen. and sp., LACM 117502, skull, holotype, ventral view (reconstruction).

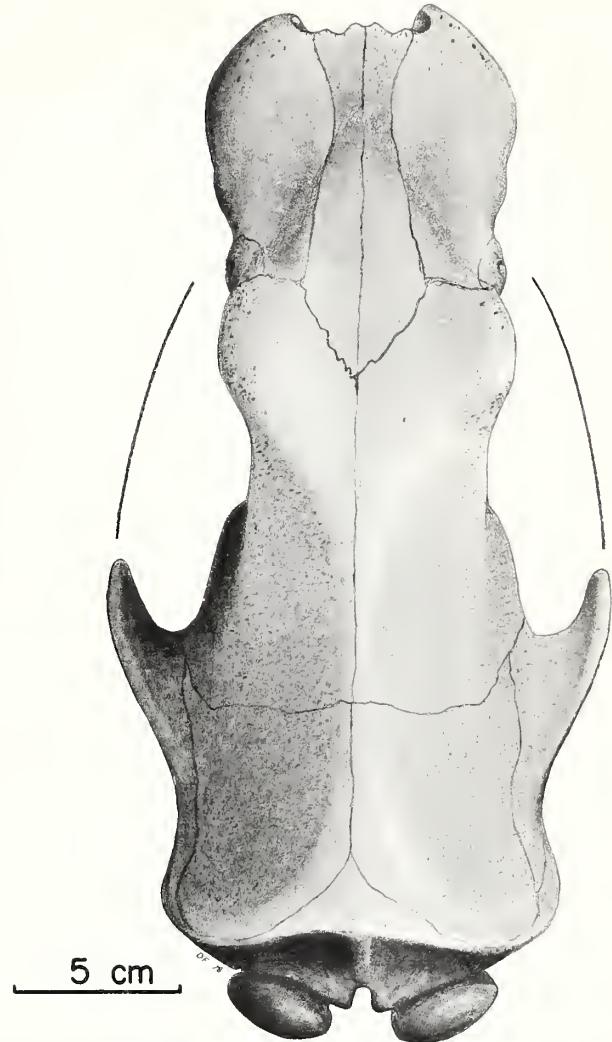


Figure 7. *Stenodon campbelli* n. gen. and sp., LACM 117502, skull, holotype, dorsal view (reconstruction).

Order Edentata Cuvier, 1798

Family Mylodontidae Gill, 1872

Subfamily Mylodontinae Gill, 1872

Stenodon campbelli, new genus and species

Figures 5, 6, 7, 8, 9A-C

HOLOTYPE. LACM 117502, skull.

TYPE LOCALITY. LACM 4418.

REFERRED MATERIAL. LACM 117503, ulna; LACM 117504, femur; LACM 117505, astragalus.

GENERIC DIAGNOSIS. Dorsal margin of skull is slightly convex and higher than the nasals. The palate extends anteriorly to M^1 and is bulbous. Tooth rows diverge slightly toward the anterior. Teeth are ellipsoid in cross section with no posterior lobation of M^5 .

ETYMOLOGY. steno, Gr., narrow; odon, Gr., m. tooth.

SPECIES DIAGNOSIS. Same as for the genus.

ETYMOLOGY. Patronymic, in honor of Dr. Kenneth E. Campbell, Jr.

DESCRIPTION. **Skull.** The specimen is fragmented, crushed and distorted to the left. The malar is missing. The extreme fragmentation of the skull and its calcareous encrustation permits discussion of only the gross features of the skull.

Dorsally, the skull appears tubular in shape, similar to *Paramylodon* but shorter, with postorbital and preorbital constrictions. Supraorbital bosses are prominent. A low and wide (10 mm) sagittal crest is indicated between the large temporal fossae. Prominent lambdoidal and occipital crests are present and confluent. Thin, paired crests are present laterally on the occipital and reach the lambdoidal crest. The occipital is hemispherical and slopes forward. The occipital condyles are large, bulbous and continue on the ventral line



Figure 8. *Stenodon campbelli* n. gen. and sp., LACM 117502, skull, holotype, lateral view (reconstruction).

of the occipital to form the most posterior part of the skull and extend ventrad as far as the pterygoids.

In lateral view, the dorsal margin is flat or somewhat convex and the nasals are slightly lower than the dorsal margin. The zygomatic process of the squamosal is wider toward the anterior, free end and narrows toward the squamosal. The lacrimal protuberance and lacrimal foramen are large and situated above M^2 . The hard palate is approximately 10 mm ventrad to the alveolar borders or M^{2-5} .

Ventrally, the skull widens anteriorly from its narrowest point immediately posterior to M^5 (67 mm) to its widest point across the predentary bosses (128). The distance between the left and right M^5 's is 32.5; between M^1 's it is 57.3. The predentary portion of the palate is inflated and bulbous with a shallow fossa at the midline. The postpalatine fossa is large, broadly U-shaped and bounded laterally by widely flaring pterygoids. The basioccipital is trapezoidal in shape.

On the posterior part of the basioccipital, the area of origin of the *M. rectus capitus ventralis* is deeply sculpted. Occipital condyles are fully separate from other basicranial structures. The paroccipital process and mastoid process are equal in size and do not extend ventrad to the basioccipital. The groove for the carotid artery is open. The posterior lacerate foramen is small, barely larger than the carotid canal. The condyloid foramen is compressed into a slit rather than the circular foramen more normal in mylodontids, but this may be due only to the distortion of the fossil.

Dentition. All teeth are missing on the specimen and the following discussion is based on the alveoli.

Five upper teeth were present, here designated M^{1-5} . All the teeth are remarkable in their simple, ellipsoid occlusal shape with lobation indicated in only one tooth, M^1 . In M^1 , the lateral half of the alveolus is enlarged. The second and third upper alveoli are flexed with a concave border toward the anterior. The labial margins of the alveoli of M^{1-5} lie on a curving line which converges on the midline of the palate. Orientation of the teeth also changes progressively toward the posterior. The M^1 is directed posterolabially and M^5 is almost transverse to the midline of the palate. The teeth are approximately equally spaced with a slight increase in separation toward the anterior. Measurements of the alveoli (length \times width): M^1 , 12.8 \times 32.5; M^2 , 12.8 \times (24); M^3 , 12.4 \times 23.9; M^4 , 12.6 \times 23.5; M^5 , 12.8 \times 20.0. Measurements between alveoli: M^{1-2} , 12.2; M^{2-3} , 8.2; M^{3-4} , 7.6; M^{4-5} , 7.2. Length of tooth row, 95.

Postcranial skeleton. The astragalus (Fig. 9A-C) has a low odontoid process which meets the external trochanter at an approximate 90° angle. The external trochanter is biconvex when viewed laterally and forms a straight articular surface when viewed tibially. The fibular facet is planar and extends between the middle part of the external trochanter and the distal part of the lateral calcaneal facet. The lateral calcaneal facet is oval in outline and concave. The proximal end comes within 10 mm of the proximal end of the external trochanter. The medial calcaneal facet is a ventral continuation of the cuboidal articular surface. It is planar and more rectangular in outline than the lateral calcaneal facet. The calcaneal facets are well separated (10 mm). The articular surfaces for the navicular and cuboid are about equal in size. The navicular surface is concave externally and convex medially. The cuboidal facet is triangular in shape and convex. Measurements: odontoid process (internal trochanter), height, 31, length, 42.1; external trochanter (length \times width), 99.7 \times 42.0; fibular facet, 37.0 \times 33.3; navicular facet, 55.9 \times 33.1; cuboid facet, 40.4 \times 40.0; external calcaneal facet, 66.5 \times 38.4; internal calcaneal facet, 42.8 \times 32.8.

DISCUSSION. A large sloth is represented in the fauna by a skull and several incomplete limb elements. This sloth is placed in the Mylodontidae on the basis of 1) its large size which is equal to that seen in *Glossotherium*; 2) the long, cylindrical skull; 3) the presence of five molariform teeth which are subequal in size and subcylindrical in shape; and 4) evenly spaced teeth (i.e., there is no anterior tusk).

The features of the astragalus further substantiate the familial identification. Astragali with the internal trochanter

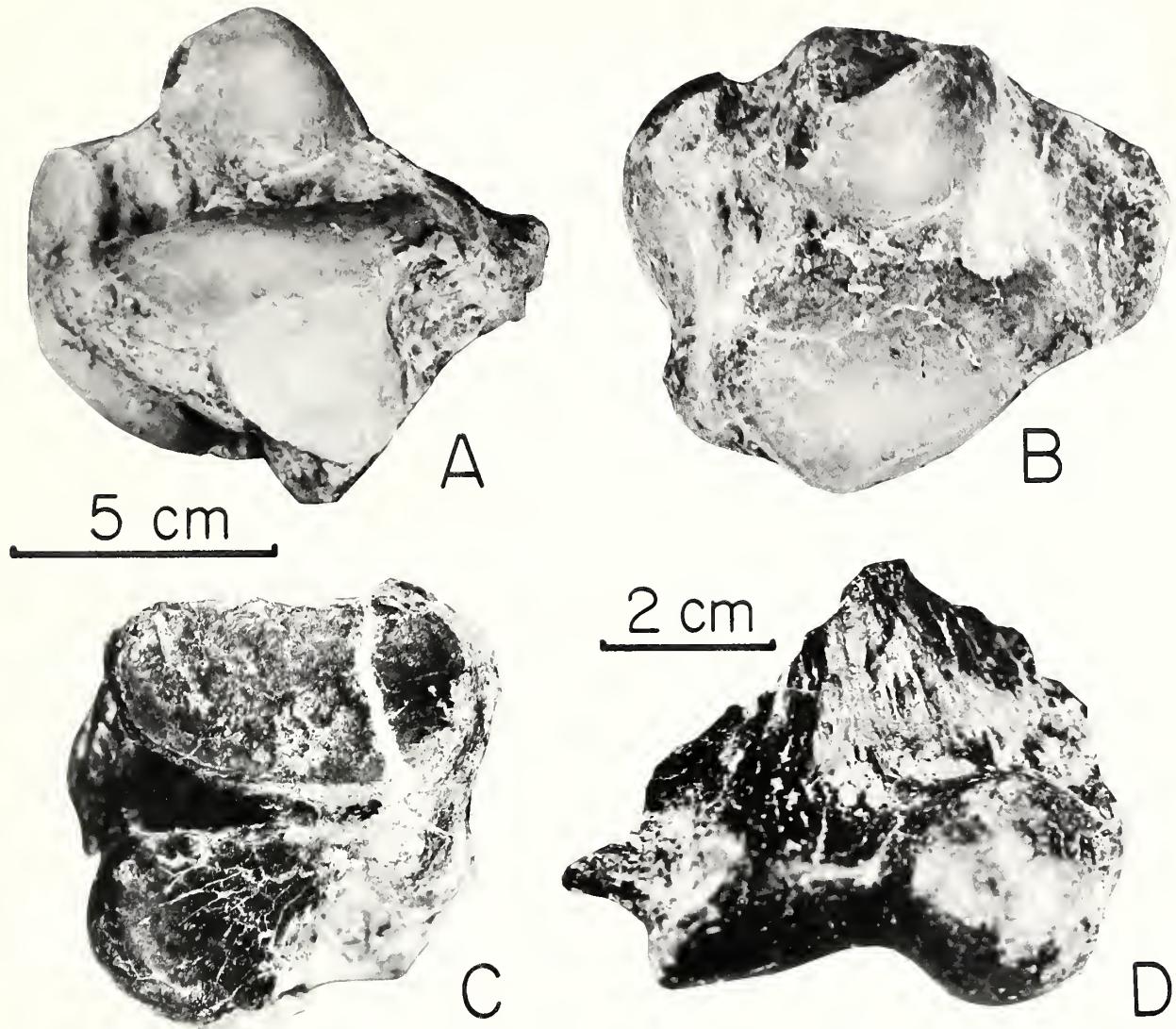


Figure 9. *Stenodon campbelli* and *Megalonychidae*. A-C, *Stenodon campbelli* n. gen. and sp., LACM 117505, left astragalus. A, Fibular view; B, trochlear view; C, calcaneal view, anterior to left. D, *Megalonychidae*, LACM 117534, distal end of left humerus, anterior view.

modified into an odontoid process are characteristic of Mylodontidae and Megatheriidae. This astragalus, unlike those of the Megatheriidae, has a straight (rather than semicircular) external trochanter and a gently concavo-convex navicular facet rather than a deep navicular pit. Completely separate calcaneal facets as in *Stenodon* is a primitive sloth feature found in the Scelidotheriinae and in most Mylodontinae (fused in *Glossotherium* Owen, 1840; *Mylodon* Owen, 1840; and *Paramylodon* Brown, 1903). The astragalus of *Stenodon* is differentiated from those of the Scelidotheriinae and resembles the Mylodontinae in that the cuboid and navicular facets are broadly continuous rather than sharply differentiated as in the Scelidotheriinae, and that the cuboidal facet is convex rather than concave.

This sloth can further be assigned to the Subfamily Mylodontinae, rather than the Scelidotheriinae, on the basis of

1) a forwardly sloping occiput; 2) a hard palate that is ventral to the level of the alveoli; 3) an anteriorly widening palate in which the tooth rows diverge as in *Glossotherium* and *Glossotheridium* Kraglievich, 1934; 4) a low and rounded paroccipital process; and 5) a groove, rather than a foramen, for the internal carotid artery.

The specimens are not, however, referable to any of the known genera of the Mylodontinae and therefore represent something new. In this genus, all the teeth are subcylindrical in shape with only a slight tendency to bilobation. The M^5 lacks a posterior elongation. The characters indicate that this genus was more primitive than either *Glossotherium* or *Glossotheridium*. The rostrum extends anteriorly to M^1 and is bulbous. The teeth appear to have been more compressed in shape (anteroposteriorly) than in the other mylodonts. This character is more like that of the Scelidotheriinae and is either

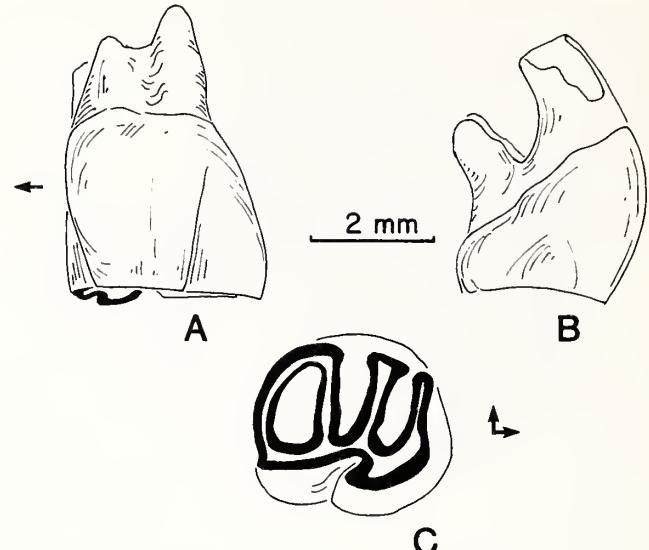
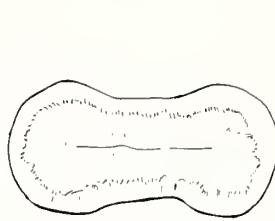


Figure 10. Pampatheriinae, gen. and sp. indet., LACM 117506, lower tooth, photograph of lateral side and drawing of occlusal surface.

convergent on the Scelidotheriinae (as I believe) or represents a shared ancestral (plesiomorphic) character. The dorsal margin of the skull is essentially flat but slopes forward at the rostrum as is also seen, although more dramatically, in *Glossotherium* and *Glossotheridium*. *Stenodon* probably is related to *Glossotheridium* and *Glossotherium* in the Mylodontinae. It is, however, more primitive than either of these respectively Pliocene and Pleistocene genera in many features although it had developed its own characteristic, derived features. As such, *Stenodon* cannot be placed in a directly ancestral position to the later genera.

Family Megalonychidae Zittel, 1893

Genus and Species Indeterminate

Figure 9D

MATERIAL. LACM 117534, distal end of humerus.

LOCALITY. Sandbar in Río Acre, no stratigraphic data.

DESCRIPTION. An unusually small ground sloth is identified by a humerus fragment. The external trochlea is round, bulbous and has a slight sagittal ridge medially. The internal trochlea is as broad (anteroposteriorly) as the external trochlea. The angle formed between the trochlea when the humerus is viewed anteriorly is shallow and much less than that seen in the Megatheriidae. The olecranon fossa is shallow. There is no evidence of an entepicondylar foramen on the portion of the humerus that is preserved.

DISCUSSION. The features of this specimen are similar to humeri of *Hapalops* although the Río Acre specimen is about 50 percent larger than any known species of that genus. A more striking resemblance, including correct size correspondence, is seen between this fragment and humeri of the small Pleistocene sloths of the West Indies, *Mesocnus* Matthew, 1919 and *Parocnus* Miller, 1929 (but not *Acrotocnus* Anthony, 1916). On the material available, these humeri are inseparable. The origin of these small Caribbean ground sloths is conjectural but their antecedents may have dispersed to the islands from continental South America during the Miocene or perhaps early Pliocene (Paula Couto, 1967a). This suggestion is based primarily on the similarity of the Carib-

Figure 11. Erethizontidae, gen. and sp. indet., LACM 117507, right M¹ or M². A, lingual view; B, anterior view; C, occlusal view.

bean Megalonychidae to the Early Miocene Megalonychidae. The Río Acre megalonychid suggests an alternative possibility in that small megalonychids could have existed in the Amazon Basin throughout the late Tertiary and migrated to the Caribbean islands at any time that conditions permitted, even later than the Early Pliocene. Unfortunately, the Río Acre specimen was not found associated with other fossils. It may in fact not derive from the Tertiary red beds although its preservation is the same as fossils that were found in place and is here considered to be part of the same local fauna.

Measurements are: width across trochlea, 58; anteroposterior length of external trochlea (capitulum), 33; maximum length of internal trochlea, 30.

Infraorder Cingulata Illiger, 1811

Family Dasypodidae Bonaparte, 1838

Subfamily Pampatheriinae

Paula Couto, 1954

Genus and Species Indeterminate

Figure 10

MATERIAL. LACM 117506, lower tooth.

LOCALITY. LACM 4611.

DESCRIPTION. This tooth is identified as a pampatherine on the basis of its elongate cross section, dumbbell-shaped lobation and lack of branching of the central osteo-dentine plate. The degree of molarization places this as one of the posterior molariform teeth in the lower tooth series, M₅–M₈. Measurements, length × width, are 10.2 × 5.0.

DISCUSSION. This tooth is small for a molariform tooth of *Kraglievichia* Castellanos, 1927, and more comparable in

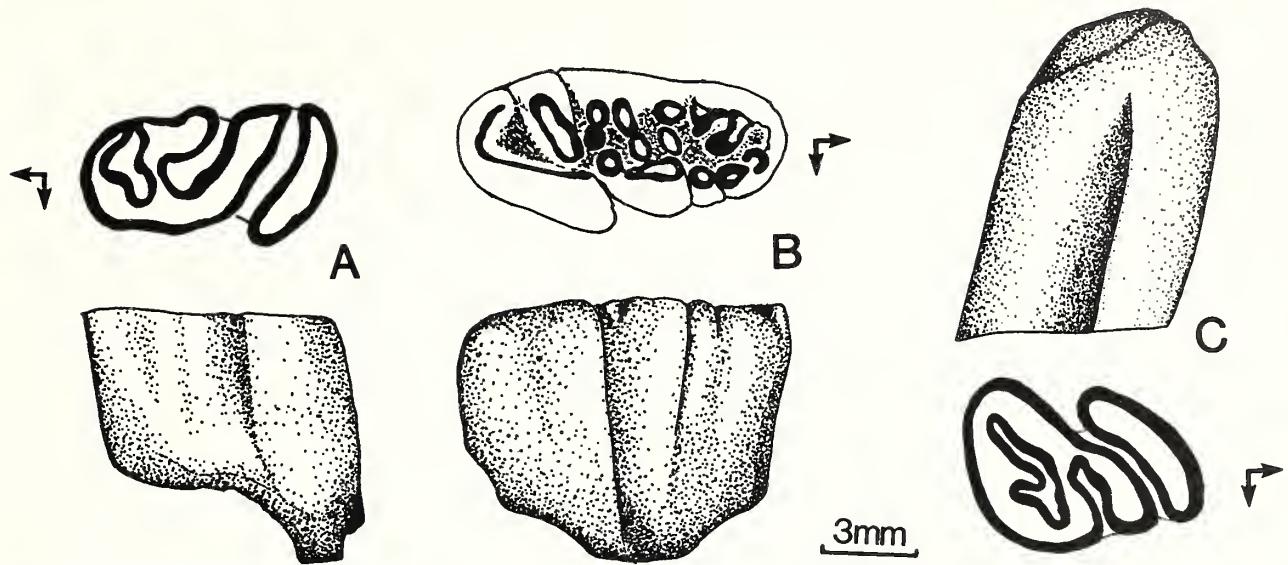


Figure 12. Dasyprotidae, gen. and sp. indet. **A**, LACM 117574, left lower tooth, occlusal and labial views; **B**, LACM 117576, right lower tooth, occlusal and labial views; **C**, LACM 117577, left M^1 or M^2 , lingual and occlusal views.

size to *Vassalia* Castellanos, 1927, the earlier (Huayquerian) pampatheres (Castellanos, 1927).

Order Rodentia Bowdich, 1821

Family Erethizontidae Thomas, 1897

Genus and Species Indeterminate

Figure 11

MATERIAL. LACM 117507, M^1 or M^2 , right.

LOCALITY. LACM 4611.

DISCUSSION. A very small porcupine is represented in the Tertiary local fauna by a single upper tooth. The tooth is relatively high-crowned for early porcupines and the crests are thin and well defined. The metaloph and posteroloph have united to form a deep oval enamel lake but the protoloph and anteroloph remain free. The sharpness of the crests and simplicity of the crown pattern is more similar to *Erethizon* Cuvier, 1822, or *Coendou* Lacépède, 1799, than to *Steiomys* Ameghino, 1887, and earlier Erethizontidae.

Family Dasyprotidae Smith, 1842

Genus and Species Indeterminate

Figure 12

MATERIAL. LACM 117574, left P_4 ; LACM 117575, left P_4 ; LACM 117576, right ? DP_4 ; LACM 117577, left P^4 .

LOCALITY. LACM 4611.

DESCRIPTION. Lower teeth. Two lower cheek teeth are represented in two stages of wear. The teeth are rounded anteriorly and one (LACM 117575) has a wear facet on the posterior surface which indicates that these teeth are P_4 s. In the less worn of the two (LACM 117574), the posterolophid is separated from the anterior lophids by a hypoflexid that

is deep on the labial margin but does not extend to the base of the crown on the lingual margin. Two additional flexids are present on the lingual margin that probably correspond to the mesoflexid and anteroflexid (assuming that the metaflexid was incorporated in the hypoflexid when the latter expanded lingually). On this species, the mesoflexid is persistent during all wear stages of the tooth. The anteroflexid, on the other hand, would soon disappear beyond the stage exhibited by LACM 117575. An ectolophid, metalophid, and anterolophid are recognizable. The ectolophid parallels the posterolophid and is equal to the posterolophid in size. With wear, as in LACM 117575, the ectolophid and posterolophid become joined lingually (around the shallow end of the hypoflexid) and centrally. The metalophid is club-shaped (enlarged toward its labial end) in these wear stages and joins the anterolophid, lingually, to create an anterofossettid from the anteroflexid. From the present height of these teeth and their advanced stage of wear, the teeth apparently were hypodont and may never have formed roots.

An isolated lower tooth (LACM 117576) is tentatively referred to this taxon as a DP_4 . It is only slightly worn, shows no wear facets from adjacent teeth, and the lophid pattern is complex and only partially discernable. However, this pattern and the placement and relative heights of the flexids are comparable to those of the previously described lower teeth.

Upper teeth. The more quadrangular occlusal outline and the curvature (a concave buccal surface) of LACM 117577 indicate that it is an upper tooth. A wear facet is present on the posterior surface only and suggests that this is a P^4 . The anteroloph is separated from the posterior portion of the tooth by a long hypoflexus that appears to replace the paraflexus labially. The hypoflexus extends to the base of the crown on the lingual side. The labial extent of the hypoflexus is less than half the height of the unworn crown (approximately 1 mm below this wear stage). Two additional labial

flexi are present. The posterior flexus (metaflexus) is represented labially by only a notch on the enamel wall. The more anterior of the two (mesoflexus) is also indicated only by a notch in the enamel wall but extends medially as a deep flexus. The first loph that is posterior to the hypoflexus, the protoloph, is short and irregular in outline and much larger toward the labial surface. The protoloph unites with the metaloph centrally in the tooth. The posteroloph is long and unites labially with the metaloph and lingually with the combined protoloph and metaloph. Therefore, a large fossette is enclosed. The irregular shape of this fossette is created in part by what appears to be an anterior extension of the posteroloph into it. This apparently new loph corresponds to the neoloph of some authors (see following discussion) and its appearance here as a new structure may be phylogenetically significant.

DISCUSSION. These teeth are referred to the Dasyproctidae on the basis of the presence of four distinct lophs and lophids in which the anteroloph and posterolophid are fully separate until advanced wear. Furthermore, the posterior lophs unite and converge on the hypocone and the anterior lophids unite and converge on the protoconid. These features are used by Patterson and Wood (1982) in their emended diagnosis of the Oligocene genus *Incamys* Hoffstetter and Lavocat, 1970, from Salla, Bolivia, but these features are still evident in this much later genus. The distinctness of these features is remarkable in that the dental similarities are perhaps closer between *Incamys* and this unknown genus than between other known fossil dasyproctids which are closer to *Incamys* in age. Furthermore, the similarities are apparent despite the much larger size and hypsodonty of the teeth from the identified genus. The two genera differ in their dental patterns in the placement of the metaloph, which in the Río Acre genus unites with the protoloph rather than with the posteroloph. This feature correlates with the much greater size of the metaflexus on the Río Acre specimens. Secondly, in the upper teeth, *Incamys* does not have a neoloph but the Río Acre form does have a small loph in this position. The presence of this new loph in a later form but not in one of the earliest occurring caviomorph genera argues for the primitive presence of only four lophs in Caviomorpha (as in *Incamys*) and the later modification of the dental pattern by the addition of a neoloph as an extension of the posteroloph (the interpretation of Wood in several papers; see Wood, 1974; and Patterson and Wood, 1982:493–503, for reviews of this argument).

The alternative interpretation, as expressed by Lavocat (1974, 1976), is that the primitive caviomorph dental pattern is five-crested and that the metaloph is a small projection from the posteroloph. The mesoloph of Lavocat (the metaloph of Wood) occupies a central position in the primitive caviomorph tooth between his protoloph and metaloph. From this viewpoint, the dental evolution of the Río Acre dasyproctid would not have been from a four-crested *Incamys*-type tooth but would have been from a five-crested pattern in which the metaloph (of Lavocat, the neoloph of Wood) was reduced. A simpler, four-loph pattern was thus achieved with a remnant of the metaloph yet remaining (or perhaps

forming again) in this late occurring genus. This four-crested pattern is thought to be the advanced caviomorph type according to Lavocat.

The nearest contemporary dasyproctid is *Neoreomys* Ameghino, 1887, of Santacrucian and Friesian ages (Savage and Russell, 1983). The teeth of *Neoreomys* are similar to the Río Acre specimens in hypsodonty and size and to both these and *Incamys* in dental pattern. However, the teeth of *Neoreomys* differ markedly in the rapid union of the anteroloph and posterolophid with the rest of the enamel pattern and in the early formation of fossettes and fossettids unlike the Río Acre specimens in which these features are only seen in late wear stages.

Family Caviidae Waterhouse, 1839

Subfamily Cardiomyinae Kraglievich, 1930a

Genus and Species Indeterminate, A

Figure 13

MATERIAL. LACM 117508, M¹ or M².

LOCALITY. LACM 4611.

DESCRIPTION. This single tooth is composed of two cordiform (heart-shaped) prisms of equal size and separated by a deep internal flexure. Only a faint external flexure, situated slightly posterior to the termination of the internal flexure, is present. The enamel is discontinuous on the labial side of each prism. The tooth is hypsodont and probably unrooted, although the base is broken in the specimen and this cannot be clearly determined. In anterior view, the tooth is strongly convex lingually. Measurement: crown (length × width), 3.3 × 3.0.

DISCUSSION. The simple biprismatic cordiform pattern with interrupted enamel identifies this tooth as a specimen of the Cardiomyinae, the most primitive of the Caviidae (Pascual et al., 1966). This tooth is smaller than all known Cardiomyinae and about 25 percent smaller than *Procardiomys* Pascual, 1961.

Subfamily Cardiomyinae Kraglievich, 1930a

Genus and Species Indeterminate, B

Figure 13

MATERIAL. LACM 117578, lower tooth.

LOCALITY. LACM 4611.

DESCRIPTION AND DISCUSSION. A second, unidentifiable caviid rodent is represented in this local fauna by a single, damaged lower tooth. A portion of one prism and one enamel wall of another together with the cement between is preserved. The tooth is hypsodont with narrow, cordiform prisms that are widely separated by a deep hypoflexid. The hypoflexid maintains a constant width over the length that is preserved. This genus is not the same as that previously described (Cardiomyinae, A) because this tooth is taller and the prisms and hypoflexid wider. Nonetheless, this is a related

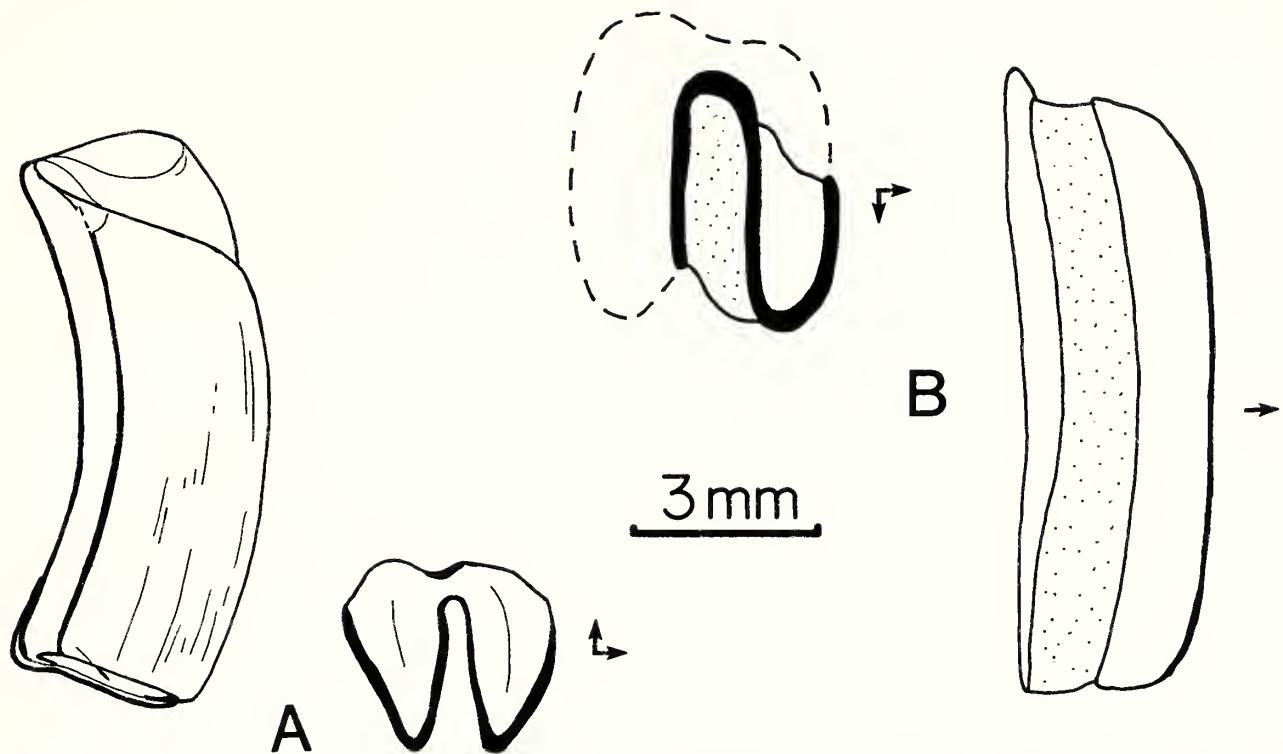


Figure 13. Cardiomysinae. A, Genus A, LACM 117508, right M^1 or M^2 , anterior and occlusal views. B, Genus B, LACM 117578, lower tooth, anterior and occlusal views.

taxon and indicates a diverse cardiomysine fauna was present at this time.

Family Hydrochoeridae Gill, 1872

Subfamily Cardiatheriinae Kraglievich, 1930b

Kiyutherium Francis and Mones, 1965

Kiyutherium orientalis

Francis and Mones, 1965

Figures 15, 16

MATERIAL. LACM 117509, M_1 or M_2 ; 117510, M_3 ; 117511, ? P^4 ; 117512, 117513, 117514, 117578, M^1 or M^2 ; 117515, 117516, 117517, M^3 ; 117579, tooth fragment.

LOCALITIES. All from LACM 4611 except LACM 117578 and 117579 which are from LACM 5158.

DESCRIPTION. Lower teeth. A single broken and worn specimen (LACM 117509) is either M_1 or M_2 . For this discussion of characters, an exact identification is not necessary as characters are essentially the same in these two teeth in capybaras. Prisms I, IIa, and IIb are approximately of equal width and h.p.i. and h.f.e. (see Fig. 14 for terminology) are approximately of equal depth. The h.s.i. is shallow, less than 1 mm, but present for the length of the tooth that is preserved. The h.t.i. is deep, reaching two-thirds the length of Pr. IIa, and cuts off a small Pr. IIc which is triangular in occlusal

outline. The h.p.i. is very deep and reaches the most external part of the tooth where it is bordered by a thin enamel loop. The h.f.e. is equally as deep as the h.p.i. The h.s.e. is a shallow, broad, U-shaped flexid about 1 mm in depth. Measurements are 8.5×5.5 (length \times width).

One M_3 is preserved in the Rio Acre sample. The M_3 is highly diagnostic in *Kiyutherium* and in capybaras in general. The relative proportions of prisms and flexids as described previously for M_1 or M_2 are also seen in M_3 . The h.s.i. and h.s.e. are reduced to slight incisions with the h.s.e. slightly deeper and broader. The h.t.i. extends approximately two-thirds the length of Pr. IIa and the h.p.i. nearly bisects the occlusal surface leaving only a narrow enamel loop on its labial border. The h.f.e. is as deep as the h.p.i. and sharply bent in occlusal view. The outer surface of the enamel of this tooth is rugose with small bumps arranged in rows that parallel the occlusal surface. Measurements are 11.3×7.8 (length \times width).

Upper teeth. The upper teeth, P^4-M^2 and the anterior prism of M^3 , are very similar in their structure and will be discussed as a unit. Each tooth has a deep h.p.e., approximately 2 mm, that divides the anterior prism into two unequal parts and a shallow (1 mm deep) h.s.e. Another very shallow flexus (unnamed) is evident in one specimen (LACM 117514) on the external portion of Pr. I posterior to the h.p.e. This flexus is visible as a shallow groove for the height of the preserved portion of this tooth. The h.f.i. is deep and reaches the external margin of the tooth where the h.f.i. is bordered by a

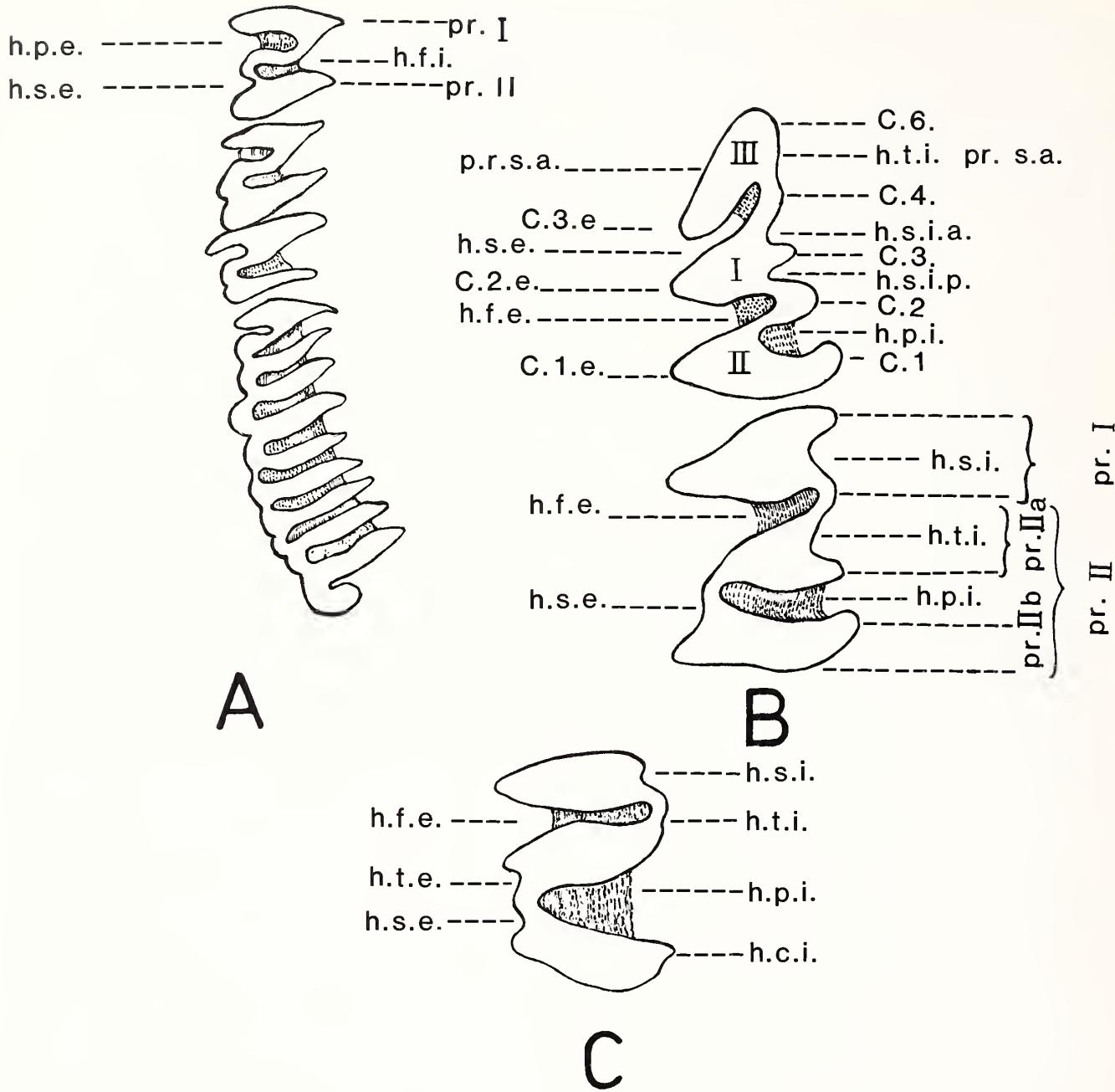


Figure 14. Dental nomenclature of Hydrochoeridae. A, P^4-M^3 , right; B, P_4-M_1 , left; C, M_3 , left. In order to conform to previous publications on the Hydrochoeridae, terminology and abbreviations are given in Spanish and follow Pascual and Bondesio (1961) who modified the terminology of Kraglievich (1940a) and Rusconi (1939).

Lower teeth—h.f.e., hendedura fundamental externa (primary external flexid); h.s.e., hendedura secundaria externa (secondary external flexid); h.t.e., hendedura terciaria externa (tertiary external flexid). h.p.i., hendedura primaria interna (primary internal flexid); h.s.i. hendedura secundaria interna (secondary internal flexid); h.t.i. hendedura terciaria interna (tertiary internal flexid); h.c.i. hendedura cuarta interna (fourth internal flexid). h.s.i.a., hendedura secundaria interna anterior (secondary, anterior internal flexid); h.s.i.p., hendedura secundaria interna posterior (secondary, posterior internal flexid). h.t.i.pr.s.a., hendedura terciaria interna de la prisma secundaria anterior (this was called the h.t.i. by previous authors but it is not homologous to the h.t.i. of M_{1-3}). In occlusal view, lower teeth are composed of two moieties called prisms. The prisms are indicated by Roman numerals. On P_4 , Prism I separates around a deep h.s.e. in all Hydrochoeridae and creates a third prism, Pr. III or prisma secundaria anterior (pr.s.a.). C indicates a column, a term that is falling out of usage because of its near synonymy with prism but which I have retained in order to designate the characteristic C.3 in P_4 . Prism II is divided by h.f.i. into an anterior part, Prism IIa, and a posterior portion, Prism IIb. A deep h.t.i. creates another prism, Pr. IIc (my usage) from the anterior portion of Pr. IIa in M_{1-3} in some genera (ex. *Kiyutherium*, *Cardiatherium*, and modified in later genera).

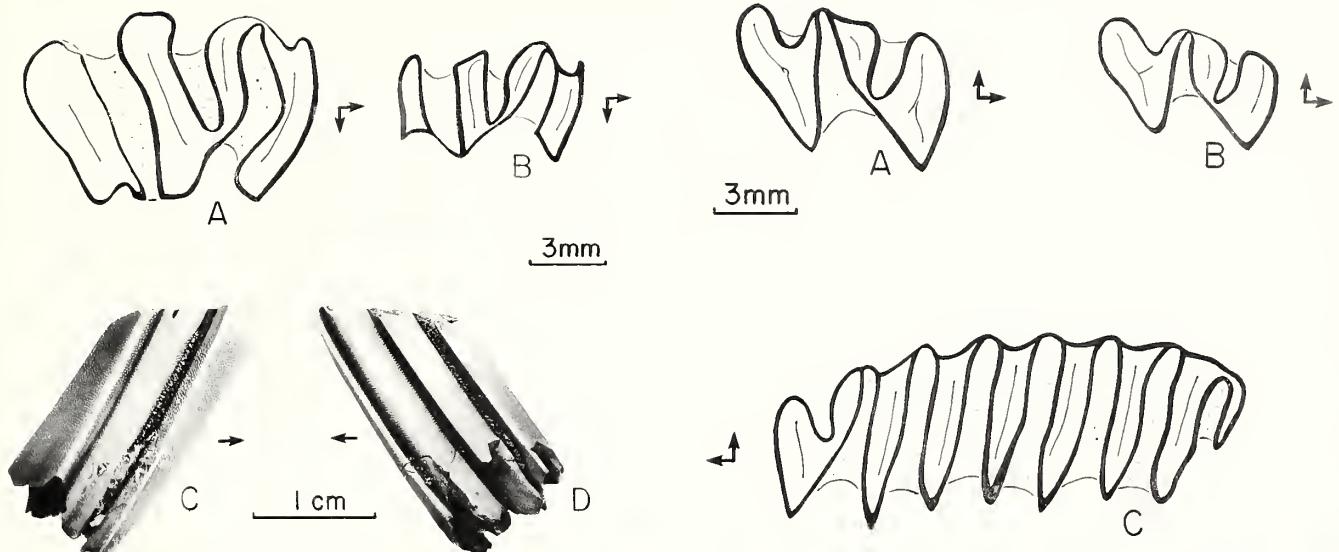


Figure 15. *Kiyutherium orientalis*. A, LACM 117510, right M_3 , occlusal drawing; B, LACM 117509, right M_1 or M_2 , occlusal drawing; C-D, LACM 117510, right M_3 ; C, labial view; D, lingual view.

thin loop of enamel. The teeth are hypodont, with a strong, labially concave curvature. The posterior prism is more slender than the anterior. All the upper teeth are irregularly pitted on the labial enamel. The prisms of one specimen (LACM 117511) are less wide than those of the other teeth and this tooth may be a P^4 rather than an M^1 or M^2 . Measurements (length \times width) are: LACM 117511, 7.1×5.0 ; 117512, 7.0×5.8 ; 117513, 8.1×7.0 ; 117514, 8.0×5.4 .

Three M^3 's are preserved in this sample although one is water-tumbled and badly worn (LACM 117517) and another is broken and preserves only the last six prisms (LACM 117516). The complete M^3 's (LACM 117515, 117517) have eight prisms (Pr. I and seven laminae, the last two joined labially). Prism I has the appearance of those of P^4 - M^2 . Prisms II-VII are narrow bands that are connected labially by a thin border of enamel. The labial end of Prisms I-VII is marked by a flexus that is large in Prism I (the h.p.e.) but very shallow (less than 1 mm) in Prisms II-VII. The prisms gradually increase in width to Prism VI and then decrease rapidly. Prism VIII varies in width. In LACM 117515, it is about one-half the width of Prism VII and about four-fifths the width of Prism VII in LACM 117516 and 117517. Measurements (length \times width) are: LACM 117515, 17.5×7.6 ; 117516, $- \times 8.6$; 117517, $17.8 \times (7.3)$.

DISCUSSION. These specimens are referable to *Kiyutherium* on the basis of laminate lower teeth each with a minute h.s.i., moderately deep h.t.i., and deep h.f.e. The lower teeth are very similar to those of the holotype of *K.*

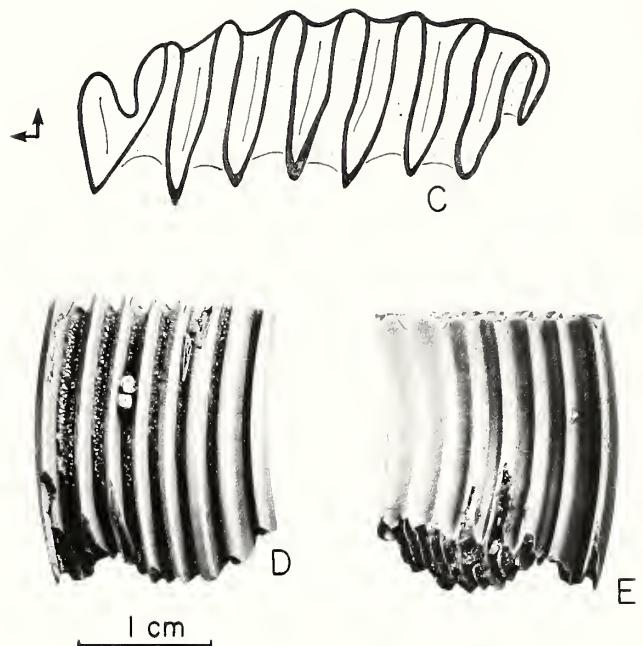


Figure 16. *Kiyutherium orientalis*. A, LACM 117514, right M^1 or M^2 , occlusal drawing; B, LACM 117511, right $?P^4$, occlusal drawing; C-E, LACM 117515, left M^3 ; C, occlusal drawing; D, lingual view; E, labial view.

orientalis (within limits of variation established by Mones, 1975) and reference to this species seems reasonable. However, in the relative sizes and orientations of some dental features, the Río Acre specimens agree more with a specimen of *Kiyutherium* from Argentina, a partial cranium and articulated upper and lower dentitions (Pascual and Bondesio, 1968, 1982). Uncertain of the variation in this species, Pascual and Bondesio (1982) cautiously identified the specimen as *Kiyutherium aff. orientalis*.

No P_4 is available for comparison but M_{1-3} of *Kiyutherium* in the Río Acre Local Fauna share several features with *Kiyutherium aff. orientalis* that differ from the holotype. In M_1 or M_2 , for example, the h.s.e. is similarly open, and the depth

←

Upper teeth—h.p.e., hendedura primaria externa (primary external flexure); h.s.e., hendedura secundaria externa (secondary external flexure). h.f.i., hendedura fundamental interna (primary internal flexure). Upper teeth are divided by h.f.i. into anterior and posterior prisms, Pr. I and Pr. II. Additional prisms added to M^3 are numbered consecutively beyond II.

Table 3. Comparative dental features within the Hydrochoeridae.

| Upper teeth | <i>Paleocavia</i> (Caviidae) | <i>Xenocardia</i> | <i>Anchimysops</i> | <i>Kiyutherium</i> | <i>Carditherium</i> | <i>Hydrochoeropsis</i> | <i>Protohydrochoerus</i> | <i>Neohoerus</i> | <i>Hydrochoerus</i> | |
|------------------------------|---|---|--|---|--|--|--|------------------------|-------------------------|--------|
| P ⁴ | h.p.e. h.s.e. h.f.i. | m. ¹ deep deep | slight deep | m. deep deep | ? | deep m. deep deep | deep deep open | deep deep open | deep deep open | |
| M ¹ | h.p.e. h.s.e. h.f.i. | m. deep deep | m. deep deep | m. deep shallow | deep | deep shallow deep | deep deep open | deep deep open | deep deep open | |
| M ² | h.p.i. h.s.i. h.f.i. | m. deep deep | m. deep deep | deep shallow | deep | deep shallow deep | deep deep open | deep deep open | deep deep open | |
| M ³ | h.p.e. h.s.e. h.f.i. | m. deep m. deep deep | m. deep shallow | m. deep shallow | m. deep shallow | deep shallow | deep shallow to m. deep open ⁴ | deep absent open | deep deep open | |
| Number of prisms | | 2 | 6 | 6 | 8 | 10 | 13 | 17 | 16 | 13 |
| Shape, excluding Pr. I | cordiform | cordiform, slender | lanceolate | lanceolate | lanceolate | lamine | lamine | lamine | lamine | lamine |
| Lower teeth | <i>Paleocavia</i> (Caviidae) | | <i>Phugatherium</i> | | <i>Kiyutherium</i> | | <i>Anchimys</i> | | <i>Procardiatherium</i> | |
| P ₄ | h.f.e. h.s.e. h.p.i. h.s.i.p. h.s.i.a. h.t.i. C.3 | present present, pos- terior to h.f.e. | deep deep deep single, shallow single, shallow | deep deep deep present, smaller than h.s.i.a. | deep deep deep single, shallow | deep deep deep deepens (as deep as h.s.i.a.) | deep | deep | deep | |
| M ₁ | h.f.e. h.s.e. h.p.i. h.s.i. h.t.i. | deep deep present shallow | deep deep deep shallow | deep m. ¹ deep deep shallow deep | deep slight deep shallow shallow | deep faint absent | deep | m. deep | deep | |
| M ₂ | h.f.e. h.s.e. h.p.i. h.s.i. h.t.i. | deep deep present, post- erior to h.f.e. | deep deep deep small | deep small deep m. deep | deep slight deep deeper than <i>Phugatherium</i> | deep | deep | small | deep | |
| M ₃ | h.f.e. h.s.e. h.t.e. h.p.i. h.s.i. h.t.i. Pr. IIa | deep small small present small | deep small small deep, narrow small | deep small deep v. ² small deeper oblique | deep m. deep footnote ⁵ deep small deep oblique | deep small deep deep deep oblique | deep | deep | deep | |
| Number of prisms | | 2 | 3, Pr. I thin | 3, Pr. I cordiform | 3, Pr. II, oblique | 3, Pr. II, oblique | | | 3 | |

Table 3. Continued.

| Lower teeth | <i>Cardiatherium</i> | <i>Protohydrochoerus</i> | <i>Chapalmatherium</i> | <i>Hydrochoeropsis</i> | <i>Neochoerus</i> | <i>Hydrochoerus</i> |
|------------------|---|--|---|--|--|---|
| P ₄ | h.f.e. h.s.e. | deep deep, anterolingual | v. deep deep | deep deep | deep deep | deep deep, anterolingual |
| | h.p.i. h.s.i.p. | deep deep, as in <i>Procardiatherium</i> | deep v. deep | deep m. deep | deep deep | deep deep |
| | h.s.i.a. h.t.i. C.3 | present faint present | reduced deep present | deep deep present | m. deep deep ill-defined | m. deep deep present |
| M ₁ | h.f.e. h.s.e. h.p.i. h.s.i. h.t.i. | deep m. deep v. deep deep deep | open m. deep open deep deep | open m. deep open deep deep | open m. deep v. deep deep open | open m. deep open deep open |
| M ₂ | h.f.e. h.s.e. h.p.i. h.s.i. h.t.i. | deep m. deep v. deep deeper than <i>Procardiatherium</i> | open m. deep open deep m. deep | open m. deep open m. deep | open m. deep open m. deep | open m. deep open m. deep |
| M ₃ | h.f.e. h.s.e. h.t.e. h.p.i. h.s.i. h.t.i. Pr. IIa | deep small small v. deep m. deep v. deep oblique | open absent open open v. deep open transverse | open absent open open deep open transverse | open v. deep open open v. deep open transverse | open open open open v. deep open transverse |
| Number of prisms | | 3 | 3 | 3 | 3 | 3 |

¹ m. = moderately.² v. = very.³ Last two h.f.i. in series closed.⁴ All h.f.i. open except last one in series.⁵ Present in "Eucardiodon."

of the h.f.e. extensively overlaps the depth of the h.s.i. (particularly in M₁). Also in the M₂, Pr. IIb is more laminate in the referred specimens and the anterior lobe is less conspicuous than in the holotype. In M₃, both share a narrower h.f.e. (as a result of the deep h.t.i.). These are probably all advanced features with the exception of the open h.s.e.

The holotype of *Kiyutherium orientalis* and the Río Acre specimens, however, share certain features that differ from those of *Kiyutherium aff. orientalis*. For example, the wider laminae and the lesser obliquity of the h.p.i. on M₃ (both primitive) contrast with the Argentinian specimen. Other characters that appear to be advanced are found only on the Río Acre specimens: the h.p.i. of M₁₋₂ is wider and the h.t.i. is deeper (i.e., Pr. II is more deeply divided); and the h.s.e. of M₃ is narrower.

In the upper teeth of the Río Acre specimens, and in par-

ticular M³, the prisms are noticeably more inflated and more transversely situated (both plesiomorphic characters) than corresponding features in *Kiyutherium aff. orientalis*. No upper dentition is present with the holotype.

Of the three specimens, those from the Río Acre Local Fauna are the smallest but the range does not seem significant (length of M₃ is 11.3 for *Kiyutherium* from the Río Acre; 12.0 for *Kiyutherium aff. orientalis*; and 13.75 for the holotype).

The expanded hypodigm of *Kiyutherium* demonstrates some variation in dental features. At present, the variation appears to be within the limits of a species and there is no consistency in character polarity that would suggest other than one species. The known specimens of *Kiyutherium* that can be identified to the species level are therefore assigned to *K. orientalis*.

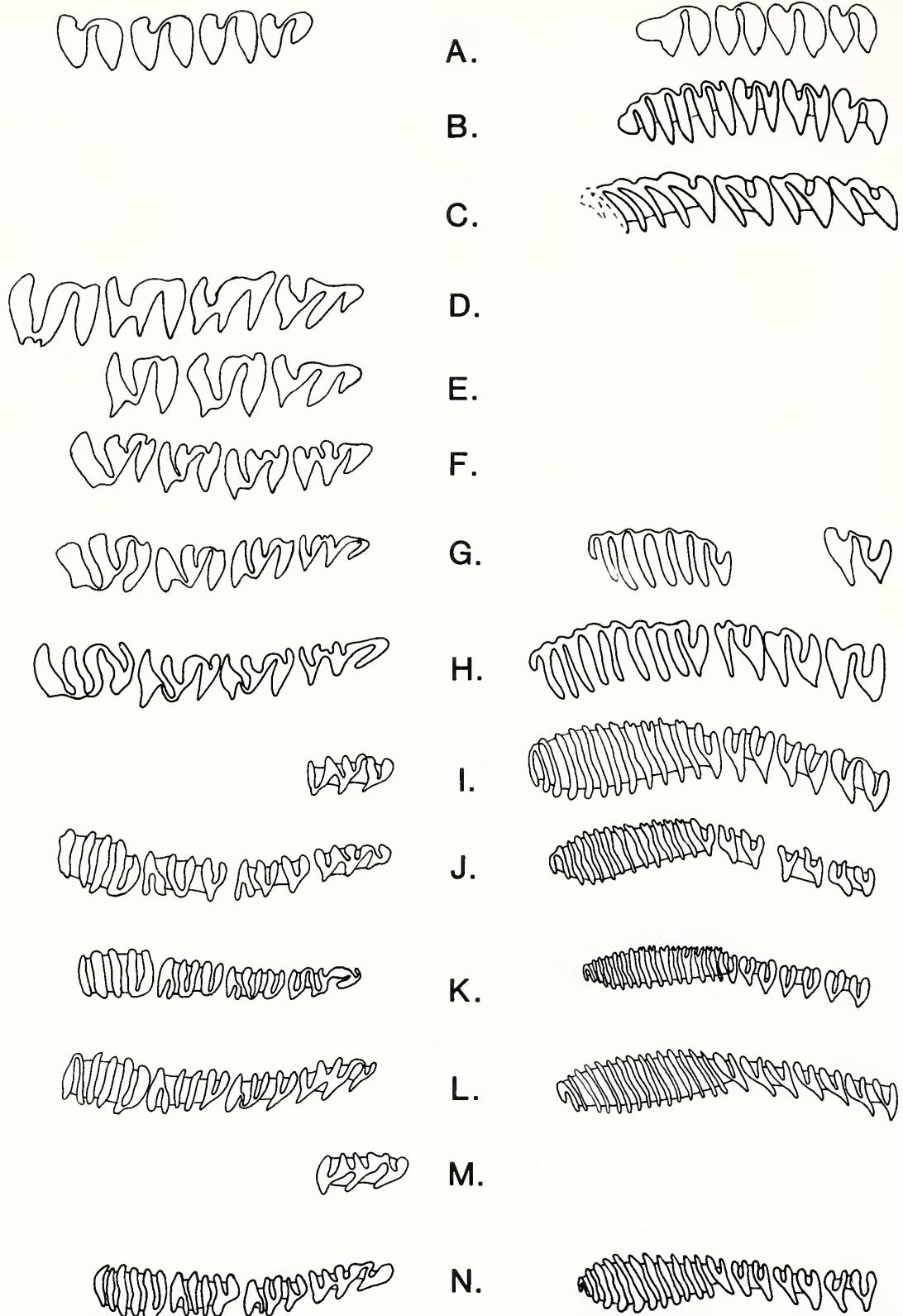


Figure 17. Occlusal patterns of genera of Hydrochoeridae discussed in cladograms (Figs. 18, 19). Left, lower right dentition; right, upper right dentition. Dentitions are not to scale. **A**, *Paleocavia* (Caviidae); **B**, *Xenocardia*; **C**, *Anchimysops*; **D**, *Phugatherium*; **E**, *Anchimys*; **F**, *Procardiatherium*; **G**, *Kiyutherium*; **H**, *Cardiatherium*; **I**, *Hydrochoeropsis*; **J**, *Chapalmatherium*; **K**, *Protohydrochoerus*; **L**, *Neochoerus*; **M**, *Nothydrochoerus*; **N**, *Hydrochoerus*. (Sources: Pascual and Bondesio, 1961, 1963, 1968; Pascual et al., 1966.)

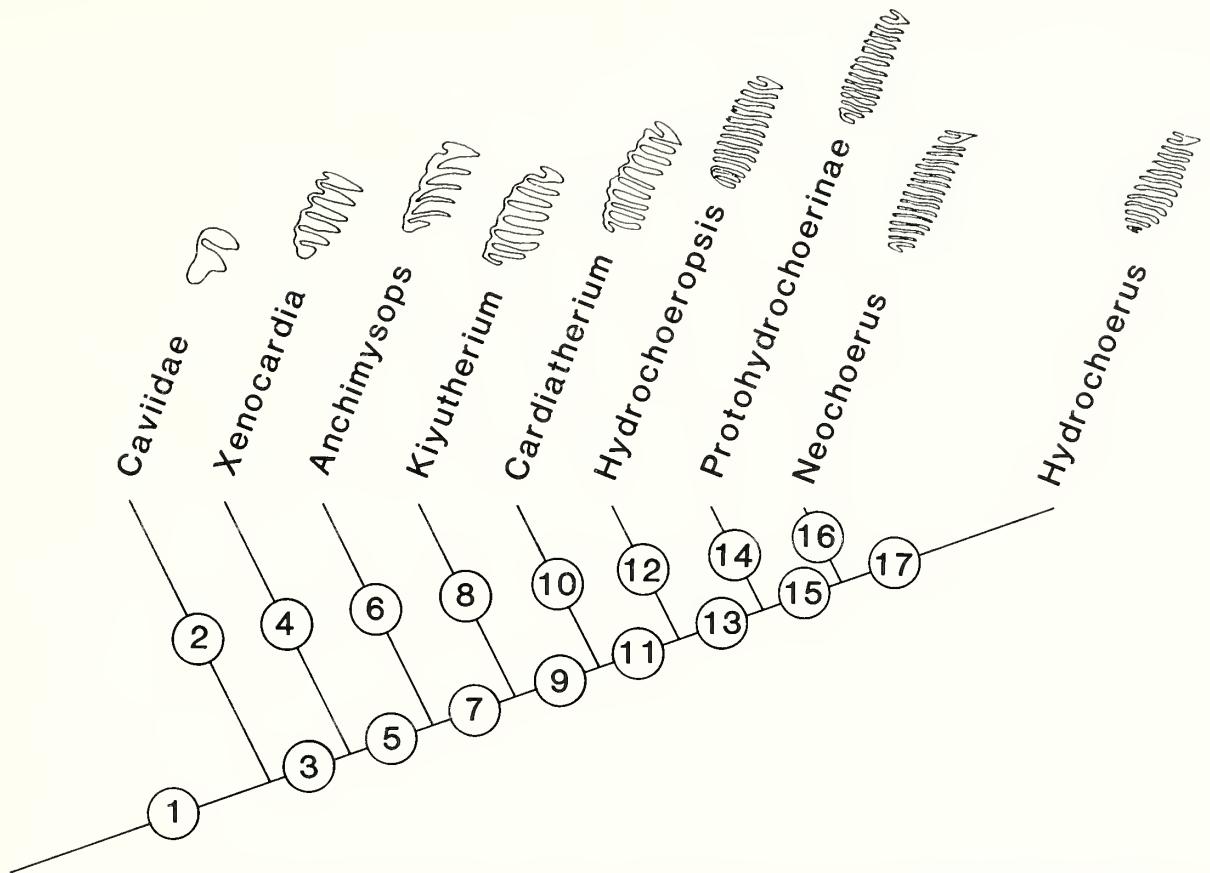


Figure 18. Cladistic relationships among genera within the Hydrochoeridae using features of the upper dentition. A sketch of M^3 is included for each genus. Some genera are known only by the upper dentition.

Kiyutherium was described by Francis and Mones (1965) from a single ramus from the Kiyú Formation of Uruguay. This formation was dated faunally by Francis and Mones as “Mesopotamian.” In the view of Pascual and Bondesio (1968) the “Mesopotamian” is not a unified faunule but rather is comprised of several faunules, and correlative in part to the Huayquerian (Late Miocene) and in part to the Montehermosan (Pliocene). The Argentinian record of *Kiyutherium* is from Huayquerian sediments (Pascual and Bondesio, 1968, 1982). A third specimen, a partial M^3 with the number of laminae hypothesized for *Kiyutherium* (Mones, 1975) and equal to that seen in M^3 's from Río Acre, is briefly mentioned by Mones (1976) from Huayquerian sediments in Venezuela. *Kiyutherium* is then seen to have a wide geographic range, the broadest known of any of the Cardiatheriinae, that included Huayquerian and probable Huayquerian sediments in La Pampa Province, Argentina (Pascual and Bondesio, 1968); San José Department, Uruguay (Francis and Mones, 1965); Estado Falcón, Venezuela (Mones, 1976, a questioned referral of a single specimen); and now the western margin of the Amazon Basin.

These new sediments from the Río Acre permit further discussion of the position of *Kiyutherium* within the Cardiatheriinae. *Kiyutherium* is acknowledged to be a highly derived member of the most primitive subfamily of the Hy-

drochoeridae, although probably not in the direct line which led to the more advanced Subfamilies Protohydrochoerinae and Hydrochoerinae (Francis and Mones, 1965; Pascual and Bondesio, 1968). Genera of the Cardiatheriinae are broadly contemporaneous in the Late Miocene and Early Pliocene with the morphologically more advanced genera (*Procardiatherium* Ameghino, 1885, *Kiyutherium* and *Cardiatherium* Ameghino, 1883) being the earlier known and longer ranging (Mones, 1976). Authors have therefore tended to avoid conventional phylogenetic trees and instead speak of more primitive and more derived genera (Francis and Mones, 1965; Pascual and Bondesio, 1968; Mones, 1976). The position of *Kiyutherium* when viewed cladistically as a progression of characters within the Hydrochoeridae (Figs. 17, 18, and 19 and Tables 3, 4, and 5) is therefore roughly equivalent to previous authors' usages although presentation in this manner clarifies the relative positions of genera without introducing implications of ancestry.

The evolutionary development of dental characters (all that is known of Cardiatheriinae with the exception of the undescribed partial skull of *Kiyutherium*) can be seen as an addition of flexures and flexids that indented the cordiform prisms inherited from a caviid ancestor, and the anteroposterior compression of the prisms that created first lanceolate and then laminate teeth. The number of laminae of M^3 steadily

Table 4. Characteristics of the upper dentition used in constructing the cladogram of Hydrochoeridae (Fig. 18).

1. Teeth with 2 prisms, no h.p.e., h.s.e. present, situated posteriorly to h.f.i., h.f.i. deep, M³ with 2–5 prisms.
2. Caviidae. No h.p.e., M³ with fewer than 6 prisms, prisms cordiform.
3. h.p.e. present (strongest on M^{1–3}); M³ has 6 or more prisms; prisms of all teeth become more slender (lancolate rather than cordiform).
4. *Xenocardia*. M³ with 6 prisms. h.p.e. equals h.s.e. in depth on M^{1–2}.
5. Prisms become more slender. h.p.e. separates Pr. I into anterior part (Pr. Ia) and small, triangular in cross section, Pr. Ib.
6. *Anchimysops*. h.f.i. directed posterolabially, deep h.p.e. and shallow h.s.e.
7. Number of prisms in M³ increases to 8. h.p.e. and h.s.e. deepen.
8. *Kiyutherium*. Fewer than 10 prisms in M³. All flexures shallower than in sister-group.
9. M³ prisms number 10 or more. h.t.i. present on M^{1–2}, prisms narrower.
10. *Cardiatherium*. h.t.i. well developed. Largest of the Cardiatheriinae.
11. Enamel no longer continuous on labial side of M³, more than 12 prisms on M³, anterior and posterior prisms separated on M^{1–2}, h.p.i. and h.s.e. equally deep.
12. *Hydrochoeropsis*. h.f.e. not perforate on P⁴, 3 posterior laminae (at least) of M³ connected.
13. h.f.e. perforate on P⁴, never more than 2 laminae of M³ connected.
14. *Chapalmatherium* (Protohydrochoerinae). Prisms of P⁴–M² widely separated, thick, and directed lingually rather than anterolingually. h.p.e. and h.s.i. more medially placed in prism.
15. No labial grooves on M³ (Hydrochoerinae).¹
16. *Neochoerus*. Prisms very thin. M³ with 14–17 prisms. Large size (twice that of *Hydrochoerus*).
17. *Hydrochoerus*. M³ with 12–13 prisms. M₂ composed of three prisms.

¹ Ahern and Lance (1980) describe a new species of *Neochoerus* that has labial grooves. I suspect this is the first North American record of *Hydrochoeropsis*.

ily increases at the generic level although it varies within limits in individuals (Mones, 1975).

In reference to Figures 18 and 19, *Neoanchimys* Pascual and Bondesio, 1961, is synonymized under *Phugatherium* Ameghino, 1887, following Mones (1972), and *Eucardiodon* Ameghino, 1891, is synonymized with *Anchimys* Ameghino, 1886, following Mones (1975). *Nothydrochoerus* Rusconi, 1935, is poorly known. The revised diagnosis of this genus (Pascual et al., 1966) relies on features which are highly variable (Mones, 1975). *Nothydrochoerus* could be referred to

Table 5. Characteristics of the lower dentition used in constructing the cladogram of Hydrochoeridae (Fig. 19).

1. h.p.i. present and posterior to h.f.e., no h.s.i., P₄ with two prisms (i.e., no h.s.e.), M₃ undifferentiated.
2. Caviidae. Prisms cordiform, h.s.i. absent, h.p.i. shallow, no Pr. III on P₄, h.s.e. absent.
3. Prisms narrow, small h.s.i., h.p.i. deep, Pr. III present on P₄ (deep h.s.e.), slight h.s.e. present.
4. *Phugatherium*. h.s.e. very deep on M_{1–2}, h.p.i. deep, narrow, Pr. I thin.
5. Pr. II sits oblique to ramus (rather than transverse), h.s.i. deepens on M_{1–3}, h.t.i. present on M_{1–3}.
6. *Anchimys*. h.t.e. present.
7. h.t.i. deepens on M_{1–3}, h.s.i.a. and h.s.i.p. present on P₄, new structure, C.3, develops on P₄, h.s.e. on M₃ reduced.
8. *Procardiatherium*. h.p.i. on P₄ reduced.
9. h.f.e and h.t.i. on M_{1–3} deepen, h.s.e. and h.f.e. deepen on P₄.
10. *Kiyutherium*. h.s.i., h.s.e. small on M_{1–3}, h.p.i. wide on M_{1–3}.
11. h.t.i. deepens on P₄, h.p.i. on M_{1–2} deepens and narrows, h.s.i. deepens on P₄–M₃, h.s.e. deepens on M_{1–2}, laminae thin.
12. *Cardiatherium*. h.t.i. and h.s.i. on M_{1–2} only half as deep as in sister-group. All prisms connected on each tooth.
13. h.t.i. deep on P₄, Pr. I and Pr. II of M_{1–3} separate (h.f.e. and h.p.i. open, only on M₂ and P₄ of *Neochoerus*), h.s.i. and h.s.e. deep.
14. *Hydrochoeropsis*.
15. h.t.i. perforate on M₃, h.s.i. on P₄–M₃ very deep, h.f.e. perforate on M_{1–3}.
16. *Chapalmatherium* (Protohydrochoerinae). h.p.i. open on M_{1–2}, h.s.e. absent, C.6 on P₄ directed posterolingually. (*Protohydrochoerus* has h.s.i.p. on P₄ deep, h.s.i.a. absent, h.s.i. and h.t.i. very deep on M_{1–2}, h.s.i. very deep on M₃, h.i.e. deep and medially directed.)
17. Deep h.s.e. on M₃, h.t.i. open on M₂.
18. *Neochoerus*.
19. *Nothydrochoerus*, *Hydrochoerus*. h.s.e. on M₃ perforate, h.p.i. open on M_{2–3}. *Nothydrochoerus* is much larger than *Hydrochoerus* but may not be a valid genus.

Neochoerus Hay, 1926 (which is the same size), *Hydrochoerus*, or simply declared a *nomen dubium*.

Family Dinomyidae Alston, 1876

Subfamily Potamarchinae Simpson, 1945

Potamarchus Burmeister, 1885

Potamarchus murinus Burmeister, 1885

Figures 20, 21

MATERIAL. LACM 117518, right P⁴; GB 677, left P⁴; GB 676, M¹ or M²; LACM 117580, M³; LACM 117519,

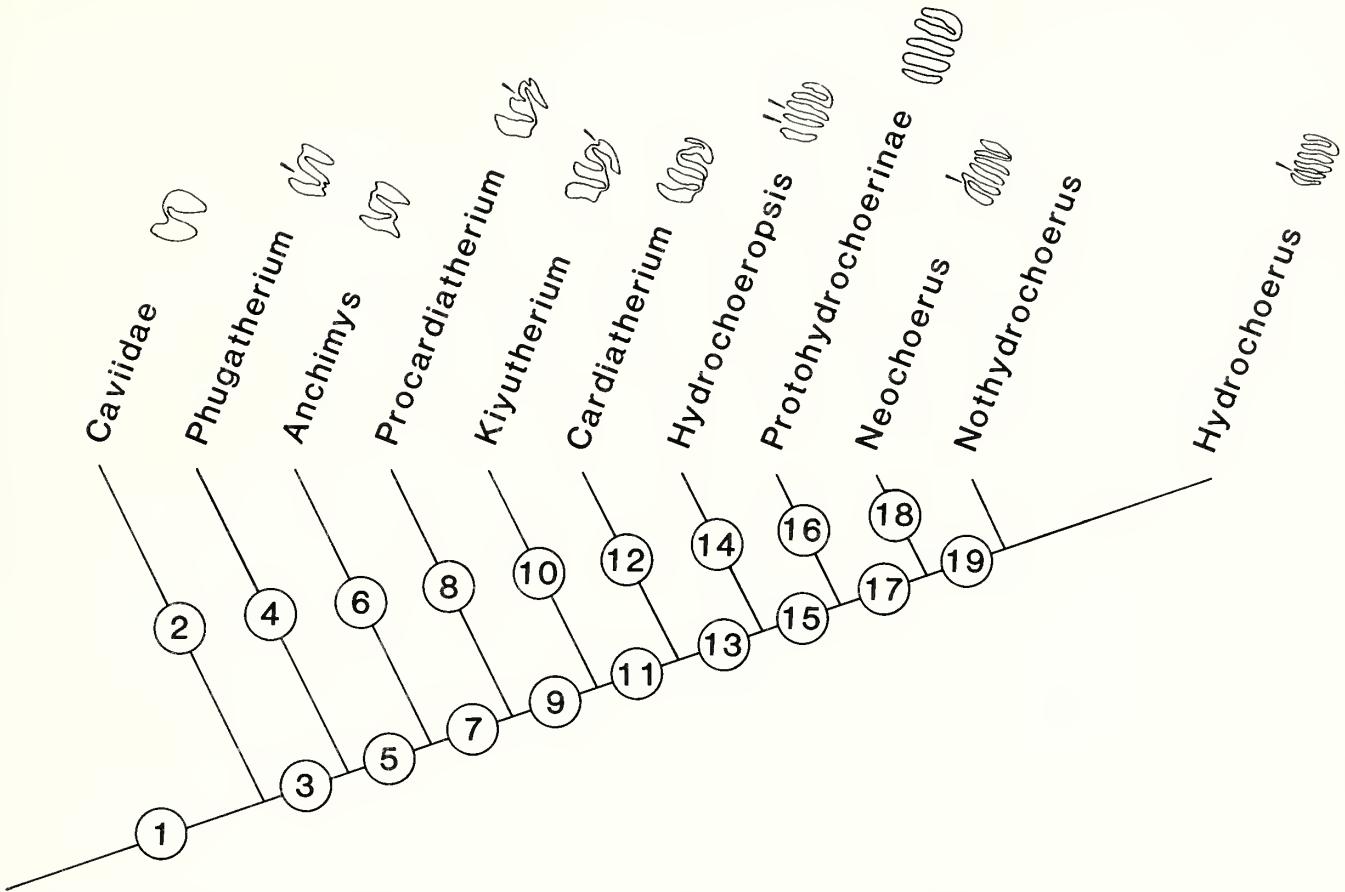


Figure 19. Cladistic relationships among genera within the Hydrochoeridae using features of the lower dentition. A sketch of M_3 , if known, is included for each genus. Arrows denote taxonomic features discussed in the text. Some genera are known only by the lower dentition.

partial ramus with M_{1-3} ; LACM 117520, M_3 ; LACM 117521, 117522, 117581, teeth fragments.

LOCALITIES. LACM 117520–2, LACM 4606; LACM 117518–9, LACM 4611; GB 676–677, Río Acre, west of Cobija, Depto. del Pando, Bolivia; LACM 117580–117581, LACM 5158.

DESCRIPTION. Lower teeth. The lower molars consist of parallel lophids that are slightly concave anteriorly and are oriented obliquely to the line of the ramus. In M_{2-3} and possibly M_1 at an earlier wear stage, the metalophid and hypolophid are not smoothly concave but rather are S-shaped. Four lophids are present in M_1 , apparently a reduction due to wear, and five each in M_2 and M_3 . The anterior border of each lophid is crenulated. Hypoflexids are persistent and obvious on each tooth (small on M_1) but internal flexids are present only on M_3 at this wear stage. The identification of these internal flexids is difficult but I suggest that the internal flexids present on M_3 are the mesoflexid and anteroflexid with a new and unnamed flexid situated anteriorly to the anteroflexid. The occlusal outline becomes increasingly elongate from M_1 to M_3 .

An isolated M_3 recovered from LACM 4606, LACM 117520, is only slightly worn and shows features of *Potamarchus* that were heretofore unknown. Five lophids are

present and all are separate. The anteriomost lophid is divided into two unequal parts that lie in the same transverse plane. Three ectoflexids and four entoflexids are present. The hypoflexid is the most persistent flexid (and the most readily identifiable) and extends to within 2 mm of the base of the crown. The anterior two ectoflexids are short (2 mm to less than 1 mm for the more anterior). All the entoflexids are short and would disappear after one-third of the crown was worn away. The posteriormost entoflexid appears to be the remnant of the metaflexid. The heights of the entoflexids, from the anterior, are 3.0, 4.6, 4.4, and 2.0. Crown height is 14.8.

Measurements of lower teeth are as follows: M_1 , 6.3×5.6 ; M_2 , 7.5×6.4 ; M_3 , 8.5×6.7 (LACM 117519). M_1 (GB 677), 6.8×5.7 ; M_3 (LACM 117520), 8.9×6.0 (measured in the middle of the tooth, a position that corresponds to the wear stage of the other specimens).

Upper teeth. The least worn P^4 , LACM 117518 (Fig. 21A, B), consists of eight oblique lophs that are gently concave towards the posterior. The anterior five lophs extend the width of the tooth; the sixth reaches only three-quarters the width, the seventh only about half the width of the crown, and the eighth is minute. The lophs are approximately the same thickness with the exception of the posterior two lophs

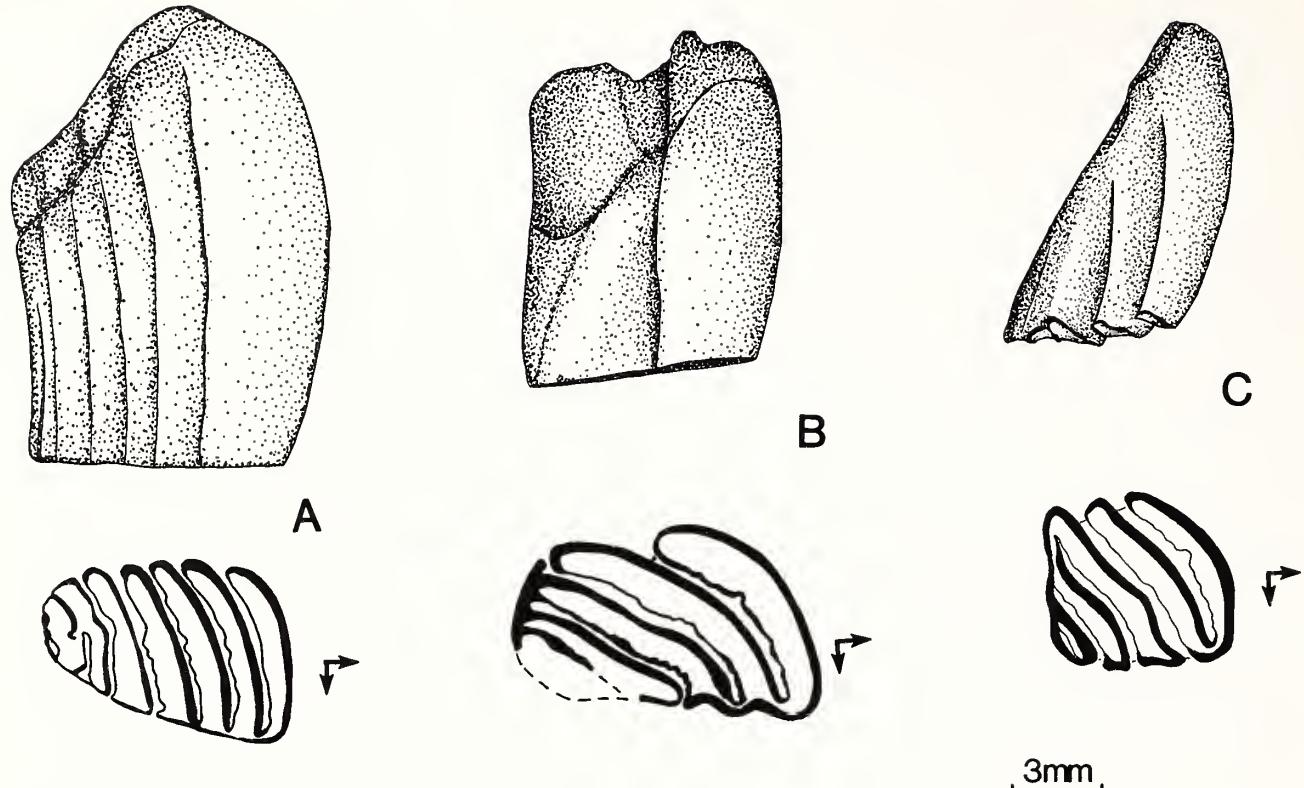


Figure 20. *Potamarchus murinus*. A, LACM 117580, left M^3 ; B, GB 676, left M^1 or M^2 ; C, GB 677, left P^4 . Lingual and occlusal views of each.

that are thin and would have been the first lophs to be worn away. The anterior enamel rim of each loph is thicker than that of the posterior. The posterior enamel rim is highly crenulated and variable in thickness. The posterior five lophs are confluent both labially and lingually. With wear the anterior lophs would progressively become united with the posterior block. The occlusal outline is rectangular. A single broad, shallow groove is present on the vertical midline of the labial surface. On the lingual surface, a fissure is present after each of the first three lophs. At this wear stage, the anteriormost fissure extends to the base of the crown; the second approximately half this length; and the third approximately one-fifth the distance. Cement is present between the lophs. Four roots have formed; the labial roots are situated more toward the crown than are the lingual roots (lateral hypsodonty). Measurements are 8.7×7.6 , length \times width.

A single isolated tooth (GB 676) is identified as a left M^2 . This tooth consists of three complete and one broken lamina with the postero-external portion of the crown missing. The anterior two laminae are convex to the anterior and the posterior two have a gentle S-curve. The posterior border of each loph is thin and crenulated. A large, antero-internal flexus is present for nearly the entire length of the crown. Two minor flexi persist, one internal and one external, but each less than 1 mm deep at this wear stage with about half the tooth gone. Measurements are 9.6×6.9 , length \times width.

The M^3 in this sample, LACM 117580, has seven lophs

although the posterior two are not fully formed in this early wear stage. The thin posterior enamel wall of each loph is crenulated but not to the extent of other teeth in the sample. Morphological variation rather than variation due to wear is indicated in that the thin posterior enamel walls of the equally little-worn P^4 (LACM 117518) are highly crenulated. The lophs are closely appressed with only a faint indication in the posterior lophs of what may with wear become S-shaped flexures. The anterior four lophs are united labially by the enamel wall. The posterior two are united by enamel on all margins of the occlusal surface. The labial flexi are short and with only an additional 1 mm of wear all the lophs would be united on their labial surface. On the lingual surface of M^3 , the flexi extend to the base of the crown. The anterior portion of the crown is much higher than the posterior and the lingual enamel surface is longer than the labial surface. Five roots are present. Two large anterior roots are connected medially and support the anterior portion of the crown. Behind this root crest are two smaller, medial roots and a large root that is situated under the posterior apex of the crown. On the lingual margin of the tooth, lophs 1 and 2 are supported by the anterior root; 3 and 4 by the medial root, and 5, 6, and 7 by the posterior root. On the labial margin, lophs 1, 2, and 3 are supported by the anterior root; 4, 5, and 6 by the medial root; and 7 is supported by the terminal root. Measurements of M^3 (length \times width) are 8.9×6.9 .

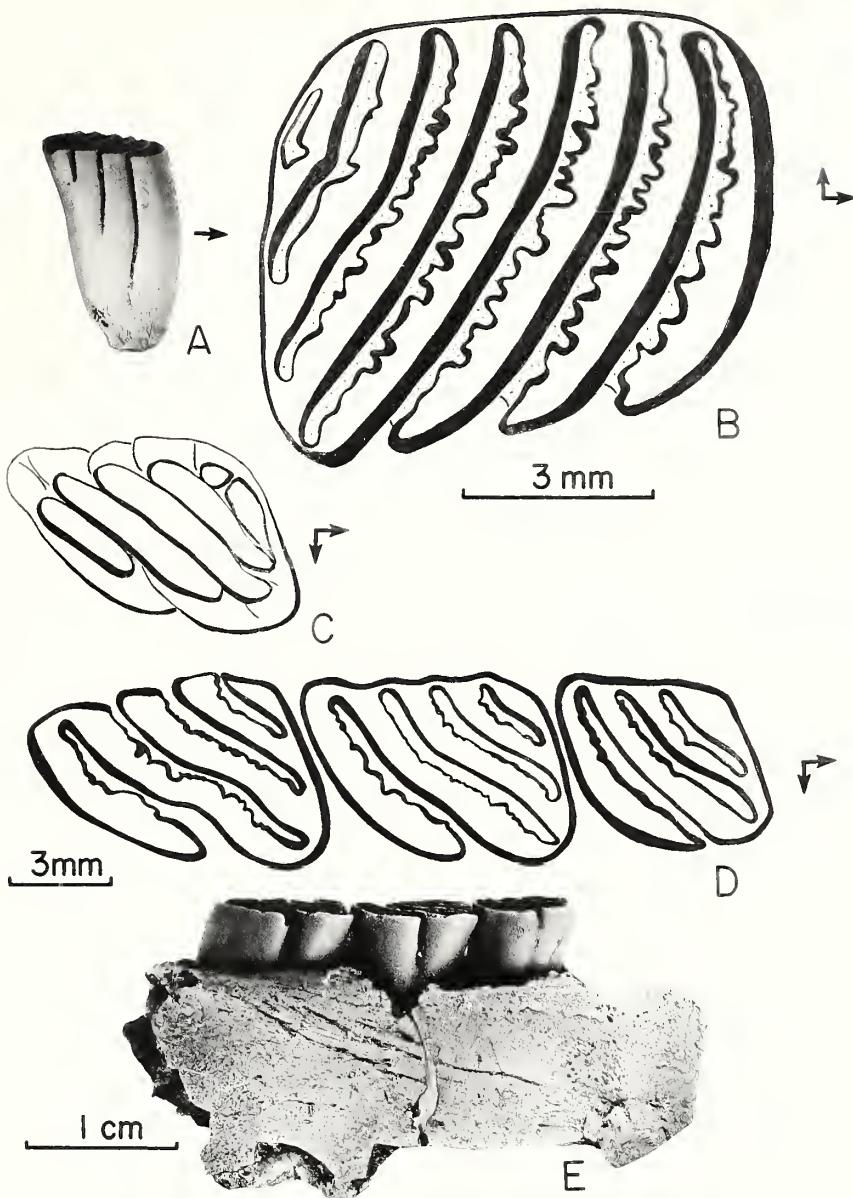


Figure 21. *Potamarchus murinus*. A-B, LACM 117518, right P⁴; A, lateral view; B, occlusal drawing; C, LACM 117520, right M₃, occlusal drawing; D-E, LACM 117519, ramus with M₁₋₃; D, occlusal drawing; E, labial view. A and E are to the same scale.

DISCUSSION. These specimens are referred to the Potamarchinae because the teeth are hypsodont and comprised of closely appressed, parallel lophs and lophids that in the lower teeth are convex posteriorly, and in which the hypoflexid and hypoflexus are the most persistent re-entrants.

In the Potamarchinae, these teeth resemble those of *Potamarchus* in having the lophids of the lower teeth fully separated laterally and medially when unworn but united laterally (except for the hypoflexid) with early wear. In the upper teeth, the degree of obliqueness of the lophs is less than in the lowers. These teeth differ from those of *Simplimus* Ameghino, 1904, the only other genus of Potamarchinae, in having lophs that are more oblique and that are closely ap-

pressed with no cement evident between them (see Kraglievich, 1930c).

The specimens from the Río Acre have numerous crenulations in the thin anterior enamel blade of each lophid that are characteristic of *Potamarchus murinus* Burmeister, 1885, and not *P. sigmodon* Ameghino, 1891. Furthermore, the lophids appear not to be as S-shaped as those of *P. sigmodon* although a definite S-shape is discernable. Considerable variation in enamel crenulation and lophid curvature was apparent in the small sample recovered from sites along the Río Acre and as a result species referral is somewhat dubious. With additional specimens, the features that are used to separate these two species may prove invalid.

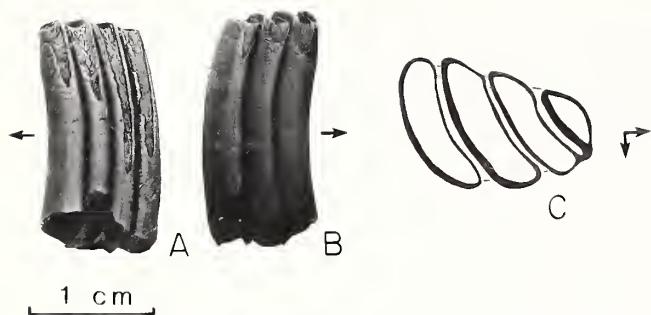


Figure 22. *Tetrastylus* sp., LACM 117535, right P₄. A, lingual view; B, labial view; C, occlusal drawing.

Potamarchus murinus is found in the Arroyo Chasicó Formation (of Chasicoan age) and possibly in the Epecuen Formation (Huayquerian age) (Pascual et al., 1966). *Potamarchus sigmodon* is probably contemporaneous but is found in the "Paraná fauna" (Ameghino, 1891). The Paraná fauna is difficult to date precisely due to an apparent mix of Miocene, Pliocene, and even some Pleistocene taxa (Pascual and Bondesio, 1961). The age indicated by the majority of the taxa is Huayquerian and possibly Montehermosan (Pascual and Odreman Rivas, 1971).

Subfamily Eumegamyinae Kraglievich, 1932

Tetrastylus Ameghino, 1886

Species Indeterminate

Figure 22

MATERIAL. LACM 117535, right P₄.

LOCALITY. LACM 4611.

DESCRIPTION. This P₄ is lophate, hypodont, and concave on the anterior face. The occlusal surface consists of four parallel lophids that increase in width toward the posterior (measurements, 2.6, 4.0, 5.0, 5.3) and also in thickness (0.5, 0.9, 1.1, 1.5). The lophids are closely appressed with a thin sheet of cement between them. The anterior two lophids are connected labially. All the other lophs are fully separate on the preserved part of the crown in this specimen. Measurements, length × width, are 9.0 × 5.5.

As defined by Pascual et al. (1966), four arcuate lophids that are united on the labial surface only and that decrease in size anteriorly are characteristic of lower teeth of the Eumegamyinae. The size of this tooth dictates its assignment to the smallest genus of the subfamily, *Tetrastylus*. *Tetrastylus* is a Chasicoan and Huayquerian genus (Pascual et al., 1966) and serves as a good time indicator for the local fauna.

Telicomys Kraglievich, 1926a

Telicomys amazonensis new species

Figures 23, 24, 25

HOLOTYPE. LACM 117523, partial skull, missing zygomatic arches, nasal and premaxillary bones, and incisors.

Table 6. Comparative measurements between *Telicomys amazonensis* and *Telicomys giganteus* (measured from Rovereto, 1914).

| | <i>T. giganteus</i> | <i>T. amazonensis</i> |
|---|-------------------------|---------------------------|
| Condyllobasal length | 297 | (263) |
| Occiput: height (condyle to inion) width, maximum | 74 124 | 62 84 |
| Maxillary tooth row: length width of palate between anterior margins of P ⁴ s | 71 | (65) 7.6 |
| width of palate between poste- rior margins of M ³ s | 45 | 47 |
| Width of braincase | 80 | (90) |
| Least interorbital width | 92 | (75) |
| Palatal length, from premaxillary- maxillary suture to anteriomost point on posterior edge of pal- ate | 105 | (96) |
| Postpalatal length | 99 | 77 |
| Tympanic bulla: length width | 34 18 | 29 18 |
| P ⁴ (length × width) | 16.8 × 12.4 | 15.3 × 10.8 |
| M ¹ (length × width) | 16.1 × 11.1 | 10.6 × 10.7 |
| M ² (length × width) | 14.8 × 11.4 | 11.2 × 10.0 |
| M ³ (length × width) | 16.5 × 11.4 | 15.5 × 9.6 |

TYPE LOCALITY. LACM 4418.

DIAGNOSIS. Smaller than *Telicomys giganteus* (Ameghino) 1904, with narrower occiput and shorter postpalatal length. P⁴ approximately equal in size to M³ and both are larger than M¹ and M² which are of equal size.

DESCRIPTION. Skull. In dorsal view, the skull is flat and wide. The temporal fossae are deep but narrow and appear in this view as right triangles that do not meet centrally, i.e., there is no sagittal crest.

In lateral view the dorsal margin of the skull is straight, the depth of the skull increases to a maximum over the tooth row. The occiput is flat and nearly vertical.

Ventrally, the tooth rows are straight and well separated. The palate is triangular and vaulted; the postpalatine notch is V-shaped and terminates posterior to M³. The basisphenoid and basioccipital are short, flat, and broad. The auditory bullae are large but do not contact the paroccipital processes.

In posterior view the occiput is low and wide. The paroccipital processes are large but short. Lateral to the occipital condyles are accessory condyles. These are flat, oval articular processes that are situated between the paroccipital processes and occipital condyles and are confluent with the latter.

Upper teeth. The upper cheek teeth each have four major lophs in which the posterior two are connected lingually and which are separated by thin sheets of cement. The M² has a small fifth loph that would be incorporated into the fourth loph with slightly more wear. The M³ has six lophs, although

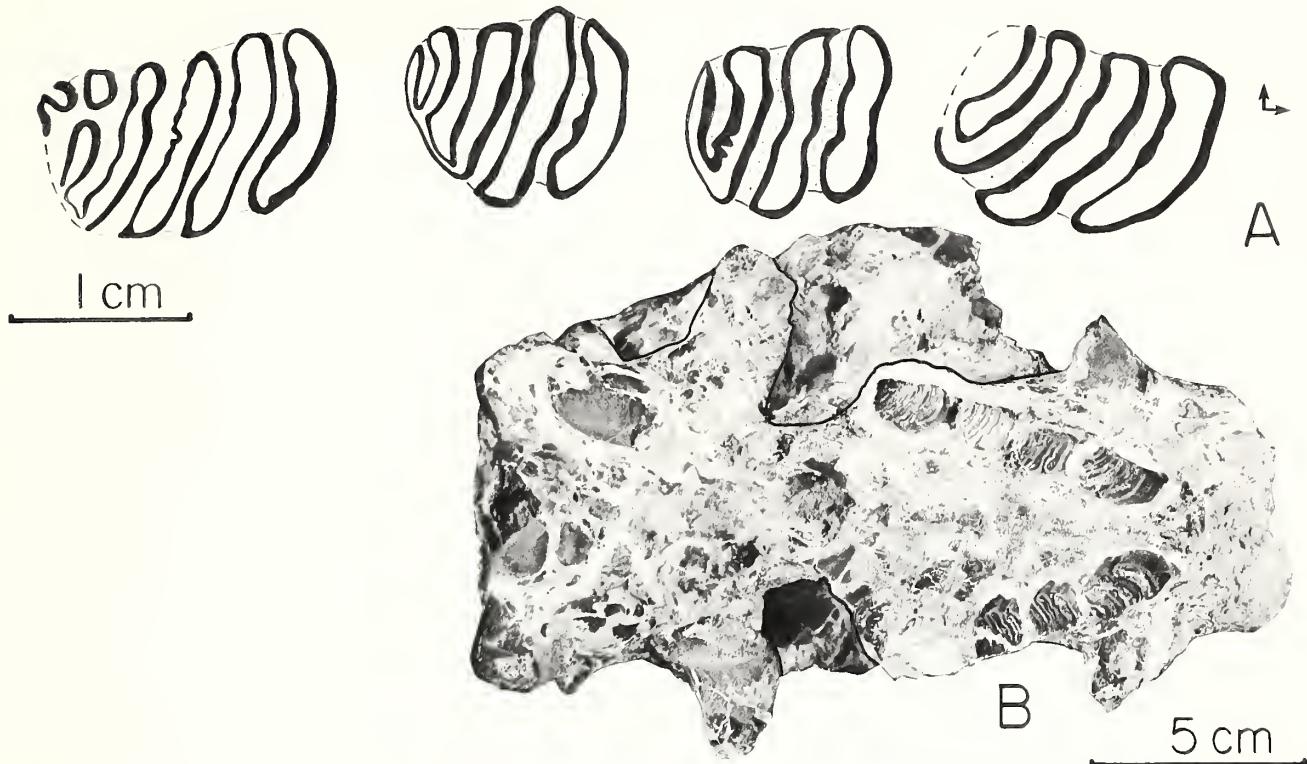


Figure 23. *Telicomys amazonensis* n. sp., LACM 117523, skull, holotype. A, right upper dentition, occlusal drawing; B, palatal view.

the sixth is nearly worn away even at this early wear stage. The fifth loph of M^3 is comprised of two enamel loops that are not yet confluent into a single loph but probably would be with more wear. The fourth and fifth lophs are continuous on the lingual side. The upper premolar and M^3 are approximately equal in size and larger than M^{1-2} which are also approximately equal in size. On this skull, the teeth are separated by 2–3 mm, an apparent distortion due to preservation.

Comparative measurements of the teeth and skull are given in Table 6.

DISCUSSION. The Subfamily Eumegamyinae was named by Kraglievich (1932) but not fully defined until much later (Pascual et al., 1966; Francis and Mones, 1968). In those features that can be compared to the description of Pascual et al., *Telicomys amazonensis* agrees in having a flat, broad skull, restricted temporal fossae and short sagittal crest, and similar shape of the basicranium and occiput. The lateral, accessory occipital condyles (paracondyles in the terminology of Pascual et al., 1966) are unique in this subfamily of Mammalia.

The large specimens of two species of *Tetrastylus* (*T. giganteus* Ameghino, 1904, a skull, and *T. gigantissimus* Ameghino, 1909, a mandible, both known only from the holotypes) were put in a new genus by Kraglievich (1926a). These two species of *Telicomys* were synonymized without comment by Pascual et al. (1966) as *Telicomys giganteus*. Kraglievich (1926a) stated that the principal differences, other

than size, between *Telicomys* and *Tetrastylus* are the relatively wider and lower occiput, position of the postpalatine notch posterior to M^3 , and the disproportionately large size of the incisors in *Telicomys*. The incisors are missing on the Rio Acre specimens but the size, occiput, and postpalatine notch are like *Telicomys giganteus*.

The usefulness of a wide and low occiput as a taxonomic character in large rodents is somewhat doubtful in that the same relative relationship of this feature in *Tetrastylus* and *Telicomys* can also be seen between *Castor* and *Castoroides*. The latter two genera are related and both are Castoridae, but they are probably less closely related than are *Telicomys* and *Tetrastylus*. *Castoroides*, the more derived genus in this feature, does not follow *Castor* in age (the lineages are in fact separate from the Middle Miocene to the Pleistocene: Larry D. Martin, pers. comm.). It may be that the shape of the occiput is more a function of size and weight of the head than an indicator of phylogeny. Curiously enough, the morphological similarity continues in that the occipital condyles of *Castoroides* are very flat and laterally expanded to provide articular surfaces similar to the unique accessory occipital condyles of the Eumegamyinae. This further suggests that many of the diagnostic features of these large rodents result from their very large size.

Those features of the posterior half of the skull of *Telicomys amazonensis* that differentiate this species from *T. giganteus* are primitive features. The great lateral expansion of the occiput and postpalatal length of the skull, and the

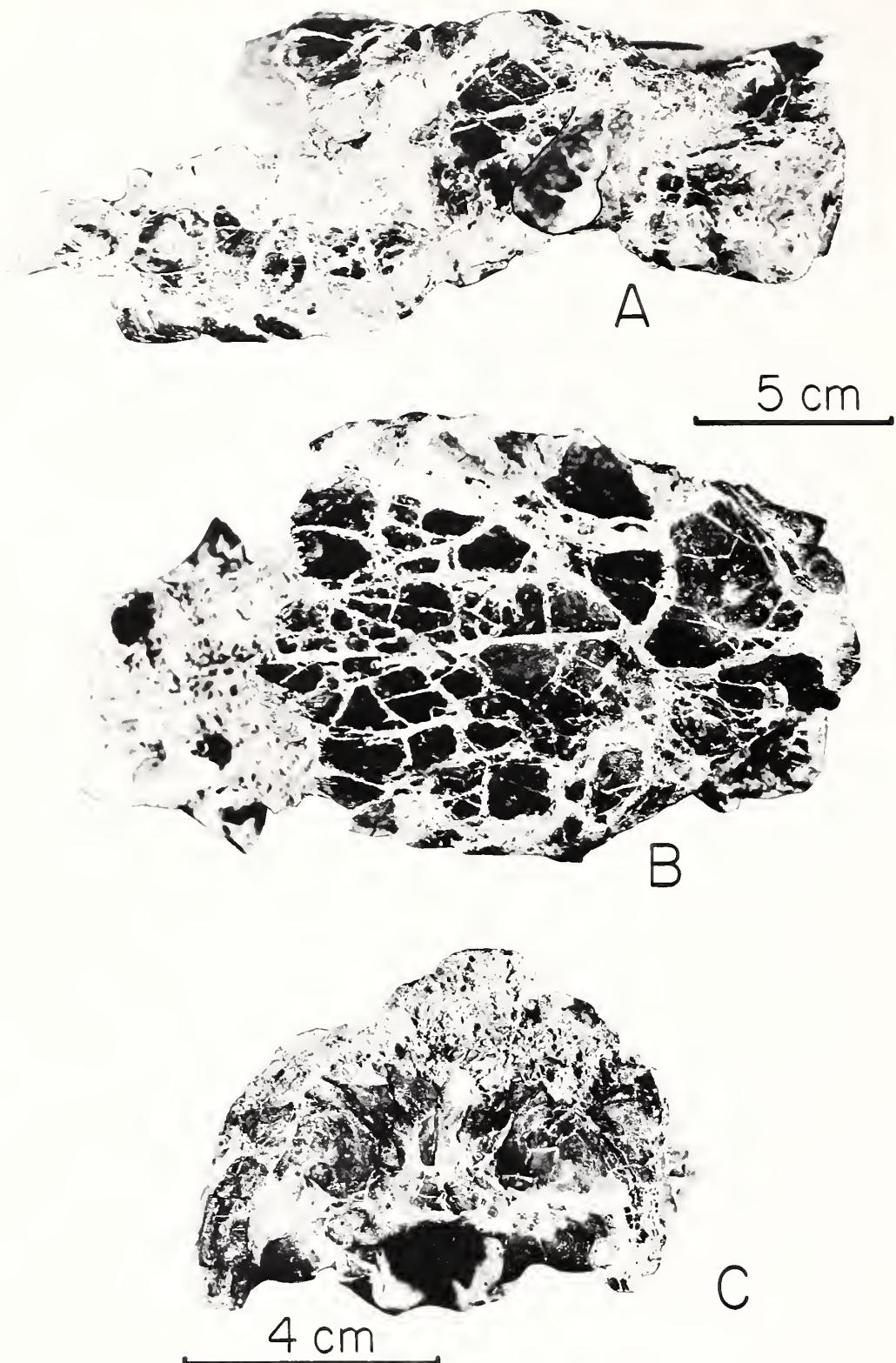


Figure 24. *Telicomys amazonensis* n. sp., LACM 117523, skull, holotype. A, left lateral view; B, dorsal view; C, occipital view. Note that C is to a different scale.

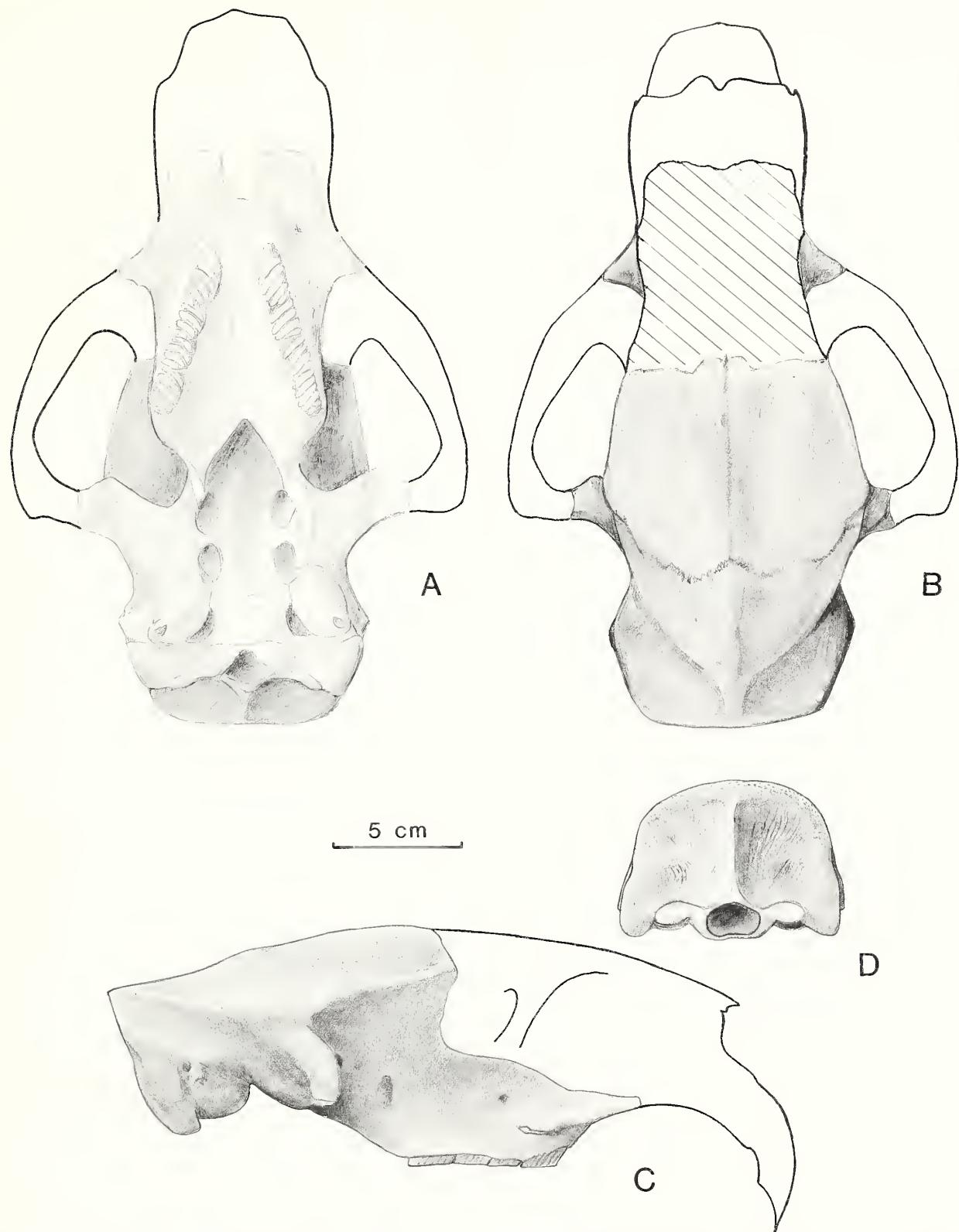


Figure 25. *Telicomys amazonensis* n. sp., LACM 117523, skull, holotype (reconstruction). A, palatal view; B, dorsal view; C, right lateral view; D, occipital view.

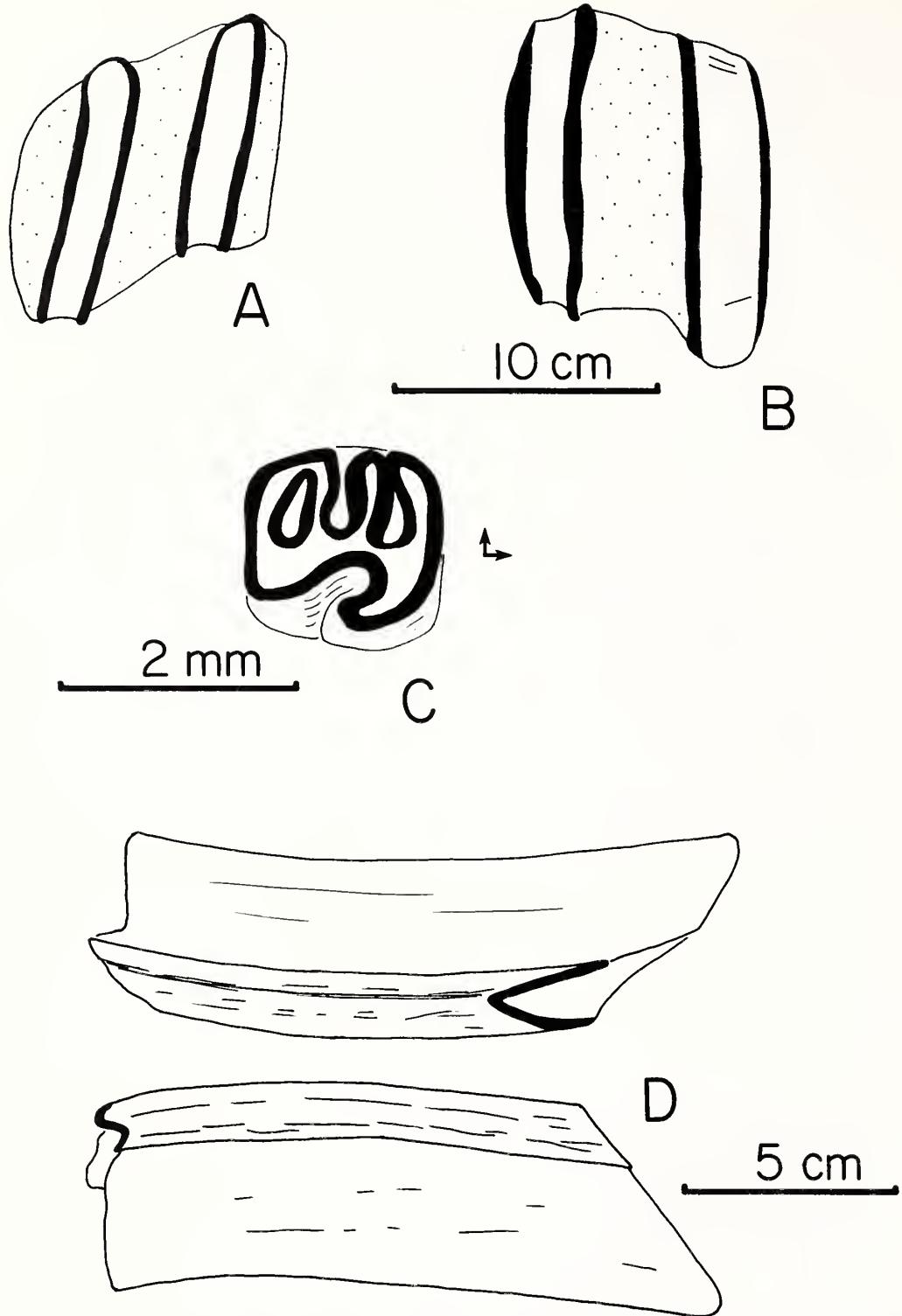


Figure 26. Neoepiblemidae, Heteropsomyinae, and *?Synastrapotherium* sp. A-B, Neoepiblemidae, gen. and sp. indet., lower cheek teeth, occlusal drawings; A, LACM 117524; B, LACM 117525. C, Heteropsomyinae, gen. and sp. indet., LACM 117526, right M¹ or M², occlusal drawing. D, *?Synastrapotherium* sp., LACM 117531, upper canine, lateral and medial views.

greater importance of the dorsal neck muscles that was probably concomitant with the enlargement of the incisors, is not evident in *Telicomys amazonensis*.

The holotype skull of *Telicomys giganteus*, the type species, was found in the Montehermoso Formation and the mandible, the holotype of “*Tetrastylus gigantissimus*,” was found

in the Chapadmalal Formation of Argentina (Kraglievich, 1926a). *Telicomys* therefore has a known temporal distribution of Montehermosan to Chapadmalalan (Early to Late Pliocene) in temperate South America. This new species from the Río Acre Local Fauna extends both the temporal and geographic ranges of the genus into the Huayquerian (Late Miocene) of western Amazonia as it adds a second, more primitive, species to this genus.

Superfamily Chinchilloidea
Kraglievich, 1940

Family Neoepiblemidae Kraglievich, 1926a

Genus and Species Indeterminate

Figures 26A, B; 28B

MATERIAL. LACM 117524, 117525, isolated lower teeth.
LOCALITY. LACM 4611.

DISCUSSION. Kraglievich (1926a) erected the Family Neoepiblemidae to include large rodents with ever-growing teeth in which the teeth are composed of subparallel laminae that are fully separated by cement. Two genera were included by Kraglievich, *Neoepiblema* Ameghino, 1889, and *Dabbenea* Kraglievich, 1926a, both known from deposits along the Río Paraná in the Province of Entre Ríos of Argentina. These deposits are Huayquerian and possibly Montehermosan in age (Pascual and Odreman Rivas, 1971). Bondesio et al. (1975) extended the family to include the Santacruzan rodent *Scotaeumys* Ameghino, 1887, and *Perimys* Ameghino, 1887, and thereby expanded the familial diagnosis to include small forms with rooted teeth in which the enamel laminae are connected labially (on the upper teeth) or lingually (on the lower teeth).

The specimens from the Río Acre Local Fauna are placed in this family on the basis of the large, ever-growing cheek teeth in which the laminae are straight, parallel, and unconnected. The laminae are furthermore widely separated by cement, more so in fact than in either *Dabbenea* Kraglievich, 1926a, or *Neoepiblema* Ameghino, 1889, the larger genera to which the Río Acre specimens most conform. In addition, these teeth are intermediate in size between those of *Dabbenea* and *Neoepiblema* and cannot be clearly referred to either genus. The discovery of these teeth along the Río Acre extends the range of the Neoepiblemidae into the Amazon Basin, identifies the probable existence of another genus of the larger neoepiblemids, and establishes a temporal connection to the deposits along the Río Paraná in Argentina.

Family Echimyidae Miller and Gidley, 1918

Subfamily Heteropsomyinae Anthony, 1917

Genus and Species Indeterminate

Figure 26C

MATERIAL. LACM 117526, right M¹ or M².

LOCALITY. LACM 4611.

DESCRIPTION. This tooth is brachydont with four lophs. The posteroloph and metaloph have joined and closed off

the posterior labial flexure (metaflexus) as a fossette. The anteroloph and protoloph have united and created a fossette from the anterior flexure (paraflexus). The protoloph and metaloph are separate at this wear stage. The hypoflexus is broad and directed anteriorly. The occlusal shape of the tooth is quadrate. The tooth has three roots but the medial root is large and appears to be two fused roots. Measurements (length × width) are 1.65 × 1.62.

DISCUSSION. Heteropsomyine features seen in this tooth are the quadrate outline, four separate lophs until moderate wear is reached on the upper molars, and a broad, anteriorly extended hypoflexus (Pascual et al., 1966; Patterson and Pascual, 1968). The Heteropsomyinae range from the Early Oligocene (*Sallamys* Hoffstetter and Lavocat, 1970) to the Recent in South America.

Order Litopterna Ameghino, 1889

Family Proterotheriidae Ameghino, 1887

Genus and Species Indeterminate

Figure 27C, D

MATERIAL. LACM 117527, right metatarsal III.

LOCALITY. LACM 4611.

DESCRIPTION. The proximal end is gently convex plantodorsally and concave transversely for articulation with the ectocuneiform. Only a small facet for articulation with the cuboid is present laterally. The lateral margin of the proximal end is deeply sculpted for metatarsal IV but the medial margin is only slightly so for metatarsal II. The shaft is flattened for appression of the secondary metatarsals along the proximal two-thirds of its length and only slightly more rounded beyond. The shaft is therefore trapezoidal in cross section. The narrowest part of the shaft is at the proximal one-fifth of its length. The carina extends with uniform prominence around the distal articular facet. Two large (7 mm) facets are placed one each in the lateral and medial fossae of the distal end. These look like articular facets but are more likely unusually smooth attachment areas for the collateral ligaments.

DISCUSSION. This single metatarsal is not sufficiently diagnostic for generic identification. It has the size and proportions of those of *Epecuenia* Cabrera, 1939, and *Eoauchenia* Ameghino, 1887, both Huayquerian genera. Measurements: length, 95.5; proximal end, length × width (15) × 21.2; mid-shaft, length × width, 10.9 × 15.2; distal end, length × width, 15.8 × 22.1.

Family Macrauchiidae Gill, 1872

Unnamed New Genus

Figures 27A–B, E–F and 28E–F

MATERIAL. LACM 117528, right mandibular ramus with DP₄–M₁; LACM 117529, left premolar; LACM 117530, right metatarsal III.

LOCALITIES. LACM 117530, LACM 4418; LACM 117528 and 117529, LACM 4611.

DESCRIPTION. The ramus maintains a uniform depth

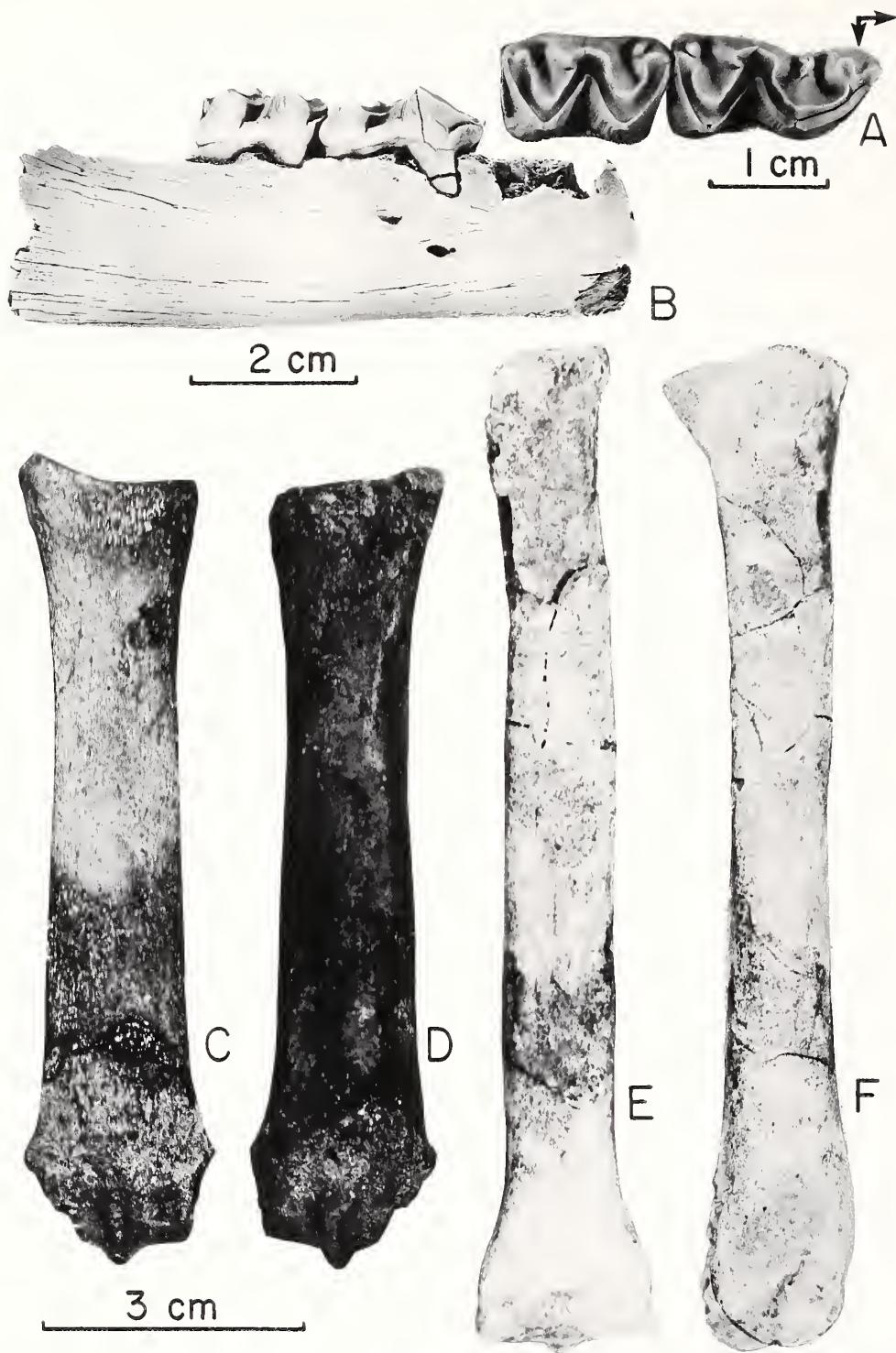


Figure 27. Macraucheniidae, Proterotheriidae, and Macrauchenidae. **A-B**, Macraucheniidae, unnamed new genus, LACM 117528, right mandibular ramus with DP₄-M₁; **A**, occlusal view; **B**, labial view. **C-D**, Proterotheriidae, gen. and sp. indet., LACM 117527, right metatarsal III; **C**, anterior view; **D**, posterior view. **E-F**, Macrauchenidae, unnamed new genus, LACM 117530, right metatarsal III; **E**, anterior view; **F**, lateral view.

(18 mm) beneath the alveoli of DP₃. Two mental foramina are present, one beneath the anterior root of DP₄ and another posterior and dorsal to the first and beneath the center of DP₄.

The DP₄ and M₁ are brachydont, with metastylids separate from the metaconids, and with prominent anterior, posterior, and labial intercolumnar cingulae. The prominence of the labial cingulae, and the openness of the ectoflexids, separate these teeth from those of the proterotheres. Small accessory cusps are present posterior to the paraconid (large on DP₄) and anterior to the termination of the hypolophid. With wear these produce bifurcations in the paralophid and hypolophid. On DP₄, a small accessory cusp is placed between the paraconid and metaconid on a small crest that extends to the apex of the protoconid. This situation is analogous to the placement of the entoconid in the posterior half of the permanent teeth of most macraucheniiids genera. The appearance of this additional cusp on a deciduous premolar is evidently the retention of a primitive character (the true paraconid?) that is not duplicated in the adult teeth. The entoconid is either lost or has been reduced and has migrated to form the small accessory cusp at the termination of the hypolophid. On DP₄ the anterior half of the tooth is elongated and equals almost twice the length of the posterior half. Measurements, length × width: DP₄, 17.3 × 18.5; M₁, 14.0 × 8.9.

The single isolated lower premolar, probably P₂, possesses a very small paraconid that is connected to the protoconid by a labial crest and also to the metaconid by a lingual crest. The metaconid is only slightly lower than the protoconid to which it is connected by a crest. A single crest descends from the metaconid to the most posterior part of the tooth and divides the talonid into two oblique surfaces, the lingual being the smaller. The tooth is two-rooted.

Metatarsal III is slender. It is the same length as that of *Theosodon* Ameghino, 1887, but equally as slender as those of *Cullinia* Cabrera and Kraglievich, 1931. The articular facet for the ectocuneiform is narrow and slightly convex plantodorsally and slightly concave transversely. The plantar hook is large and has a large oblique articular facet for metatarsal IV. The lateral side of the proximal end is sculpted and the shaft is flat for the proximal two-thirds of its length to receive metatarsal IV. A small (3 mm) facet is present on the dorsomedial side of the proximal end for the articulation with metatarsal II and the shaft is flattened on its medial side for only one-half of its length. The proximal shaft is therefore subquadrate and the distal part, approximate one-half, is oval in cross section. The distal end flares widely toward the articular surface. The carina is large and located plantarly and distally with a slight ridge reaching the dorsal surface. Measurements are: overall length, 120; proximal end, length × width, 22.0 × 13.9; mid-shaft, length × width, 11.7 × 13.1; distal end, length × width, (18) × 21.3.

DISCUSSION. The Santacrucian-Chasicoan genus *Theosodon* and the rare Chasicoan genus *Cullinia* are the geologically youngest macraucheniiids that are comparable in size to the Río Acre genus. This Río Acre macraucheniiid is more derived than either of the known genera in having the metaconid and metastylid well separated and in lacking an ento-

conid. The slenderness of the metatarsal is unlike that of *Theosodon* but similar to metatarsals of *Cullinia*. These specimens differ from known macraucheniiids to the extent that a new genus is probably represented. However, additional and better material is needed to be certain of this.

The discovery of this macraucheniiid adds to the diversity of the family during the Late Miocene. During the Chasicoan, *Theosodon* and *Cullinia*, both small forms, were present while in the succeeding Huayquerian Land Mammal Age a larger genus, *Promacrauchenia* Ameghino, 1904, was the representative of the family (Savage and Russell, 1983). This small genus from the Amazon is dentally more advanced than *Promacrauchenia* in having lost the entoconid (previously known to have been lost only in *Macrauchenia* Owen, 1840).

Order Astrapotheria Lydekker, 1894

?*Synastrapotherium* Paula Couto, 1976

Figure 26

MATERIAL. LACM 117531, isolated canine.

LOCALITY. Sandbar in Río Acre, no lithologic association.

DISCUSSION. The Order Astrapotheria is represented in the Río Acre Local Fauna by a single tusk that was found as float material. The latest occurrence of an astrapothere is that of *Xenastrapotherium* Kraglievich, 1928, of the Friasian of Venezuela and Colombia (Cabrera, 1929). This tusk is of the size expected for *Xenastrapotherium* although none is described for the genus.

The Order Astrapotheria is an indicator of Middle Miocene (Friasian) or older time and is therefore at variance with the Late Miocene (Huayquerian) age indicated by other faunal members. Either the Astrapotheria survived until more recent time in the Amazon Basin or the Río Acre Local Fauna is not a unified local fauna but rather is mixed. It is my belief that this is a single local fauna and that this record constitutes a late occurrence of the Order Astrapotheria. This is based on the absence of older strata (or any other formation) along the Río Acre that could have been the source of the astrapothere specimen and in the same preservation of the astrapothere tusk and the other fossils.

Synastrapotherium amazonense was described by Paula Couto (1976) from several cheek teeth found on the Río Juruá of Brazil. The Río Juruá and the Río Acre are part of adjacent river systems. *Synastrapotherium* was dated as Oligocene on the basis of its relative stage of evolution, but there was no associated fauna to support this age assignment. However, the type locality for *Synastrapotherium* as described by Paula Couto (1976) and the geologic section of the Río Juruá as figured by Paula Couto (1978) appears to be the same as that cropping out along the Río Acre. Although there are no comparable specimens of the astrapotheres from the Río Juruá and the Río Acre, the tusk from the Río Acre is questionably referred to *Synastrapotherium* on the basis of the probable origin from the same stratum. A Huayquerian age assignment for *Synastrapotherium amazonense* of the Río Juruá based on stratigraphy and faunal association of an astrapothere

from the nearby Río Acre seems as reasonable as an Oligocene date based on morphological comparisons alone.

Order Sirenia Illiger, 1811

Family Trichechidae Gill, 1872

?*Ribodon* Ameghino, 1883

Figure 28

MATERIAL. LACM 117532, left lower molar.

LOCALITY. LACM 4611.

DESCRIPTION. This tooth has a simple crown pattern that consists of two transverse crests, one anterior cusp, and one posterior cusp with no accessory cusps. Following the terminology of Pascual (1953), the anterior cusp is the paraconid (not present on any of Pascual's specimens), the first transverse lophid is comprised of the metaconid and protoconid, the second lophid is composed of the hypoconid and entoconid, and the single posterior cusp is the hypoconulid.

The paraconid and hypoconulid are similar in that each points away from the crown (anteriorly and posteriorly, respectively) at an approximate 60° angle. Each cusp is also attached higher on the labial side but low on the lingual side (identifiable as a separate crest to the level of the lingual cingulum). The hypoconulid is the larger cusp and has a slight terminal bifurcation.

The protoconid is slightly taller than the metaconid and sits anterior to the metaconid. Both cusps are distinguishable at this slight wear stage but their distinctness would soon disappear into a single transverse lophid (actually slightly oblique because of the position of the protoconid). The posterior transverse crest is the same height as the protoconid, and the hypoconid and entoconid are only faintly discernable as distinct cusps. A low crest unites the protoconid with the center of the posterior lophid. This tooth is much more elongate than those of *Ribodon limbatus* and has a figure eight rather than a rectangular occlusal outline. The inferior margin of the enamel is about 2 mm higher on the lingual side of the crown. The tooth is double-rooted. The posterior root bends slightly to the anterior and is approximately twice the height of the crown. Measurements (length × width): 16.9 × 8.7.

DISCUSSION. The simple bilophate pattern, large hypoconulid, and long roots are typical of *Ribodon* (Pascual, 1953). The bilophate pattern is reminiscent of primitive perissodactyls and cause for its original placement with the Tapiridea (Ameghino, 1883). The Río Acre specimen differs greatly from lower teeth of *Ribodon limbatus* in being slightly higher crowned although this may merely reflect less wear, in having a large paraconid (wholly absent in *Ribodon limbatus*), and in having a smaller hypoconulid. These may, however, be primitive conditions in the Trichechidae. The Río Acre specimen can be only questionably referred to the genus *Ribodon*.

Only a very few specimens of Tertiary manatees are known in South America. The oldest specimen of Trichechidae, *Sire-*

notherium pirabensis Paula Couto, 1967b, consists of an upper tooth and a few skeletal fragments from early Miocene deposits on the northern coast of Brazil that cannot be directly compared with the lower molar from the Río Acre. However, the upper molar is very similar in its compactness to those of *Ribodon*, in which the lower molars are also compact and not so elongate as the Río Acre tooth. *Sirenotherium* is in fact sufficiently similar to *Ribodon* to perhaps merit reference to that genus.

The generic holotype of *Ribodon* and the best specimens are from exposures along the Río Paraná in Argentina (Ameghino, 1883; Pascual, 1953). The fossils from these deposits are now referred to the Huayquerian or possibly Montehermosan land mammal ages (Pascual and Odreman Rivas, 1971).

Reinhart (1951) described a single lower molar from the La Venta Fauna (Middle Friasian) of Colombia as the holotype of *Potamosiren magdalenensis*, but Pascual (1953) thought this species was more likely referable to *Ribodon*. The molar of "*Potamosiren*" *magdalenensis* is more similar to lower teeth in *Ribodon* than is the Río Acre molar and indicates that the features of *Ribodon* were established at least by the Middle Miocene if not the Early Miocene (in *Sirenotherium*). This would support a generic separation of the Río Acre specimen from the Colombian and Argentinian specimens in that the lineages of these two groups would necessarily have had to diverge prior to the Middle Miocene.

A second possible specimen of *Ribodon* is a fused parietal-supraoccipital from the Río Juruá, Acre, Brazil. The Río Acre forms part of the southern border of Acre, and the Río Juruá probably exposes the same geologic section as the Río Acre (see discussion of Río Acre geology). This skullcap could have come from the same level as did the isolated tooth. Unfortunately, the stratigraphic occurrence of this skullcap is not known and Paula Couto's (1956) reference to *Trichechus manatus* (a Pleistocene and Recent species) is beyond further comment at this time.

Iñapari Member A Local Fauna
Holocene

Order Edentata Cuvier, 1798

Family Megatheriidae Owen, 1843

Subfamily Nothrotheriinae
Kraglievich, 1923

Nothropus Burmeister, 1882

Nothropus priscus Burmeister, 1882

Figures 29, 30, 31, 32

MATERIAL. LACM 117533, skeleton, missing left hind-limb and both hind feet.

LOCALITY. LACM 4609.

DESCRIPTION. **Skull.** When discovered, the left side of the skull was exposed. As a result, the left malar, squamosal, and most of the left frontal and parietal are missing. The skull is highly fragmented but intact.

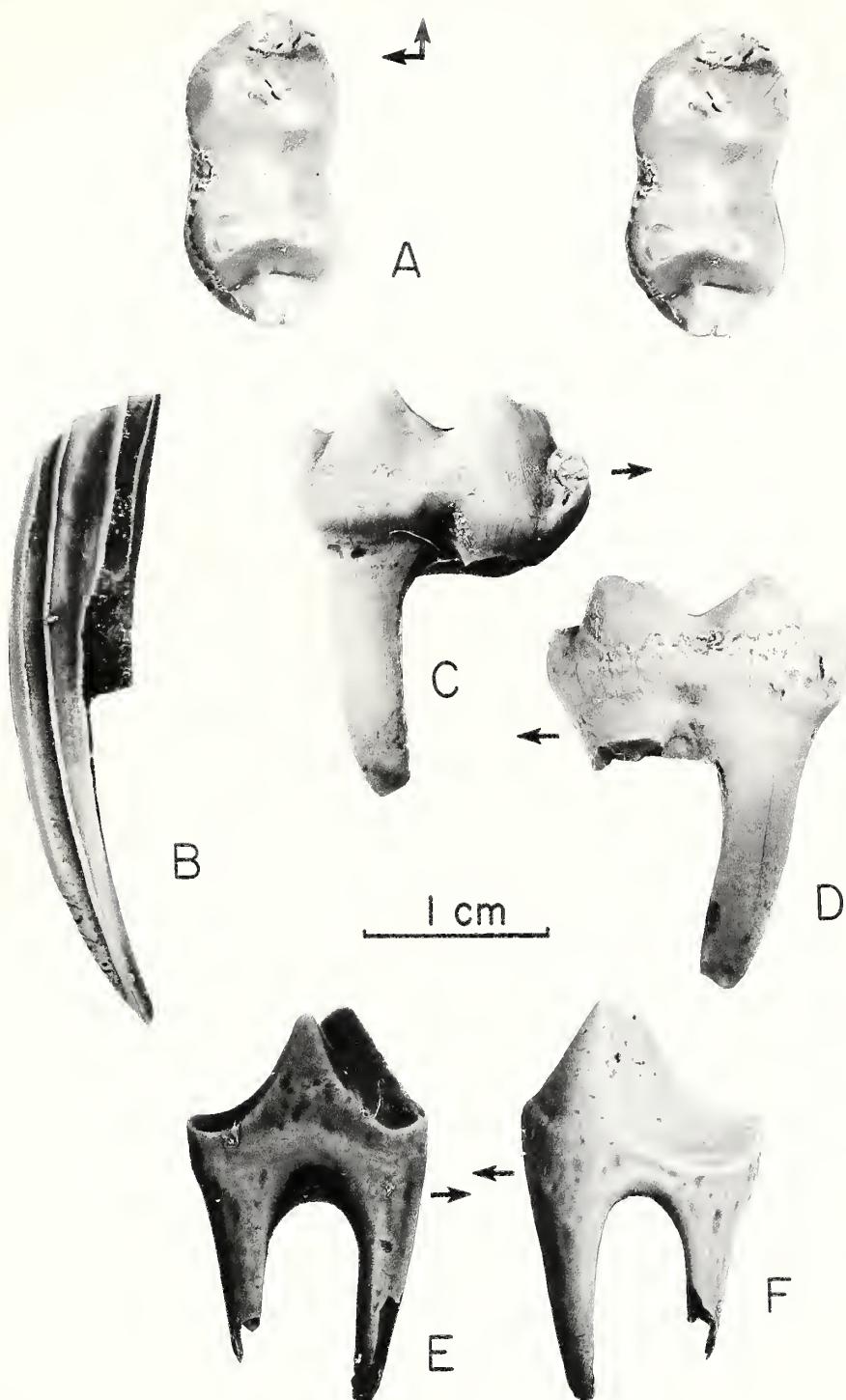


Figure 28. *?Ribodon* sp., Neoepiblemidae, and Macraucheniiidae. A, *?Ribodon* sp., LACM 117532, left lower molar, stereoscopic occlusal view; B, Neoepiblemidae, gen. and sp. indet., LACM 117525, lower tooth, side view. C-D, *?Ribodon* sp., LACM 117532, left lower molar; C, lingual view; D, labial view. E-F, Macraucheniiidae, unnamed new genus, left premolar, LACM 117529; E, lingual view; F, labial view.

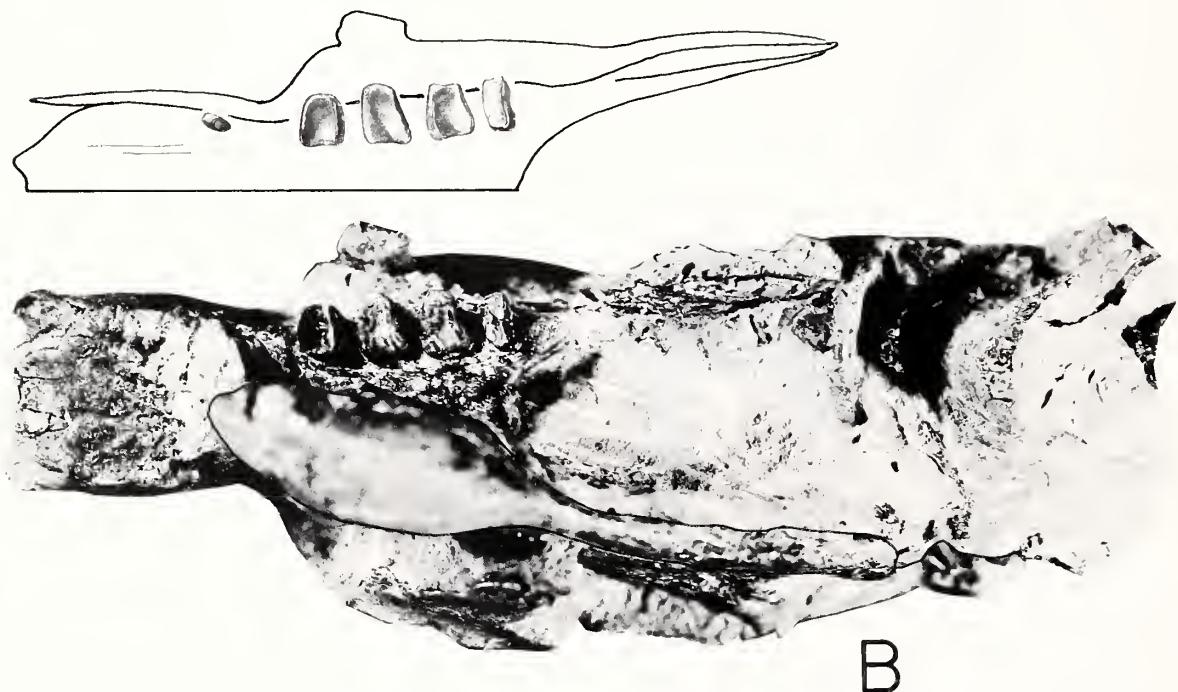
In dorsal view, the skull has a bulbous cranium and a narrow rostrum. A strong declivity is present between the lambdoidal crest and the zygomatic process. The rostrum is constricted anteriorly to the malar and then flares slightly

toward the external nares. The temporal fossa is marked by a low ridge that extends to within 25 mm of the lambdoidal ridge and to within 20 mm of the sagittal suture. Postorbital processes are present but small and are placed over M^3 . A



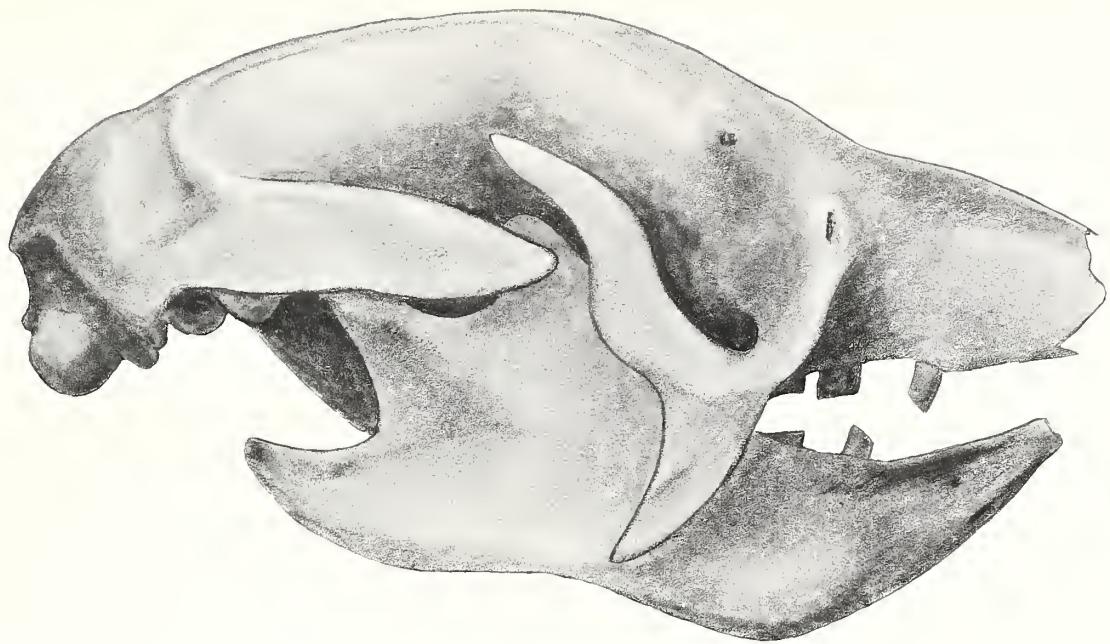
A

5 cm



B

Figure 29. *Nothropus priscus*, LACM 117533, skull and right ramus. A, lateral view; B, palatal view with occlusal drawing of teeth.



5 cm

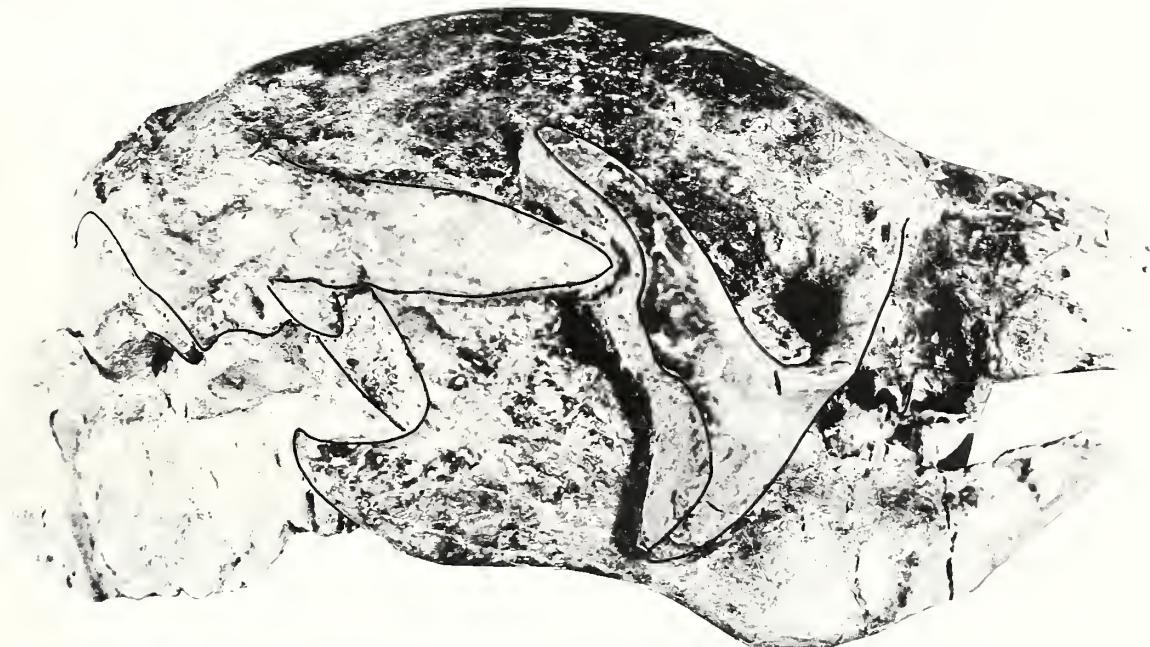


Figure 30. *Notropus priscus*, LACM 117533, skull and mandible, lateral view.

supraorbital foramen is present anterior to the postorbital process. The malar and zygomatic portions of the squamosal do not flare widely but instead are nearly parallel to the cranium.

In lateral view, the skull is domed with the highest point

above the anterior tip of the zygomatic process. The occiput is vertical with the occipital condyles situated immediately ventral to the inion. The paraoccipital and mastoid processes are equal in size, low and rounded. The dorsal margin of the external auditory meatus, ventral margin of the orbit, and

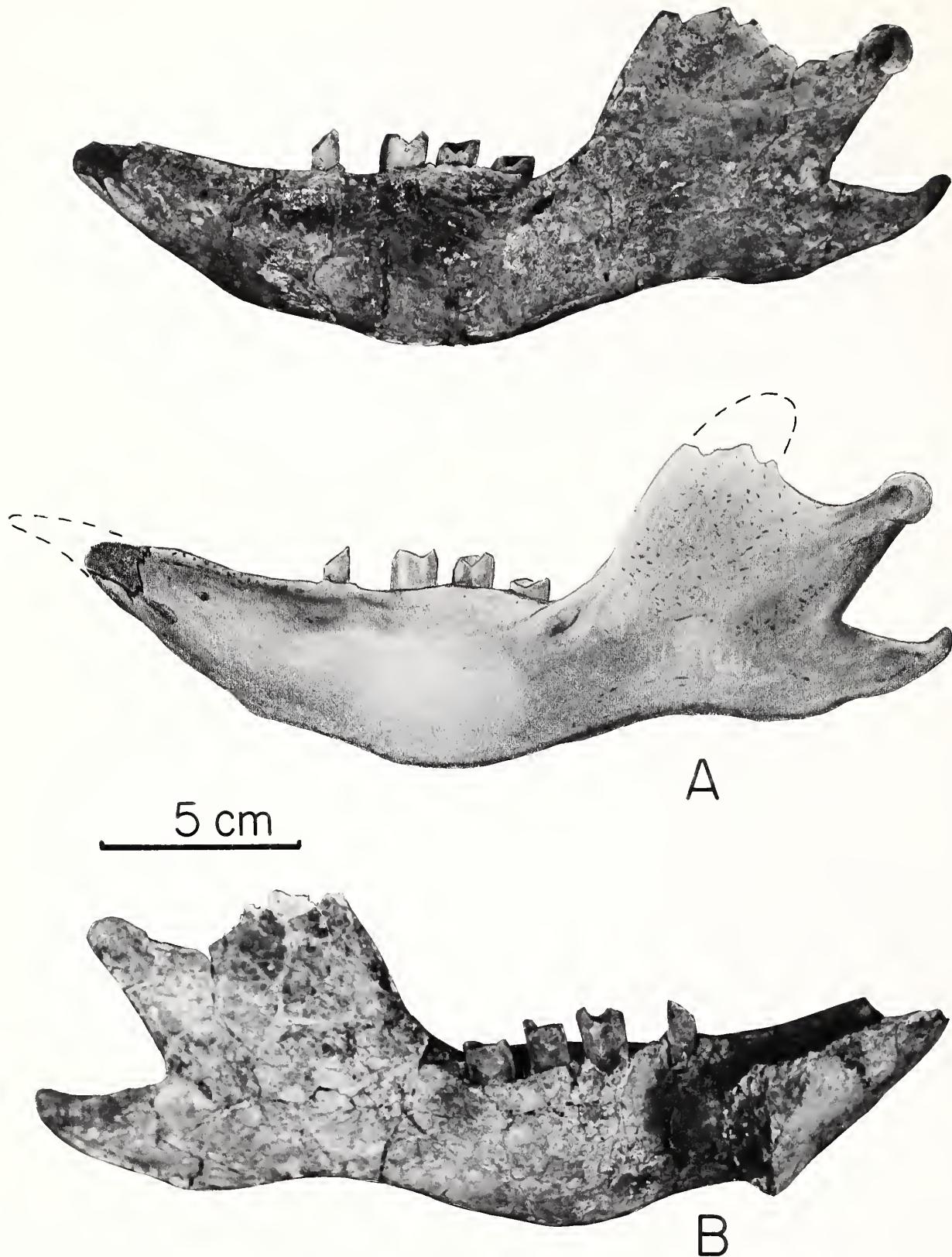


Figure 31. *Nothropus priscus*, LACM 117533, left ramus. A, lateral view, photograph and drawing; B, medial view.

alveolar border of the maxilla are on the same plane. The zygomatic portion of the squamosal narrows anteriorly and does not contact the malar (10 mm gap). The ascending portion of the malar is thin and directed dorsocaudally with a shallow notch for the zygomatic process. The descending portion of the malar is triangular and directed ventrocaudally. The lacrimal foramen is small (6.5 mm). A deep buccinator fossa is present above C¹-M². The pterygoids are semicircular in lateral view and extend from a point immediately anterior to the external auditory meatus to within 15 mm of M⁴. They are apparently only slightly expanded at their posterior base. The rostrum is short and narrows to its anterior termination.

The palate is constricted anteriorly to M¹ (the buccinator fossa) and elevated between M¹⁻³. The postpalatine fossa is U-shaped and begins at M⁴. The facets for the premaxillae are large (14 mm) and ventrolaterally placed. The premaxillae are missing in the specimen.

Upper teeth. Five upper teeth are present and are designated C¹, M¹⁻⁴ to conform to other discussions of Nothrotheriinae in which only four cheek teeth, the molariforms, are present.

The upper caniniform tooth is small and oval in cross section. It is posteriorly recurved with an oblique shear facet facing posteriorly. Measurements (length × width) are: 6.1 × 4.9.

The M¹ is trapezoidal in occlusal outline with the broad base medially. The central basin of the tooth is widely open anteromedially. The anterior border of the tooth extends farther ventrally than the posterior border. Measurements (length × width) are: 10.0 × 10.7.

The M²⁻³ have the same modified trapezoidal occlusal outline in which the medial border parallels but is longer than the external border and the posterior border is curved and concave posteriorly. The central basin is open postero-medially. The anterior edge of the tooth is higher than the posterior edge. Although M¹⁻⁴ have a slight external depression, only M²⁻³ have a distinct but shallow external groove. Measurements (length × width) are: M², 10.6 × 13.2; M³, 10.4 × 13.5.

The M⁴ is flat and anteriorly recurved. A single, anteriorly facing oblique shear facet is present on the occlusal surface. Measurements (length × width) are: 5.0 × 12.2.

Lower teeth. Four lower teeth are present and designated in this paper as C₁, M₁₋₃ to correspond with the upper teeth.

The first tooth, C₁, is caniniform, oval in cross section and with an anterior-facing, oblique shear surface. The lower and upper caniniform teeth will not occlude when the molariform teeth are in occlusion. The lower caniniform and M₁ are separated by a short diastema (10.5 mm).

The first and second lower molariform teeth are rectangular in cross section with the central basin opening externally. The anterior and posterior crests are equal in height in M₁. Both internal and external grooves are present in M₁₋₂. In M₂ (and M₃) the anterior crest is lower than the posterior. Measurements of M₁ and M₂ (length × width) are: 9.5 × 12.7; M₂, 9.7 × 13.3.

The M₃ is rounded medially and the anterior and posterior

crests slightly diverge laterally. The central basin opens anterolaterally. Measurements (length × width) are: 10.8 × 12.5.

Mandible. The postdental portion of the ramus is trifid with strong and elongate coronoid and angular processes. The condylar process is equally placed between the coronoid and angular processes. The condyle is flat, narrow, and directed ventrolaterally. The angular process is sculpted along its medial, ventral margin and the posterior tip is curved medially. The dentary portion of the ramus is thick and deep and reaches a maximum curvature beneath M₂₋₃. The posterior external mandibular foramen is laterally placed at the base of the ascending ramus immediately posterior to M₃. The posterior internal mandibular foramen is placed on the level of the alveoli approximately 30 mm posterior to M₃. The predentary portion of the ramus is elongated into a U-shaped spout. Two mental foramina are present. The larger of the two is situated near the ventral symphyseal line and the smaller foramen is posterior and dorsal to the first.

DISCUSSION. The members of the Subfamily Nothrotheriinae exhibit numerous primitive sloth features that are characteristic of Santacrucian genera (*Hapalops* Ameghino, 1887, for example, is a frequently mentioned near-relative although I can find no derived features that are shared by this genus and the nothrotheres). The most notable of features in common are the elongate and subcylindrical skull, simple dentition, trifid postdental ramus, and spout-like predental ramus. The nothrotherine genera are larger than Early Miocene genera, have inflated frontals and pterygoids, vertical grooves on the teeth, and postdental rami that incline laterally rather than parallel the axis of the tooth row. *Nothropus* is more primitive than *Nothrotherium* and *Nothrotheriops* in that the caniniform teeth are not lost and the angular process of the ramus is not reduced. However, the shape of the skull is relatively advanced, and more like the Megatheriinae Gill, 1872, in the presence of a domed forehead and a small, tubular nasal area. The mandible also has Megatheriinae features in the long symphyseal spout and the bulbous ventral margin. Comparative measurements of nothrother genera are given in Table 7.

Nothropus was previously known from only three specimens, each one a holotype. *Nothropus priscus* Burmeister, 1882, and *Nothropus taricensis* (Burmeister), 1887, are represented by partial rami in which the distinguishing feature is the presence of C₁. *Nothropus nordenskioldi* Kraglievich, 1926b, was named for a humerus that is of the proper size and not referable to any better known ground sloth. Its reference to this genus is questionable and therefore the validity of this species is doubtful. *Nothropus priscus* and *N. taricensis* have typically quadrangular nothrotherine dentitions with lateral grooves in the teeth but, unlike *Nothrotherium* and *Nothrotheriops*, an anterior caniniform tooth is present. In *N. taricensis*, this C₁ is minute. The mandible of LACM 117533 has a large C₁ that is comparable to *N. priscus*. The holotype of *N. priscus* was probably a juvenile animal (Ameghino, 1907) and slight variations in tooth shape and jaw proportions between the holotype and the new specimen are attributable to age (the length of the tooth series and the



Figure 32. *Nothrotherium priscus*, LACM 117533, left ramus, occlusal view, photograph and drawing.

diastema are longer in LACM 117533). In fact, other than the substantial difference in size of the caniniform teeth (that may be due to sexual dimorphism), teeth of *N. priscus* and *N. taricensis* differ only slightly in occlusal outline (highly variable in other ground sloths) and in size (*N. taricensis* is slightly larger).

The lack of good material has retarded systematic consideration of *Nothrotherium*. In reference to the size of C_1 , Ameghino (1907) suggested that the lineage progressed from *Nothrotherium priscus* to *N. taricensis* and ended with the complete loss of C_1 in *Nothrotheriops* (including at that time *Nothrotheriops*). This transformation series would require that *N. priscus* con-

siderably predated *N. taricensis* and other nothrotheriine genera. However, a radiocarbon date from a wood sample taken from a lignite lense beneath the channel where *N. priscus* was found dated this specimen as younger than 7145 ± 150 years b.p. Other dates from Member A and the underlying Acre Conglomerate Member range from between $5575 (\pm 105)$ and $10,075 (\pm 150)$ years b.p. (Campbell and Frailey, 1984). This age spread may represent varying degrees of contamination or may indicate a cycle of channel cut and fill in this area. In either event, the maximum age of *Nothropus priscus* leaves little time for the sequence envisaged by Ameghino (1907).

Without supporting his proposal, Paula Couto (1971) suggested that *Nothropus* and *Nothroteriops* (which Paula Couto separated from *Nothrotherium* in the same paper) formed a collateral group to *Nothrotherium*. With the additional material of *Nothropus* now available, it appears that Paula Couto's premonitory placement is accurate. *Nothropus* and *Nothroteriops* share (in contrast to *Nothrotherium*) several derived features that include a highly domed skull with convex frontals, the presence of a supraorbital foramen, a narrow dorsal prong of the malar, a posteroventrally directed descending malar, and possibly (the polarity is uncertain) an elongate angular process on the ramus. *Nothropus* resembles *Nothrotherium* in features that I believe have less taxonomic weight such as the same overall size, a zygomatic process that is fully separate from the malar and a subsequently shallower zygomatic notch on the malar, placement of the postorbital process above M^3 rather than M^2 , and the alignment of the inferior border of the orbit with the maxillary alveolar border.

In addition, the generic identification of *Nothropus* can now be expanded to include such features as the position of the postpalatine notch (at M^4 and more posterior in *Nothroteriops* and *Nothrotherium*) and straight ventral margin of the predental spout on the mandible as well as a number of certainly primitive features such as the trifid postdental ramus, relatively uninflated pterygoids, and the large caniform teeth.

Nothroteriops is a North American genus that inhabited an arid or semiarid habitat (Hansen, 1978). If *Nothropus* shared the habitat preference of its near relative, this would strongly suggest an alternative vegetation zone to the tropical deciduous forest that surrounds the Río Acre today. The spread of arid grasslands into the Amazon Basin is postulated to have occurred several times in the Pleistocene and each time the forest elements were restricted into patches, the "tropical forest refugia" (Haffer, 1969, 1974, 1979; Vanzolini and Williams, 1970; see Prance, 1982, for a review). The tropical forest refugia model largely depends on the patchwork distributions of some extant Amazonian species that are inexplicable by modern physiographic barriers. Evidence based on fossils that bears on this question is avidly sought. This discovery of a genus that has an otherwise Andean (*N. nordenskioldi*, Peruvian altiplano), Sub-Andean (*N. taricensis*, Tarija Basin, Bolivia), and pampean (*N. priscus*, near Rosario, Argentina) distribution and which is related to the desert-dwelling genus (*Nothroteriops*) argues in favor of drier conditions in the western part of the Amazon basin during

Table 7. Measurements of skull and ramus of *Nothropus priscus* compared with *Nothrotherium maquinense* and *Nothroteriops shastense*.

| | <i>N. priscus</i> | <i>N. maqui- nense</i> ¹ | <i>N. shastense</i> ¹ |
|---|-----------------------|---|--------------------------------------|
| Skull | | | |
| Length from anterior end of nasals to posterior end of supraoccipital | 272 | 216, (250) | 336.3 |
| Width across anterior ends of zygomatic pro- cesses of squamosals | (105) | 93, (115) | 115.6 |
| Distance between lacri- mal foramen and the occipital | 177 | 162, (180) | — |
| Distance between lower border of foramen magnum and posterior border of palatine | (120) | 106, (120) | — |
| Height of skull above pterygoids | 98 | 84, 94 | — |
| Length of palate, from anterior end of maxil- laries to postpalatine notch | 106 | —, 96 | 135.8 |
| Greatest width across oc- cipital condyles | 72 | —, — | 77.6 |
| Ramus | | | |
| Length from anterior end of symphysis to poste- rior end of condyle | (120) | (151), 185 | 272.8 |
| Distance from anterior end of symphysis to posterior end of angu- lar process | (230) | (135), (140) | (268.1) |
| Greatest height from an- gle to coronoid process | (90) | 77, (80) | 110.8 |
| Height of mandible un- der last tooth (M_3) | 41 | 35, 35 | 45.5 |
| Height of mandible un- der first molariform | 43 | 35, 29 | 56.8 |
| C_1-M_1 diastema | 10.6 | — | — |

¹ From Paula Couto, 1971. Two specimens of *N. maquinense* and an average measurement of 2–5 specimens of *N. shastense*.

some part of the Holocene. The radiocarbon dates for Member A and the underlying Acre Conglomerate Member of the Iñapari Formation indicate a Holocene age for this formation. Forest fragmentation could have occurred during cool, dry periods several times during the late Pleistocene and Holocene. Datable cool, dry periods occurred 20,000–13,000

years b.p., 11,000–9500 years b.p., and 3500–2800 years b.p. (Haffer, 1979). Member A of the Iñapari Formation, and *Nothropus priscus*, could date from the second of these periods.

DISCUSSION AND CONCLUSIONS

The strata exposed along the Río Acre west of Iñapari, Peru, represent two formations and at least two time periods, Late Miocene and Holocene. These strata appear to be part of a widespread depositional pattern in the western Amazon Basin for they correlate with the published description of the geologic section of the Río Juruá, Brazil, 500 km northwest of the explored part of the Río Acre and with strata exposed along the Río Beni, Bolivia, 300 km to the southeast (Campbell and Frailey, 1984; Campbell et al., 1985). The lower formation, unnamed in this paper and identified only as the Tertiary red beds, is composed of variegated clays with calcitic stringers and has an eastward dip of 10–15° presumably as a result of the Andean orogeny.

The fossils recovered from the Tertiary red beds provide the greatest taxonomic diversity yet known from a single assemblage in the Amazon Basin and significantly add to the total number of fossil taxa that are known from this area. Fourteen new taxa are added to the fossil fauna. Most of this material is derived from the Tertiary red beds and is a true death assemblage of fossils rather than isolated elements as were most previous discoveries. As such, these fossils yield a more definite age assessment and a better basis for zoogeographic and paleoclimatic comparisons than was previously possible. The Río Acre Local Fauna, including reworked material found in the overlying Iñapari Formation, is dated as Huayquerian (Late Miocene) in age. This age assignment is made on the presence in the local fauna of such characteristic Huayquerian taxa as *Kiyutherium orientalis* (Francis and Mones, 1965), *Tetrastylus* (Pascual et al., 1966), and possibly *Potamarchus murinus* (Ameghino, 1891). *Potamarchus murinus* has a Chasicoan and possible Huayquerian distribution (Pascual et al., 1966).

The recognition of new taxa is not unexpected in the description of a local fauna from an area as paleontologically unknown as the Amazon Basin. The description of only the second species of the dinomyid genus *Telicomys* extends the geographic range of this genus northward and into tropical South America for the first time. *Telicomys amazonensis* is more primitive in features of the basicranium and occiput than *T. giganteus* (of Montehermosan–Chapadmalalan age in Argentina) and the placement of *Telicomys amazonensis* with a Huayquerian local fauna is therefore reasonable. In addition, a new genus and species of mylodontine ground sloth, *Stenodon campbelli*, is present that shows affinities with *Glossotherium* and *Glossotheridium* but is unique in the shape of its palate and upper teeth. No ancestral or descendant forms for this new genus can be identified among known ground sloths. A new genus of Macrauchenidae is recognized but not named for lack of adequate material.

A single lower tooth of a marsupial that cannot be referred to any known marsupial family may represent a wholly new

group that was equivalent ecologically to the Procyonidae. A compressed trigonid and the position of the hypoconulid near the entoconid indicate a marsupial, but this tooth also has a singularly wide and basined talonid that is procyonid-like, and very unlike marsupials, in its appearance.

A single tooth of a manatee, tentatively referred to *Ribodon*, marks the first appearance of this order in the Tertiary fossil record of the Amazon Basin. Manatees are rare among South American fossils with previous Tertiary discoveries in the Friasian of Colombia (Reinhart, 1951) and Huayquerian or Montehermosan of Argentina (Pascual, 1953).

One element, although relatively undiagnostic on the basis of a single canine tooth, is nevertheless interesting at the ordinal level. The Astrapotheria are thought to have become extinct at the end of the Friasian (Pascual et al., 1966). The presence of an astrapothere in the Río Acre Local Fauna may indicate that the Astrapotheria survived beyond Friasian time in the Amazon Basin.

A number of fossils cannot be identified to lower taxonomic levels. Nonetheless, several of these specimens represent first records of taxonomic categories in the Amazon Basin owing to the virtual absence of mammalian fossils from this part of South America. Taxa thus represented include Pampatheriinae, Proterotheriidae, Macrauchenidae, Erethizontidae, Dasyprotidae, Neoepiblemidae, Caviidae (Cardiomysinae), and Echimyidae (Heteropsomyinae). These groups, now known only from isolated teeth and fragments, indicate that a substantial Amazonian Tertiary fauna existed and can yet be amplified with additional work.

Overlying the Tertiary red beds is a thick formation to which the Iñapari Formation of ONERN (1977) was restricted by Campbell and Frailey (1984). This formation comprises four readily apparent units. The lowermost identifiable unit is a characteristic marker bed, the clay-pebble conglomerate that is termed the Acre Conglomerate Member by Campbell et al. (1985). Above the Acre Conglomerate Member (and overlying the Tertiary red beds where the Acre Conglomerate is missing) is a unit composed primarily of channel-sand deposits with lenses of clay, sand, and lignite, that can be replaced laterally by buff clay. Wood fragments from these two members yielded radiocarbon dates between 5575 (± 105) and 10,075 (± 150) years b.p. (Campbell and Frailey, 1984) with the older date from the Acre Conglomerate Member and the youngest dates from lignite lenses in Member A.

Member A produced a complete skeleton of the rare nothrotheriine ground sloth, *Nothropus priscus*, that was previously known only by a single mandibular ramus from Argentina. In fact, the genus was previously represented by only three specimens, two rami and a humerus, each named as a distinct species. *Nothropus* is thought to have been closely related (Paula Couto, 1971) to *Nothrotheriops* that is known to have inhabited dry regions of southwestern North America during the Pleistocene (Hansen, 1978). If *Nothropus* shared the habitat preference of *Nothrotheriops*, its presence in the western margin of the Amazon Basin would indicate a much drier Holocene environment that is presently found there. To the extent that *Nothropus* shared the climatic preference

of its North American relative, the Río Acre discovery supports the forest refugia model of Haffer (1969, 1974), and Vanzolini and Williams (1970). Studies in a variety of fields, for example soil science, palynology, and zoogeography, have delimited several areas in tropical South America where the tropical lowland forest may have been restricted during periods of dry conditions in which grassland or savanna prevailed over much of the Amazon Basin. The areas chosen as probable sites of these refugia differ in location and size from author to author but one refugium is usually placed in the area where the skeleton of *Nothropus priscus* was found. If this individual was buried near its habitat, *Nothropus* either did not share the dry land preference of *Nothrotheriops* and was an inhabitant of this forest refugium during the early part of the Holocene or this refugium was not extant during this time. A third alternative, that *Nothropus* occupied both forest and open habitats and its fossilization in an area that may have been continually forested during the late Pleistocene and early Holocene, would mean that this specimen does not contribute to an understanding of vegetational patterns.

The Río Acre collection has doubled the known Cenozoic diversity of the Amazon Basin. Although still far from comparable to Cenozoic collections elsewhere in South America, particularly in Argentina, direct faunal comparison between the Cenozoic faunas of tropical and temperate South America is feasible and more fruitful than was previously possible. It can be determined, for instance, that many genera and at least two species were living both in the Amazon Basin and in the temperate regions during Late Miocene. Temperate South America was a savanna during the late Cenozoic (Webb, 1978) and faunal members shared in common suggest that this savanna extended into the Amazon Basin. Several genera and species, however, are included that have only been found in the tropical lowlands and were perhaps endemic. These are the pyrothere *Griphodon* (Eocene), an astrapothere, *Synastrapotherium* (probably Huayquerian), late Tertiary genera of three toxodontids, *Trigodonops*, *Abothrodion*, and *Neotrigodon*, and from this paper the ground sloth *Stenodon campbelli* and an unnamed macraucheniid. Higher taxonomic faunal distinctions are not present with the single possible exception of a new family of Marsupialia. The differences between temperate and tropical South American faunas during the Cenozoic appear to be real but are mostly at the genus and species levels. This may be a result of greater aridity in the Amazon Basin for much of its Cenozoic history that permitted more widespread grassland and grassland savanna communities than would be possible under the present climatic regime of South America.

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THE SUBFAMILIES OF EURYTOMIDAE AND
SYSTEMATICS OF THE SUBFAMILY HEMBRINAE
(HYMENOPTERA: CHALCIDOIDEA)

Gerald I. Stage and Roy R. Snelling



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THE SUBFAMILIES OF EURYTOMIDAE AND SYSTEMATICS OF THE SUBFAMILY HEIMBRINAE (HYMENOPTERA: CHALCIDOIDEA¹)

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ABSTRACT. The family Eurytomidae consists of three subfamilies: Rileyinae, Eurytominae (=Harmolitinae = Aximinae = Eudecatominae = Isosominae = Decatominae, all NEW SYNONYMY), and Heimbrinae. The subfamily Heimbrinae is compared with the other two and is described in detail for the first time. There are two genera of Heimbrinae, both limited to the Western Hemisphere: *Heimbra* in both North and South America and *Symbra* (n. gen., type-species: *S. cordobensis* n. sp.), known only from Argentina; the genus *Heimbrella* is transferred to the subfamily Eurytominae.

The two genera and seven species are separated in a key. *Heimbra* includes six known species: *H. acuticollis* Cameron (the type-species), *H. opaca* (Ashmead), *H. bicolor* Subba Rao, *H. nigra* Subba Rao, and two new species, *H. parallela* and *H. pallida*. One species, *H. opaca*, is confined to western North America, *H. bicolor* is known from Mexico and Brazil; the remaining species are known from semiarid regions of southern South America.

Pertinent illustrations of morphological features supplement the key and descriptions.

Known distribution data are cited and shown on maps.

INTRODUCTION

The present paper was begun many years ago by the senior author, while still at the Division of Biological Control, University of California, Berkeley, California. The essentially finished manuscript languished for some years. The junior author assumed the responsibility for updating the manuscript and arranging its publication; however, the bulk of the systematics and of taxonomic decisions must mostly be credited to the senior author.

SPECIMENS EXAMINED

During the course of this study we have been able to study material from the following collections: American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), California Academy of Sciences (CAS), Canadian National Collections (CNC), Natural History Museum of Los Angeles County (LACM), United States National Museum of Natural History (USNM), University of Arizona (UNAR), University of California at Berkeley (UCB), Davis

(UCD), and Riverside (UCR), University of Kansas (UKAN), and the personal collection of J.A. Halstead (HALS).

HISTORICAL RESUME

The genus *Heimbra* was originally described by Cameron (1909) for a single species, *H. acuticollis*, from Mendoza, Argentina. He placed the new genus among the typical eurytomids in the tribe Eurytomini. Another species, *H. opaca* (Ashmead, 1894) originally described in *Euperilampus*, was transferred to *Heimbra* by Burks (1958). At that time Burks assigned the genus to a position between *Eurytoma* Illiger and *Eudecatoma* Ashmead. Peck (1963) placed *Heimbra* near *Ipideurytoma* Bouček and Novicky in the Eurytominae.

The groupings of the genera within the family Eurytomidae have been more or less stable since Ashmead treated them in his 1904 revision of the Chalcidoidea. At that time he recognized five major eurytomid groups to which he accorded tribal rank: Aximini, Isosomini, Eurytomini, Rileyini, and Decatomini. These tribes have all been raised to subfamily rank by various more recent authors (e.g., Burks, 1971) and it has been necessary to change some of the names for nomenclatorial reasons. Nevertheless the group concepts have remained essentially the same through the years. Thus in Peck's catalog of the Nearctic Chalcidoidea (1963), five eurytomid subfamilies were recognized: Harmolitinae (=Isosomini), Aximinae, Rileyinae, Eurytominae, and Eudecatominae (=Decatomini). Unfortunately no authors have been able to offer clear characters to distinguish these groups as a whole, except in the case of the Rileyinae. In Ashmead's key the rileyines are distinguished primarily by their thirteen-

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segmented antenna with two or three ring segments. In the same key the other groups are distinguished by characters far more subtle and variable, such as the shape of the thorax, whether or not the head is cornute, and the nature of the wing venation. Ferrière (1950) in his key to the subfamilies occurring in Europe used essentially the same characters as did Ashmead although his wording in the couplets was more explicit. Nevertheless, from his key it was still apparent that Rileyinae was the only group truly distinct from the remaining groups within the Eurytomidae. Claridge (1961) added his endorsement to Ferrière's groupings but was similarly unable to clearly characterize any of the groups except the Rileyinae. The obvious solution to these problems was supplied by Peck, Bouček, and Hoffer (1964) in their work on the Chalcidoidea of Czechoslovakia. To them the only group sufficiently distinct from the rest of the eurytomids to warrant subfamily rank was the Rileyinae while the other three groups treated by them, Harmolitinae, Eudecatominae, and Eurytominae, were all placed together under the latter name.

Burks (1971) reviewed the higher classification of the Eurytomidae within which he proposed to recognize eight subfamilies; *Heimbra* was assigned to the new subfamily Heimbrinae as its sole genus. One new genus, *Heimbrella*, was added to the Heimbrinae by Subba Rao (1980), as well as two new species of *Heimbra* from Argentina and Brazil. Burks, in Krombein et al. (1979), in the most recent catalog of Nearctic Hymenoptera adhered to his 1971 arrangement.

As Burks (1971) had already noted, it was impossible to characterize the eight subfamilies that he recognized since none possessed unique sets of features. "It is an unfortunate fact that every character I have used here for separating genera will intergrade somewhere in the family. There seem to be no absolute characters in the Eurytomidae . . . The world genera . . . fall into apparently natural groups . . . [that] . . . cannot always be segregated by non-integrating key characters. It has not been possible to take out all the genera of a group at one place in a key." Why it should have seemed necessary to establish or continue the use of these undefined groups was neither explained nor justified and is, we believe, unsupportable.

Subba Rao (1980) expressed doubt that a family with about 55 genera worldwide should be divided into eight subfamilies. Similarly, Bouček, in Bouček, Watsham, and Wiebes (1981) noted that such subfamilies as ". . . Eurytominae, Eudecatominae and Harmolitinae . . . are still maintained by some authors . . . without good reason." In spite of those sentiments, no formal steps have been taken to rectify this situation. We, therefore, propose to formally place the subfamilies Aximinae, Decatominae, Philoleminae, Harmolitinae, Prodecatominae, and Eudecatominae in synonymy with the subfamily Eurytominae (NEW SYNONYMIES), since none can be differentially defined from that subfamily.

The synonymy of the above six subfamilies within the Eurytominae includes, of course, the transfer of all their component tribes and genera to the Eurytominae. Whether the Eurytominae, as here recognized, is monophyletic remains to be determined. We suspect that it is not and that one or

more of the old subfamilies may have to be resurrected, though differently defined. This problem is beyond the scope of the present paper.

It is clear that the old subfamilies, as they have been heretofore characterized, are not separable. For this reason, we chose to synonymize them. Future systematists who wish to revive these subfamilies will be forced to advance ample justification for doing so.

If we recognize three subfamilies in the Eurytomidae, i.e., Eurytominae (*s. lat.*), Rileyinae, and Heimbrinae, it becomes relatively easy to characterize and separate them. Table 1 shows the distribution among the three subfamilies of what we consider to be the more important group characters in the family. It can be seen that the Heimbrinae possess a combination of characters as distinctive as do the other two subfamilies and are perhaps even less similar to the Eurytominae than are the Rileyinae.

Subfamily Heimbrinae

DIAGNOSIS

Members of this subfamily may be readily distinguished from all other eurytomids by the following two features in combination: the peculiarly produced scutellum (Figs. 11–14) and the dorsally flattened, heavily sclerotized, partially fused gaster (Figs. 1, 2, 12, 14).

DESCRIPTION

FEMALE. Form robust with heavy sclerotization and large umbilicate punctuation on all body sections. Head tightly adpressed to thorax with width subequal to or greater than pronotal collar; occiput roundly, deeply incised in middle; compound eyes large, parocular area elevated above inner eye margin; antennal scrobes laterally and ventrally carinate, deeply incised, capable of hiding scapes; well-developed vertical lamella present between antennal sockets; malar area large, convex; malar groove absent; genal carina well developed laterally, becoming weakly lamellate near mandibles. Antenna with 11 to 13 segments; first flagellar segment often shorter than others but not forming a ring segment; flagellar segments and club more or less uniformly subcylindrical. Mandible resting against shield on procoxa. Pronotal collar with anterior lateral margin produced forward and carinate, forming socket to receive head; prepectus subcircular and very small, diameter less than one-half width of tegula; tegula large, opaque, heavily sclerotized, and heavily punctured; mesepisternum anteriorly and ventrally carinate and ventrally produced forward along middle and forming flat plate under procoxa; scutellum strongly, acutely produced posteriorly at least to base of gaster; metanotum inverted medially with anterior margin above and behind corresponding part of posterior margin. Procoxa strongly carinate and with anterior and lateral surfaces concave.

Forewing with costal cell broad; prestigma wider than submarginal vein; marginal vein short, scarcely one-half length of submarginal; stigmal vein not conspicuously enlarged ap-

Table 1. Distribution of characters in Eurytomidae.

| Character | Rileyinae ¹ | Eurytominae ² | Heimbrinae |
|----------------------------|--|--|---|
| Antennal segmentation | 13 | 9–11 | 11 with undivided club or 13 with tripartite club |
| Ring segments | 2 or 3 | 1 | 0 |
| Antennal sexual dimorphism | Absent | Present (except Eudecatomini) | Absent |
| Malar groove | Present | Present (except Aximini) | Absent |
| Prepectus | Small, subcircular to subtriangular | Large, subtriangular | Small, subcircular |
| Tegula | Weakly sclerotized, smooth or hyaline | Weakly sclerotized, smooth or hyaline | Heavily sclerotized, punctured and opaque |
| Shape of scutellum | Not produced | Not produced (except <i>Acantheurytoma</i>) | Greatly produced posteriorly |
| Shape of gaster | Subcylindrical | Laterally compressed or subcylindrical | Dorsally flattened |
| Modifications of gaster | T 2–4 (♀) and T 2 and 3 (♂) reduced laterally with T 5 covering most of gaster | Petiole often very long and occasional minor fusion of terga along meson | T 2+3 fused and large, covering most of gaster |

¹ Genera examined: *Riley*, *Neorileya*, *Calorileya*, *Archirileya*.

² Genera examined: *Eurytoma*, *Systole*, *Chryseida*, *Tenuipetiolatus*, *Bruchophagus*, *Prodecatoma*, *Tetramesa*, *Phylloxerexenus*, *Eudecatoma*, *Axima*, *Aximogastra*, *Bephrata*, *Bephratoidea*, *Sycophila*, *Eurytomocharis*, *Ipideurytoma*, *Isosomorpha*, *Isosomodes*, *Harmolita*, *Ailomorpha*, *Gahaniola*, *Aximopsis*, *Euroxysoma*, *Conoaxima*, *Phylloxerexenoides*, *Eudoxinna*.

cally and without spur; postmarginal vein at least one-half length of marginal.

Gaster dorsally flattened or weakly concave and heavily sclerotized; petiole small, rectangular in lateral view, with large pit near upper edge; terga 2+3 indistinguishably fused, covering most of gaster; terga 4 and 5 short; tergum 6 short and fused to base of tergum 7 which is large, strongly convex so that posterior margin lies under anterior margin; tergum 8 primarily ventrally situated and often entirely anterior to most caudad part of tergum 6+7; sterna 3 and 4 fused; sterna 5, 6, and 7 greatly reduced with at most only part of sternum 7 visible externally.

MALE. Head, thorax, wings, and legs identical to those of female. Gaster with same general aspect as that of female but differing as follows: terga 2 and 3 fused and large, terga 4, 5, and 6 separate and short; sterna 2 through 8 all distinct, not fused; sternum 2 much longer than other sterna.

DISCUSSION

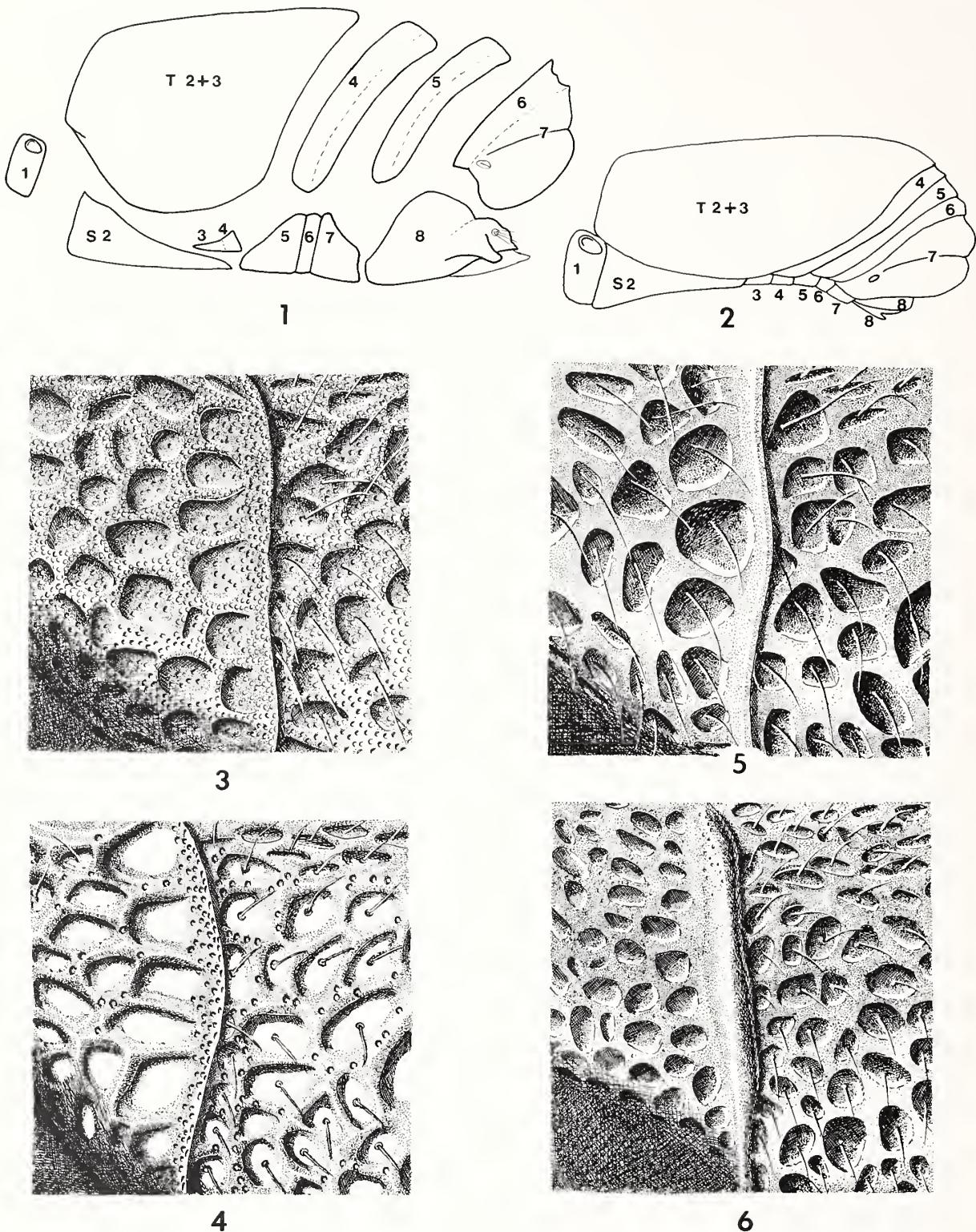
It is conceivable that new material referable to this subfamily will necessitate a broader description of Heimbrinae with many of the currently included characters perhaps being relegated to generic or specific rank. The unique character combination listed in the diagnosis, however, may be considered basie in that these features are usually conservative, varying little within other equivalent groups of eurytomids or other chalcidoids.

The unique feature of the Heimbrinae is the peculiar fusion of the gastral segments in both sexes. Specimens of *H. opaca* have been dissected and the fused segments identified. In *H. opaca* the male (Fig. 2) is least complex. All the sterna are distinct and visible in an undissected specimen. The terga are more complex since the second and third segments are indistinguishably fused. Terga 4–8 are all distinct and easily identified; laterally they approximate the corresponding sterna. The spiracle and cercus are easy means for identifying terga 7 and 8. Note that tergum 2+3 is laterally approximate to both sterna 2 and 3.

The female of *H. opaca* (Fig. 1) is more complex than the male. As is true of the male, all the sterna are distinguishable, although segments 3–6, and most of 7, are normally hidden in undissected specimens. Again, as in the male, terga 2 and 3 fused. Terga 4 and 5 are narrow but distinct. Tergum 6 is fused to 7 as a narrow basal band. Tergum 8 is large and fully visible.

The only other eurytomid genus in which the scutellum is prolonged into a spine-like process is the Bornean *Acantheurytoma* Cameron, 1911. This genus is presently believed to belong to the Eurytominae in the broad sense of this paper; Burks (1971) placed it in the Prodecatominae. In *Acantheurytoma* there is no fusion of the gastral segments, the antenna is not clavate, and the flagellar segments are elongate.

Although Subba Rao (1980) allied his genus *Heimbrella* to *Heimbra*, and thus within the Heimbrinae, we do not agree that this genus belongs here. The placement of the antennal



Figures 1–6. *Heimbra* species. 1, *H. opaca*, “exploded” lateral view of female gaster, segments numbered; 2, *H. opaca*, lateral view of male gaster, segments numbered; 3, portion of posterior margin of mesopleuron, *H. opaca*; 4, same, *H. bicolor*; 5, same *H. parallela*; 6, same, *H. nigra*.

sockets well above the level of the lower eye margin, the barely produced scutellum, and the unmodified gastral structure (tergum 1 large, following segments not fused, and gaster not dorsally flattened) are all at variance with the Heimbrinae and we suggest that *Heimbrella* should be transferred to the subfamily Eurytominae.

The following key has been prepared to facilitate the identification of the genera and species in the subfamily Heimbrinae. Since specimens of both sexes are not available for all species we do not know if the characters utilized will hold for both sexes in all species. However, with the correlated characters between the sexes of *H. opaca* as a guide we have endeavored to select for use in the couplets those features that in our opinion have a high probability of being reliably constant between the sexes in the other species.

KEY TO GENERA AND SPECIES OF HEIMBRINAE

- 1a. Antenna 13-segmented with 3-segmented club; flagellar segments broader than long (Fig. 12); scutellum with lateral, subapical margins concave in dorsal view (Fig. 11) (*Heimbra*) 2
- b. Antenna 11-segmented with undivided club; flagellar segments longer than broad (Fig. 14); scutellum with lateral, subapical margins convex in dorsal view (Fig. 13) *Symbra cordobensis*
- 2a. Mesopleuron contiguously punctured, appearing dull along posterior margin (Figs. 3, 4); tergum 6+7 (7,8) with deep, transverse groove (Figs. 10, 12) 3
- b. Mesopleuron smooth and shiny along posterior margin (Figs. 5, 6); tergum 6+7 (7,8) without transverse groove (Figs. 7-9) 4
- 3a. Umbilicate punctures on head and thorax with inner surface smooth (Fig. 4); integument generally black, pronotum orange-red *bicolor*
- b. Umbilicate punctures on head and thorax with inner surface appearing finely granulose (Fig. 3); integument unicolorous black or very dark reddish-brown *opaca*
- 4a. Marginal vein at least 1.5 times as long as stigmal vein; tergum 6+7 in lateral view, with dorsal anterior margin far behind ventral posterior margin (Figs. 7, 8) 5
- b. Marginal vein only slightly longer than stigmal vein; tergum 6+7, in lateral view, with dorsal anterior margin not far behind ventral posterior margin (Fig. 9) 6
- 5a. Integument primarily black; scutellum width about 0.65 times length *nigra*
- b. Integument primarily orange-brown; scutellum width slightly greater than 0.7 times length *pallida*
- 6a. Integument largely ferruginous, marked with blackish on face, thoracic dorsum, and side of gastral tergum 2+3, mesepimeron and propodeum largely blackish; scutellar process about 0.7 times longer than wide and moderately to strongly depressed in profile (Fig. 22) *acuticollis*
- b. Integument entirely blackish, except dusky ferruginous on some appendages; scutellar process about 0.6 times

longer than wide and not at all depressed in profile (Fig. 25) *parallela*

Heimbra Cameron

Heimbra Cameron, 1909:433-434. Type-species: *Heimbra acuticollis* Cameron, 1909; monobasic.

DIAGNOSIS

Heimbra can be distinguished from *Symbra*, the only other genus known in the subfamily, by its thick, thirteen-segmented antenna, its peculiar, laterally concave scutellum (Fig. 11) and in the female by its relatively short ovipositor (Fig. 12).

DESCRIPTION

FEMALE. Head subtriangular in front view, malar area only weakly convex; in side view, round dorsally and acute ventrally with face relatively flat; length of head (measured along middle from apex of clypeus to top of vertex) about 0.70 times width; antennal scrobe short and broad. Antenna short and thick, thirteen-segmented; scape short, not reaching median ocellus; pedicel and all flagellar segments broader than long; first flagellar segment shorter than subsequent segments and asymmetrical, dorsal length greater than ventral length; diameter of second segment slightly less than first and length not more than 1.50 times first; length of subsequent flagellar segments about subequal but diameters gradually increasing; club three-segmented, not enlarged, greatest diameter subequal to preceding segment.

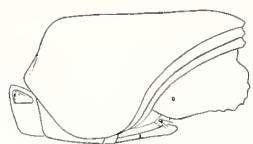
Scutellum width usually much less than 0.80 times length; lateral margin in dorsal view sinuate with basal portion convex and subapical portion concave, sides nearly parallel subapically.

Anterior lateral margin of tergum 2+3 of gaster broadly rounded where it overlaps sternum 2+3; tergum 6+7 broadly convex in lateral profile; visible portion of tergum 8 not more than about one-half length of gaster, usually much less and situated entirely anterior to most caudad portion of tergum 6+7; ovipositor sheaths short.

MALE. Similar to female in most respects except gaster is modified as indicated in description of subfamily.

DISCUSSION

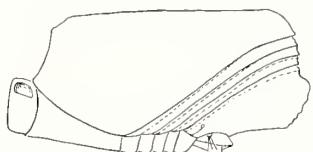
It is evident that *Heimbra* is widely distributed in the Western Hemisphere with specimens having been taken from such widely separated localities as Mendoza, Argentina and Denver, Colorado. The available distribution data suggest *Heimbra* may be more or less restricted to desert and semiarid regions. As can be seen from the maps all the North American records are from or adjacent to the arid parts of the western United States and the arid parts of northern and central Mexico, while nearly all of the South American records are from the arid parts of Argentina and adjacent countries. The



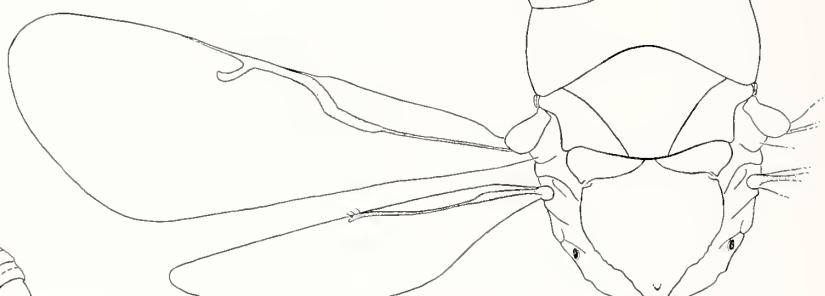
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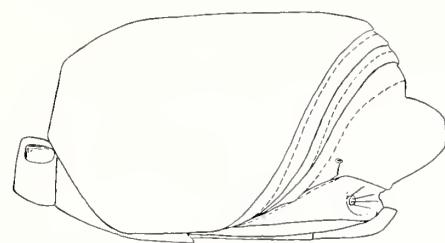
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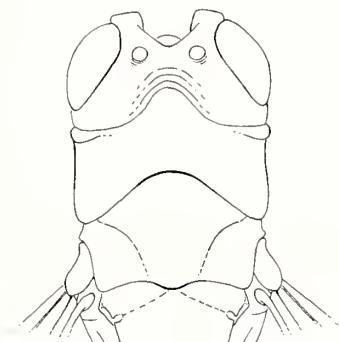
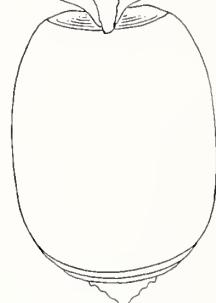
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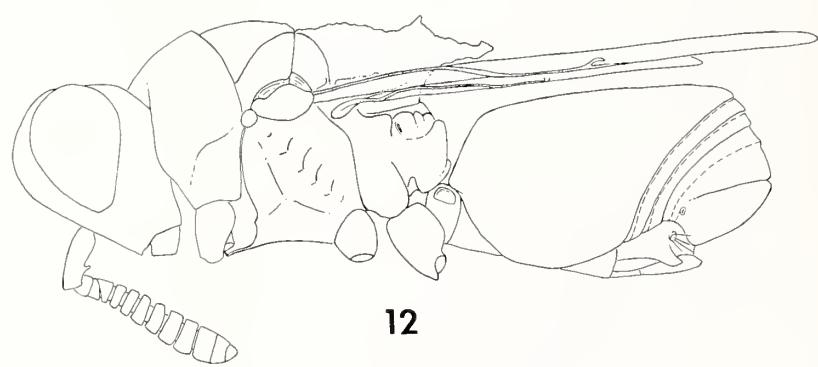
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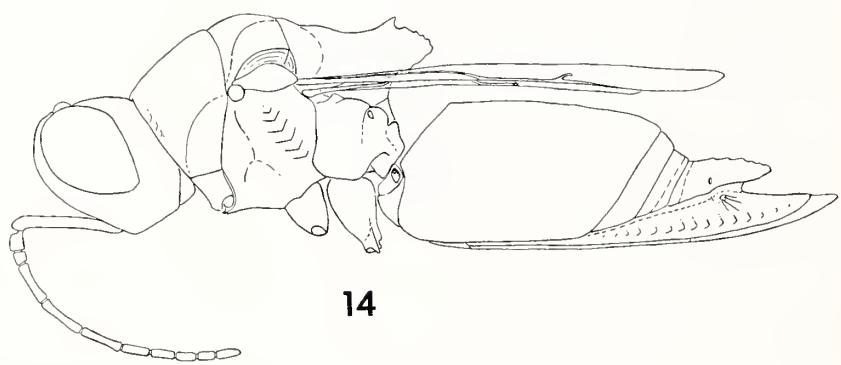
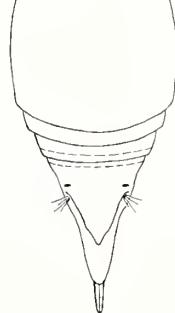
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resulting disjunct distribution is of interest since it adds another animal genus to the several botanical genera known to follow the same pattern. Among the latter, *Larrea*, *Atamisquea*, *Cercidium*, *Koeberlinia*, *Ephedra*, *Acacia*, *Caesalpinia*, *Condalia*, *Baccharis*, *Lycium*, *Prosopis*, *Mendora*, and *Hoffmannseggia* all occur on both continents while being more or less limited to xeric regions (Johnston, 1940). Unfortunately, nothing is known of the biology or hosts of the species of *Heimbra* but it would be most interesting if this genus were associated with any of these plants.

The genus *Heimbra* as presently understood contains six species, two from North America and four from South America. These six species fall into two distinct groups. The exclusively South American group includes those species in which the mesopleuron, along its posterior margin is smooth and shiny (Figs. 5 and 6), the propodeum is divided into large areolae, with smooth or weakly sculptured inner surfaces, and tergum 6+7 (♀) or 7 (♂) lacks a distinct transverse groove (Figs. 7-9). Included in this group are *H. acuticollis*, *H. nigra*, *H. pallida*, and *H. parallela*.

The second group, consisting of two species, *H. bicolor* and *H. opaca*, ranges from the United States to Brazil. In these species, the mesopleuron is punctate to the posterior margin (Figs. 3 and 4), the propodeum is dull and coarsely and irregularly sculptured and densely punctate, and tergum 6+7 (♀) or 7 (♂) has a distinct transverse groove (Figs. 10 and 12).

Those features which characterize the first, or *acuticollis* group, are shared with the one species of *Symbra*. *Symbra* is, however, readily distinguished from all species of *Heimbra* by the very long antennal scape that extends above the level of the anterior ocellus and the long, slender, nine-segmented flagellum with segments 2-9 longer than broad and segments 7-9 not forming an apical club. Females of *Symbra* possess a long ovipositor that extends beyond gastral tergum 6+7 when viewed in profile (Fig. 14). Although males of *Symbra* are unknown, they presumably will be similar to the females in antennal structure and in having the scutellar process short and, in dorsal view, with the lateral, subapical margins convex, rather than concave as in *Heimbra*.

Heimbra opaca (Ashmead)

Figures 1, 2, 3, 11, 12, 19

Euperilampus opacus Ashmead, 1894:318; ♀. Dalla Torre, 1898:358; Viereck, 1906:227; Snow, 1907:129; Schmiedeknecht, 1909:82; Essig, 1929:849; Cresson, 1928:28; Peck, in Muesebeck et al., 1951:516.

Eurytoma opaca: Crawford, 1914:69.

Heimbra opacus: Burks, in Krombein, 1958:72, 82.

Heimbra opaca: Peck, 1963:832-833. Burks, in Krombein et al., 1979:846.

DIAGNOSIS

This species may be readily distinguished from all other known species of *Heimbra* by its unique, dull punctuation.

DESCRIPTION

FEMALE. Length 4.4 to 4.6 mm. Primarily black although ventral portions and legs may become dark reddish-brown. Tarsi orange-brown.

Head with large, shallow, closely spaced, umbilicate punctures over entire surface except on clypeus and in antennal scrobes; umbilicate punctures appearing weakly and finely granulose within, each bearing a short silvery-white hair whose length is generally subequal to diameter of puncture; antennal scrobes and interspaces between punctures similarly granulose but shiny; clypeus glabrous; antennal scrobes short, length about 1.25 times greater than maximum distance between lateral carinae near antennal sockets and about two-thirds length of eyes; scrobes with lateral carinae curved along lower half; interantennal lamella small; inner eye margins nearly parallel. Antennal scape length about three times maximum width near base; relative dorsal lengths of pedicel and first three flagellar segments: 6:5:4:4. Mandible black apically, reddish-brown basally.

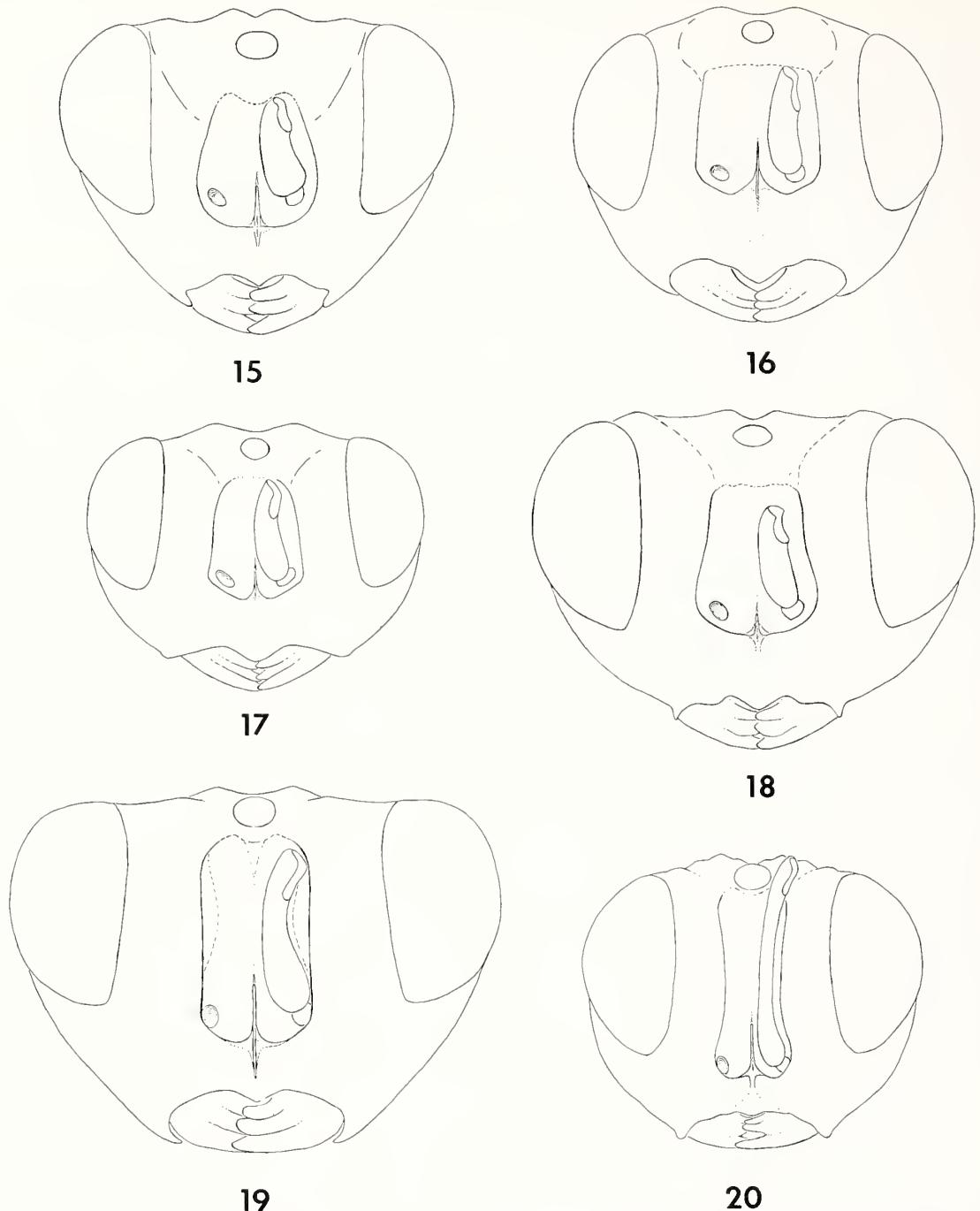
Thoracic integument dorsally with punctuation and vestiture like that on head except punctures on scutellum somewhat larger; pronotum in side view with dorsal outline convex anteriorly, somewhat flat posteriorly; lateral carina of pronotal collar very weakly oblique, nearly parallel to posterior margin; scutellum broad, width about 0.75 times length; scutellum with dorsal prominence conspicuous and acute in lateral view; mesopleuron finely, contiguously punctured along posterior margin (Fig. 3); propodeum coarsely sculptured, with large irregular ridges and finely, contiguously punctured interspaces.

Wing veins dark brown; marginal vein long (measured from angle on wing margin to base of stigmal vein), slightly over 1.5 times length of stigmal vein; postmarginal vein indistinct apically but clearly short, not more than 0.90 times length of marginal vein.

Visible parts of all gastral terga weakly, umbilically punctate, those on dorsum of tergum 2+3 merging into large reticulations; umbilicate punctures appearing finely, weakly granulose within; dorsum of tergum 2+3 medially flat; posterior lateral margin of tergum 2+3 weakly concave in lateral view; tergum 6+7 with convexity asymmetrical in lateral view, posterior margin at meson far in front of corresponding



Figures 7-14. Heimbrinae. 7, lateral view of female gaster, *H. pallida*; 8, same, *H. nigra* male; 9, same, *H. parallela* female; 10, same, *H. bicolor* female; 11-12 dorsal and lateral views of female, *H. opaca*; 13-14, dorsal and lateral views of female, *Symbra cordobensis*.



Figures 15–20. Heimbrinae, front view of head: **15**, *Heimbra bicolor*, female; **16**, *H. nigra*, male; **17**, *H. pallida*, female; **18**, *H. opaca*, female; **19**, *H. parallela*, female; **20**, *Symbra cordobensis*, female.

part of anterior margin and convexity scarcely projecting caudad of posterior margin of tergum 2+3, with deep transverse groove and lacking conspicuous keel along meson dorsally and posteriorly; exposed portion of tergum 8 short, slightly over one-half length of hind femur, lateral ridge produced posteriorly into ventrally projecting broad spine.

MALE. Length 4.0 to 4.5 mm. Similar to female in all pertinent characters described above except as follows: antennal scape bears one subapical, ocelloid spot on lower surface; scutellum narrower, width about 0.65 times length; tergum 8 without lateral ridges; punctuation of visible parts of sterna 2–8 similar to that on exposed parts of terga 5 and 6;

sternum 8 with lateral, posteriorly directed, blunt spines similar to, but smaller than, those on tergum 8 in female.

TYPE DATA

Heimbra opaca was described from a unique female collected in June at Denver, Colorado and subsequently deposited in the collection of the American Entomological Society and now in the USNM.

The only additional published distribution record (Viereck, 1906; Snow, 1907) is based on a single specimen collected in July at Oak Creek Canyon (6,000 ft. alt.), twenty miles southwest of Flagstaff, Coconino County, Arizona.

SPECIMENS EXAMINED (Map 1)

UNITED STATES. ARIZONA, *Cochise Co.*: 1♂, Texas Canyon, 5,000–6,000 ft. elev., Sept. 8, 1927 (J.A. Kusche; CAS). *Coconino Co.*: 1♀, Ashfork, June 17 (Barber and Schwarz; USNM). *Gila Co.*: 1♀, Cedar Creek, 15 mi. W Fort Apache, June 21, 1957 (G. Butler and F. Werner; UNAR). *Maricopa Co.*: 1♀, 5 mi. SE Wickenburg, Sept. 2, 1961 (P.D. Hurd; UCB), on *Euphorbia pediculifera*. *Pima Co.*: 1♂, Peppersauce Canyon, Santa Catalina Mts., Aug. 18, 1940 (J.J. duBois; LACM); 1♀, Mt. Lemmon, 9,000 ft. elev., Santa Catalina Mts., Sept. 5, 1939 (R.H. Crandall; UNAR); 1♀, 1♂, Box Canyon, Santa Rita Mts., Sept. 14, 1964 (L. and C.W. O'Brien; LACM); 1♂, Santa Rita Mts., 5,000–8,000 ft. elev., July (F.H. Snow; UKAN); 1♂, 10 mi. E Continental, July 18, 1961 (F. Werner and W. Nutting; UNAR). *Pinal Co.*: 1♂, Oracle, Aug. 25, 1934 (I. Moore; USNM). *Santa Cruz Co.*: 1♂, Canelo, July 19, 1958 (M.S. Adachi; UNAR); 1♀, same locality, Aug. 3, 1956 (G.D. Butler; UNAR); 1♀, Nogales, Aug. 24, 1939 (R.H. Crandall; UNAR); 1♂, 8 mi. NW Nogales, Sept. 8, 1957 (T.R. Haig; UCD); 1♂, 13 mi. NNW Nogales, same date and collector (USNM); 3♂♂, Patagonia, Aug. 10, 1958 (F.G. Werner, M. Adachi; UNAR); 1♂, W side, Patagonia Mts., Aug. 9, 1956 (F.G. Werner and G.D. Butler; UNAR). CALIFORNIA, *Inyo Co.*: 1♂, Antelope Springs, 8 mi. SW Deep Springs, June 15, 1961 (C.A. Toschi; UCB), on *Chrysothamnus*; 1♀, 1♂, same locality, July 1, 1961 (J.A. Powell; UCB), ♀ on *Eriogonum heermannii*. *Riverside Co.*: 1♀, Palm Desert, June 5, 1960 (R.L. Westcott; LACM); 1♂, Deep Canyon, July 1, 1964 (E.I. Schlinger; UCR). *San Diego Co.*: 1♀, 10 mi. NE Ramona, July 21, 1981 (J.A. Halstead; HALS); 2♂♂, 0.9 mi. W Oak Grove, July 25, 1979 (J. LaSalle; UCR). *Santa Barbara Co.*: 1♂, Santa Ynez Mts., June 24, 1959 (F.D. Parker; UCD). *Santa Clara Co.*: 1♀, no further data (Harkins Collection; LACM). *Tulare Co.*: 1♀, Kaweah Powerhouse Station 3, Ash Mountain, July 3, 1983 (J.A. Halstead; HALS). COLORADO, *Rio Blanco Co.*: 1♀, Meeker, ca. 6,200 ft. elev., July 20–21, 1919 (AMNH). KANSAS, *Baldwin Co.*: 1♀, Baldwin, July (J.C. Bridwell; USNM). *Scott Co.*: 1♂, no further locality, June 20, 1925 (H.O. Deny; UKAN). MONTANA, *Petroleum Co.*: 1♀, 1.5 mi W Winnett, July 28, 1970 (N.E. Rees; USNM). NEVADA, *Humboldt Co.*: 1♀, Orovada, July 14, 1962 (M.E. Irwin; UCD). NEW MEXICO, *McKinley Co.*: 1♀, Pinedale, Navajo Reservation, July 22, 1948 (L.C. Wymann; USNM). *Otero Co.*: 1♂, Moun-



Map 1. Distribution of *Heimbra opaca* (●) and *H. bicolor* (○) in North America.

tain Park, June 27, 1940 (D.E. Hardy; UKAN). *Valencia Co.*: 1♂, Sandia Mts., July 17, 1952 (R.H. and L.D. Beamer, W.E. LaBerge, C. Liang; UKAN), on *Croton*; 1♂, 2♀♀, Carrizo Arroyo, 20 mi. W Los Lunas, Aug. 1–23, 1977 (S. and J. Peck; CNC). UTAH, *Uintah Co.*: 1♂, no further locality, July 13, 1911 (USNM).

MEXICO. HIDALGO: 1♂, 18 mi. NW Pachuca, 6,400 ft. elev., June 25, 1971 (Ward and Brothers; USNM), on *Prosopis laevigata*. MEXICO: 1♂, Ixtapan la Sol, 5,500 ft. elev., Aug. 9, 1954 (J.G. Chilcott; CNC). MORELOS: 1♂, Cuernavaca, Aug. 1959 (N.L.H. Krauss; USNM); 1♂, same locality, Aug. 1, 1938 (L.J. Lipovsky; UKAN). NUEVO LEON: 1♀, Chipinque Mesa, 5,400 ft. elev., near Monterrey, July 8, 1963 (H. and A. Howden; CNC). OAXACA: 2♂♂, 7 mi. E Oaxaca, road to Guelatao, 5,400 ft. elev., July 14, 1963 (L.E. Caltagirone; LACM). SONORA: 1♂, Alamos, Aug. 12, 1960 (P.H. Arnaud, E.S. Ross, and D.C. Rentz; CAS). ZACATECAS: 1♀, 10 mi. N Fresnillo, May 10, 1962 (F.D. Parker and L.A. Stange; UCD); 2♀♀, 15 km E Zacatecas, July 30, 1951 (P.D. Hurd; UCB).

DISCUSSION

The available records indicate that *H. opaca* is widely distributed through the arid and semiarid regions of western North America. The few associated plant records may be a clue to the actual host or hosts of this species, but in all probability they merely represent adult feeding behavior since

such records by these collectors only pertain to flower visits by the insect.

Heimbra bicolor Subba Rao

Figures 4, 10, 15

Heimbra bicolor Subba Rao, 1980:308; ♀ ♂.

DIAGNOSIS

This species can be distinguished from all others known in the genus by the combined characters of the smooth, shiny umbilicate punctures, the presence of a transverse groove on tergum 6+7 (7,8) and the conspicuous coloring.

FEMALE. Length 4.0 mm. Primarily black except for bright orange-red dorsal portion of pronotum and some minor exceptions as noted below.

Head integument with large, deep, closely spaced umbilicate punctures over entire surface except clypeus and in antennal scrobes; umbilicate punctures smooth and shiny within, each bearing a short, silvery-white hair whose length is subequal to diameter of puncture; interspaces between punctures and surface of antennal scrobes appearing weakly, finely granulose but shiny; clypeus glabrous; antennal scrobe short, length only slightly longer than maximum distance between lateral carinae near antennal sockets and less than 0.75 times length of eye; scrobe with lateral carina curved along lower half; interantennal lamella large; inner eye margins weakly converging below, nearly subparallel. Antennal scape length less than three times maximum width near base; relative dorsal lengths of pedicel and first three flagellar segments: 6:4:4.5:5. Mandible nearly black apically, dark reddish-brown basally.

Punctuation and vestiture of thoracic dorsum similar to that of head except punctures slightly larger; punctures on pronotal collar as large as those on mesonotum or scutellum; pronotum in side view with dorsal outline flat anteriorly, convex posteriorly; lateral carina of pronotal collar weakly oblique to posterior margin; scutellum narrow, width about 0.65 times length; scutellum with dorsal prominence conspicuous and acute in lateral view; mesopleuron finely, contiguously punctured along posterior margin (Fig. 4); propodeum coarsely sculptured with large irregular ridges and finely, contiguously punctured interspaces.

Wing veins brown; marginal vein long (measured from angle on wing margin to base of stigmal vein), about 1.5 times length of stigmal vein; postmarginal vein indistinct apically but more or less subequal in length to marginal vein. Legs primarily dark reddish-brown, nearly black but tarsi, femora, and tibiae distally light orange-brown.

Gastral tergum 2+3 laterally and ventrally and tergum 6+7 ventrally, umbilically punctate; punctures on tergum 2+3 largest and deepest on anterior lateral portion, becoming small and indistinct on posterior lateral portion and merging into large reticulations dorsally; umbilicate punctures within and interspaces between dorsal reticulations smooth and shiny; visible portion of terga 4, 5, 6+7 anteriorly, and 8 appearing finely, weakly granulose; dorsum of tergum 2+3 medially flat; posterior lateral margin of tergum 2+3 weakly

concave in lateral view; tergum 6+7 with convexity asymmetrical in lateral view, posterior margin far in front of corresponding part of anterior margin and convexity extending slightly caudad of posterior margin of tergum 2+3; tergum 6+7 with deep transverse groove but lacking conspicuous keel along meson dorsally and posteriorly; exposed portion of tergum 8 short, slightly over one-half length of hind femur; tergum 8 with lateral ridge produced posteriorly into ventrally projecting broad spines.

MALE. Length 3.5 mm. Similar to female in all pertinent characters described above except as follows: antennal scape with one subapical ocelloid spot on lower surface; scutellum width about 0.7 times length; tergum 8 without lateral ridges; visible parts of sterna 2-8 with punctuation similar to that of exposed parts of terga 5-6; spines of sternum 8 smaller than those of female.

TYPE DATA

The type series is from Nova Teutonia, Brazil, and is deposited in BMNH; the holotype has been examined.

DISTRIBUTION

In addition to the type we have seen material of this species from Brazil, Paraguay, and Mexico (Maps 1 and 2).

SPECIMENS EXAMINED

BRAZIL. MINAS GERAIS: 3♀, Pedra Azul, Nov. 1972 (Seabra and Oliveira; CNC).

PARAGUAY. 1♂, San Bernardino (K. Fiebrig; BMNH).

MEXICO. DURANGO: 1♀, El Palmito, 6,500 ft. elev., July 17, 1964 (J.F. McAlpine; CNC). NAYARIT: 1♀, Ahuacatlan, July 18-22, 1951 (P.D. Hurd; UCB), on *Donnell-smithia hintonii*. VERA CRUZ: 1♀, 2 mi. N Cerro Azul on road to Naranjo, 1,500 ft. elev., June 9, 1963 (L.E. Caltagirone; LACM).

Heimbra parallela, new species

Figures 5, 9, 19, 25, 26

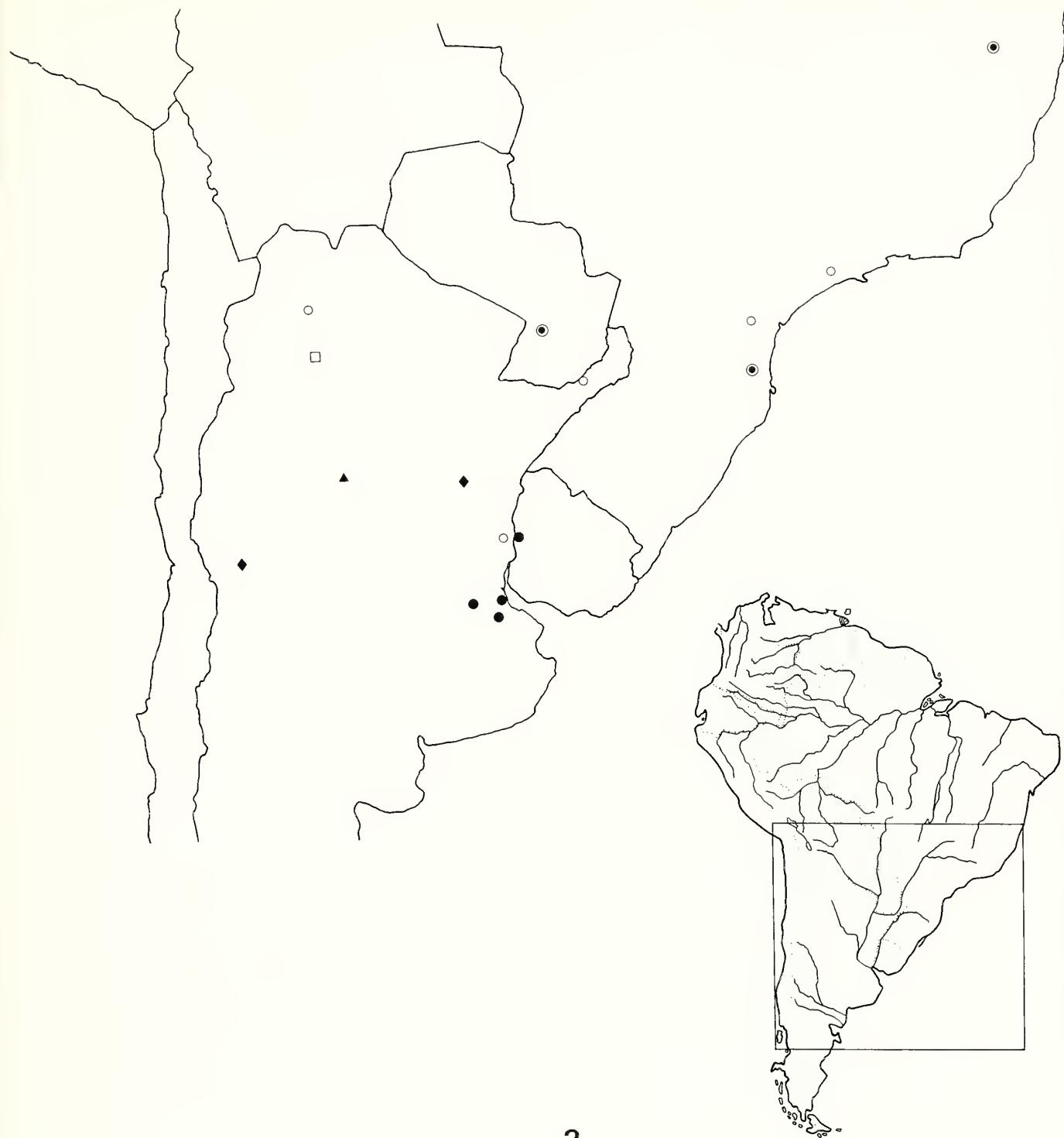
DIAGNOSIS

Heimbra parallela may be separated from all the other known species of *Heimbra* by the evenly convex seventh tergum, the short marginal vein, and the parallel carinae on the margins of the antennal scrobes.

DESCRIPTION

FEMALE. Length 5.5 mm. Primarily black but with some minor exceptions as noted below.

Head with large, deep, closely spaced, umbilicate punctures over entire surface except clypeus and in antennal scrobes; punctures smooth and shiny within, each bearing a silvery-white hair that is more than 1.5 times diameter of puncture; interspaces between punctures appearing weakly, finely, granulose but still relatively shiny; antennal scrobes with surface distinctly transversely striate and shiny; clypeus glabrous; antennal scrobe about twice as long as maximum

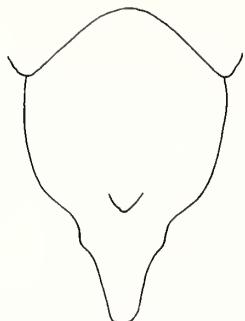


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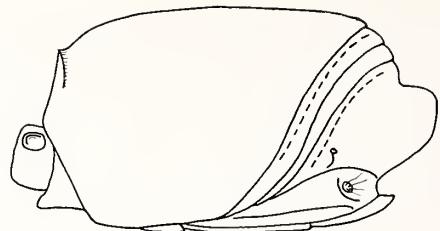
Map 2. Distribution of Heimbrinae in South America: *Heimbra acuticollis* (♦); *H. bicolor* (●); *H. nigra* (●); *H. pallida* (□); *H. parallela* (○); *Symbra cordobensis* (▲). Inset shows coverage of larger map.

distance between lateral carinae near antennal sockets and nearly equal to eye length; marginal carinae of scrobes nearly straight and parallel along lower half; interantennal lamella large; inner eye margins weakly diverging below. Antennal

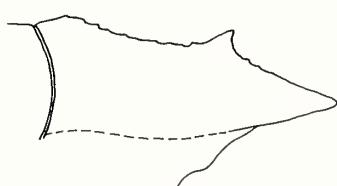
scape length nearly 3.5 times maximum width at base; relative dorsal lengths of pedicel and first three flagellar segments: 7:7:8:8. Mandible black apically, dark reddish brown basally.



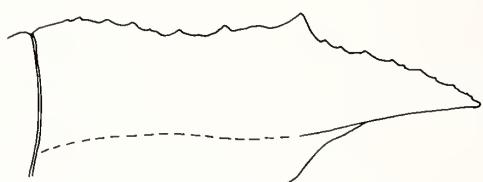
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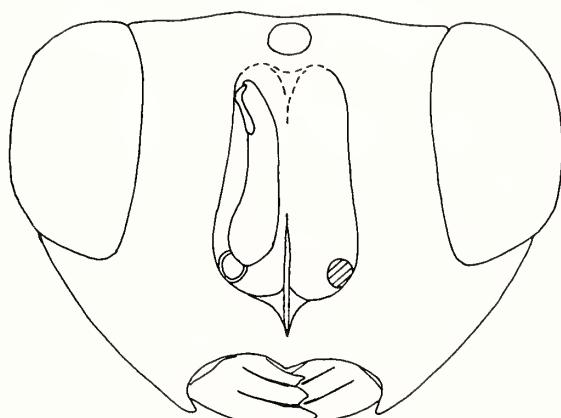
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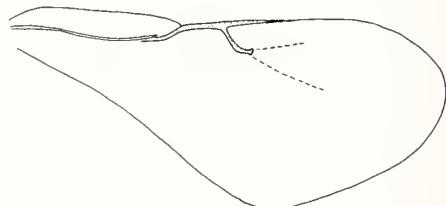
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26

Figures 21–26. *Heimbra* species. 21–24, *H. acuticollis*: 21, dorsal view of scutellum; 22, lateral view of scutellum; 23, front view of head; 24, lateral view of gaster. 25–26, *H. parallela*: 25, lateral view of scutellum; 26, forewing.

Punctuation and vestiture of thoracic dorsum similar to that of head except as follows: punctures tend to be somewhat larger and hairs more than twice longer than puncture diameter; puncture size variable, small punctures on pronotum anteriorly near meson and on mesoscutum anteriorly, larger punctures on apical portion of scutellum; pronotum in side view with dorsal outline slightly more strongly convex anteriorly than posteriorly; lateral carina of pronotal collar

strongly oblique to posterior margin; scutellum narrow, width slightly over 0.60 times length its dorsal prominence conspicuous and acute in a lateral view (Fig. 25); mesopleuron smooth and shiny along posterior margin (Fig. 5); propodeum posteriorly with two large, flat, smooth, shiny, subrectangular areolae lateral to large, shallowly depressed, irregularly sculptured diamond-shaped areola in middle.

Forewing veins dark brown; marginal vein short (measured

from angle on wing margin to base of stigmal vein), only slightly longer than stigmal vein; postmarginal vein indistinct apically, length 1.5–2.0 times length of marginal vein (Fig. 26). Legs primarily black but tarsi and ends of femora and tibiae light orange-brown.

Gastral terga laterally and ventrally umbilically punctate, punctures merging into large reticulations dorsally on tergum 2+3; punctures on terga 2+3, 4, and 5 very shallow and comparatively small; punctures on terga 6+7 and 8 large and as deep as on pronotal collar; all umbilicate punctures smooth and shiny within; area between reticulate ridges on dorsum irregular but very shiny; dorsum of tergum 2+3 medially, weakly concave, appearing medially flat in lateral view; posterior lateral margin of tergum 2+3 weakly sinuate, nearly straight in lateral view; convexity of tergum 6+7 nearly symmetrical in side view, posterior margin at meson not far in front of, but considerably ventrad of, corresponding part of anterior margin and convexity extending considerably caudad of posterior margin of tergum 2+3; tergum 6+7 with conspicuous keel along meson dorsally and posteriorly but lacking deep transverse groove; exposed portion of tergum 8 long, subequal to length of hind femur; tergum 8 with lateral ridge entire, not produced posteriorly into ventrally projecting broad spine.

MALE. Length 3.9–4.7 mm. Antennal scape without ocelloid spot. Similar to female as described above except: scutellum width 0.72–0.75 times length; tergum 8 without lateral ridges; visible parts of sterna 2–8 with punctuation similar to that of visible parts of terga 5–6; sternum 8 with short, barely evident lateral ridges instead of spines.

TYPE DATA

Holotype female: Salta, ARGENTINA, Feb. 14, 1951 (Ross and Michelbacher), in the California Academy of Sciences. Paratypes: 1♂, Pronunciamiento, Entre Ríos, ARGENTINA, Feb. 1965 (collector unknown; CNC); 1♂, Santa Anna, Misiones, ARGENTINA, no date (Dr. Cernosvitov; BMNH).

ETYMOLOGY

The specific name, Latin for parallel, refers to the parallel scrobal carinae.

DISTRIBUTION

Presently known only from Argentina and Brazil. Map 2.

DISCUSSION

In addition to the type series, we have seen one female from São Paulo, S.P., BRAZIL, Jan. 2, 1964 (V.N. Alin; AMNH) and one male from Curitiba-Villa Velho, Paraná, BRAZIL, Nov. 7, 1970 (J.W. Boyes; CNC). The female is very similar to the type. The male is likewise similar to the two paratypes, but is considerably larger, about 4.7 mm long compared to 3.9 and 4.2 mm for the two paratypes.

This species is most similar to *H. nigra*, and the male is especially similar since both lack an ocelloid spot on the antennal scape. Both sexes are readily separable from *H.*

nigra by the characteristic shape of tergum 6+7 and by the presence of a distinct tubercle on the scutellum.

Heimbra pallida, new species

Figures 7, 17

DIAGNOSIS

Heimbra pallida can be distinguished from all others in the South American species group by the ferruginous color, the long marginal vein, and the far anterior placement of the posterior margin of tergum 6+7.

DESCRIPTION

FEMALE. Length 3.3 mm. Primarily orange-brown with appendages palest and antennal scrobes, axillae, mesepisternum ventrally, tergum 2+3 dorsally, and tergum 6+7 caudally darkest.

Head with large, closely spaced, umbilicate punctures over entire surface except clypeus and in antennal scrobes; umbilicate punctures smooth and shiny within, each bearing a large, silvery-white hair whose length is nearly 1.5 times diameter of puncture; interspaces between punctures smooth and shiny except on vertex posteriorly where they appear weakly, finely granulose but still shiny; antennal scrobes with surface shiny but faintly, transversely striate; elypterus glabrous; antennal scrobes short, length slightly less than 1.5 times maximum distance between lateral carinae near antennal sockets and slightly less than 0.9 times length of compound eye; scrobes with marginal carinae weakly diverging along lower half; interantennal lamella small; inner eye margins nearly parallel. Antennal scape length about 3.5 times maximum width near base; relative dorsal lengths of pedicel and first three flagellar segments: 5:3:3:4.

Punctuation and vestiture of thoracic dorsum similar to that on vertex except puncture size varies as follows: smallest punctures on pronotum anteriorly and mesoscutum anteriorly, largest punctures on apical portion of scutellum; pronotum in side view with dorsal outline nearly evenly convex; lateral carina of pronotal collar weakly diverging ventrally from posterior margin; scutellum narrow, width slightly over 0.70 times length; dorsal prominence of scutellum weakly developed but with three distinct acuties visible in lateral view; mesopleuron smooth and shiny along posterior margin; propodeum with two large, flat, smooth, shiny subrectangular areas lateral to large, shallowly depressed, irregularly sculptured diamond-shaped area along anterior meson.

Wing veins dark brown; marginal vein long (measured from angle on wing margin to base of stigmal vein), nearly 1.6 times length of stigmal vein; postmarginal vein indistinct apically and 1.0–1.5 times length of marginal vein.

Gastral terga laterally and ventrally umbilically punctate, punctures merging into large reticulations dorsally on tergum 2+3; punctures on terga 2+3, 4, and 5 very shallow and relatively small, interspaces appearing granulose; punctures on tergum 6+7 and tergum 8 laterally as large and deep as

those on head; all umbilicate punctures smooth and shiny within; area between reticulate ridges on dorsum irregular but shiny; dorsum of tergum 2+3 broadly concave, appearing flat in lateral view; posterior lateral margin of tergum 2+3 strongly, broadly concave in lateral view; convexity of tergum 6+7 asymmetrical in side view, posterior margin at meson far in front of corresponding part of anterior margin and scarcely projecting caudad of posterior margin of tergum 2+3; tergum 6+7 lacking conspicuous keel along meson and deep transverse groove; exposed portion of tergum 8 less than 0.66 times length of hind femur; tergum 8 with lateral ridges pronounced and entire but not produced posteriorly into ventrally projecting broad spine.

MALE. Unknown but probably similar to female in most respects.

TYPE DATA

Holotype female: Trancas, Tucumán, ARGENTINA, Dec. 14, on foliage (USNM). The type is in the collection of the United States National Museum of Natural History, Washington, D.C.

DISTRIBUTION

Known only from Argentina. Map 2.

DISCUSSION

The long marginal vein of the forewing and the anterior position of the apical margin of tergum 6+7 will readily separate *H. pallida* from all species except *H. nigra*. From that species, *H. pallida* may be separated by the uniformly ferruginous color and the relatively broad scutellum. The color of *H. pallida* is similar to that of *H. acuticollis*, a species with the marginal vein short and with the apical margin of tergum 6+7 only slightly anterior to the anterior margin.

Heimbra nigra Subba Rao

Figures 6, 8, 16

Heimbra nigra Subba Rao, 1980 (1978):308; ♀.

DIAGNOSIS

Specimens of *H. nigra* can be separated from those of the other species in the South American species group by the combined characteristics of uniformly dark color, the long marginal vein of the forewing and by the apical margin of tergum 6+7 being situated much anterior to the anterior, dorsal margin (Fig. 8). The latter two features are shared with *H. pallida*, an entirely ferruginous species with broader scutellum.

The previously undescribed male is described below.

DESCRIPTION

MALE. Length 3.5–4.15 mm. Integument black except following orange-brown parts: mandible, legs except coxae, and tergum 2+3 laterally.

Head with large, deep, closely spaced umbilicate punctures over entire surface except on clypeus and in antennal scrobes; umbilicate punctures smooth and shiny within, each bearing a long silvery-white hair whose length is less than 1.5 times diameter of puncture; interspaces between punctures appearing finely granulose but shiny; antennal scrobes with surfaces shiny but faintly, transversely striate; clypeus glabrous; antennal scrobes short, length less than 1.25 times maximum distance between lateral carinae near antennal sockets and 0.80 times length of eyes; scrobes with carinae nearly parallel along lower half; interantennal lamella small; inner eye margins weakly diverging below. Antennal scape length about 3.0 times maximum width near base; lacking ocelloid spot; relative dorsal lengths of pedicel and first three flagellar segments: 6:3:4:5.

Punctuation and vestiture of thoracic dorsum similar to that on head except both punctures and hairs average slightly larger with smallest anteriorly on pronotum and largest posteriorly on scutellum; pronotum in side view with dorsal outline evenly convex; lateral carina of pronotal collar strongly oblique to posterior margin; scutellum narrow, width 0.65 times length; scutellum in side view with dorsal prominence weak and lacking acute projections; mesepimeron smooth and shiny along posterior margin (Fig. 6); propodeum with two large, shiny, finely pitted, elevated areas adjacent to deep groove along meson.

Wing veins dark brown; marginal vein long (measured from angle on wing margin to base of stigmal vein), about 1.5 times length of stigmal vein; postmarginal vein indistinct apically, length 1.0–1.5 times length of marginal vein.

Gastral terga laterally and ventrally umbilically punctate, punctures merging into large reticulations dorsally on tergum 2+3; punctures on terga 2+3, 4, and 5 shallow and small compared to those on tergum 6+7, punctures on tergum 6+7 equivalent to those on pronotal collar; all umbilicate punctures smooth and shiny within; area between reticulate ridges on dorsum irregular but shiny; dorsum of tergum 2+3 broadly concave, appearing flat in lateral view; tergum 6+7 with convexity asymmetrical in side view, posterior margin at meson far in front of corresponding part of anterior margin and slightly projecting caudad of posterior margin of tergum 2+3; tergum 6+7 lacking conspicuous keel along meson and deep transverse groove; visible parts of sterna with punctuation similar to that on lateral parts of tergum 2+3; sternum 8 with two lateral, posteriorly directed, blunt spines.

TYPE DATA

The type of *H. nigra*, a female from Burzaco, Buenos Aires, Argentina, is in the British Museum (Natural History).

DISTRIBUTION

This species is known from Argentina and Uruguay. In addition to the type, we have seen the following specimens. Map 2.

ARGENTINA. Buenos Aires: 1♂, San Isidro, Mar. 1957 (J. Daguerre; USNM); 1♀, 8♂♂, Zelaya, Feb. 1957, Nov. 1958, Dec. 1962 (J. Daguerre; USNM).

URUGUAY. 1♂, Paysandu, no date (Silveira; USNM).

DISCUSSION

Subba Rao (1980) gives the length of the holotype female as 2.3 mm. The one female, other than the holotype, that we have seen is appreciably larger, 3.8 mm. Otherwise it is very similar to the holotype. In the original description Subba Rao stressed the absence of a dorsal tubercle or elevation on the scutellum and this character is consistent in the specimens we have studied.

The male is immediately separable from those of *H. opaca* and *H. bicolor* by the lack of an ocelloid spot on the lower surface of the antennal scape. In this, it is similar to the male of *H. parallela*, from which it is separable by the lack of a dorsal prominence on the scutellum and the shape of tergum 6+7.

Heimbra acuticollis Cameron

Figures 21–24

Heimbra acuticollis Cameron, 1909:434; ♀.

This species is known with certainty only from two type specimens in the BMNH.

The color is largely ferruginous, with irregular areas of blackish on the face, the thoracic dorsum, and the side of the gaster blackish. Color aside, *H. acuticollis* most closely resembles the type female of *H. parallela*; i.e., the marginal vein is short and the anterior, dorsal margin of gastral tergum 6+7, in profile view, is only a little distad of the posterior margin (Fig. 24). However, the scrobal carinae are not parallel, the scutellar process is more slender, with the posterior one-half more depressed, as seen in profile (Fig. 22). The type is redescribed below.

DESCRIPTION

FEMALE. Length about 4.6 mm. Color primarily ferruginous, but head mostly blackish, with ferruginous mandibles, side of upper frons, center of vertex, and gena; lateral and anteromedial spots on mesoscutum, irregular axillar blotch, median blotch on scutellar process, mesopleuron (except ferruginous spot below tegula), metapleuron, and propodeum blackish; large irregular blotch on side of tergum 2+3 blackish.

Head with large deep closely spaced umbilicate punctures over all surfaces except clypeus and antennal scrobes; punctures smooth and shiny within, each bearing a silvery-white hair that is 1.2–1.5 times longer than a puncture diameter; interspaces between punctures finely granulose and slightly shiny; surface of antennal scrobe slightly shiny and apparently finely transversely striate (not readily visible because of position of antennal scapes); interantennal lamella large;

inner eye margins weakly diverging below; antennal scape length about 4.3 times basal width; relative dorsal lengths of pedicel and first three flagellar segments: 12:8:8:8.

Punctuation and vestiture of thorax similar to that of head except as follows: punctures tend to be a little larger and hairs about twice longer than a puncture diameter; puncture size variable, punctures smallest anteromesially on pronotum and mesoscutum, largest on apical portion of scutellum; pronotum, in lateral view, convex, highest at scutal margin; lateral carina of pronotal collar weakly oblique to posterior margin; scutellum broad, width about 0.65 times median length; dorsal prominence conspicuous and acute in profile (Fig. 22), apex narrowly truncate in dorsal view (Fig. 21); mesopleuron smooth and shiny along posterior margin (about as in Fig. 5); posterior face of propodeum not visible. Metacoxa black, remainder of hind leg ferruginous.

Wing vein dark brown; marginal vein (measured from angle on wing margin to base of stigmal vein) subequal to length of stigmal vein; postmarginal vein distinct for distance about equal to length of marginal vein.

Gastral terga laterally and ventrally umbilically punctate, punctures merging into large reticulations dorsally on tergum 2+3; punctures on terga 2+3, 4, and 5 very shallow and smaller than on pronotal collar; punctures on terga 6+7 and 8 a little larger and deeper, but obscured by roughened integument between punctures; all umbilicate punctures smooth and shiny within; area between reticulate ridges on dorsum irregular but very shiny; dorsum of tergum 2+3 medially, weakly concave, appearing nearly flat in lateral view; posterior lateral margin of tergum 2+3 weakly sinuate, nearly straight in lateral view; convexity of tergum 6+7 nearly symmetrical in side view, posterior margin (in profile) not far in front of, but considerably ventrad of, corresponding part of anterior margin and convexity extending considerably caudad of posterior margin of tergum 2+3; tergum 6+7 with conspicuous keel along meson dorsally and posteriorly but lacking deep transverse groove (Fig. 24); exposed portion of tergum 8 long, subequal to length of hind femur; tergum 8 with lateral ridge entire; not produced posteriorly into ventrally projecting broad spine.

DISCUSSION

Two syntypes of *H. acuticollis* are in the BMNH collection. Of these, the one in best condition is here designated and appropriately labeled as the lectotype; the second specimen is the lectoparatype.

The only additional female, other than the types, that we have seen is larger than the types, length 5.1 mm, and is almost wholly ferruginous, without the conspicuous darkened areas on the head and thorax. The gaster is distinctly brownish-ferruginous over most of tergum 2+3 and on the exposed portions of the remaining terga. This specimen differs most conspicuously from the types in the profile of the scutellar process; in profile the posterior one-half is sharply depressed below the level of the basal one-half and the erect tubercle is absent. Although this specimen may represent still

another species, it would be unwise to describe this specimen as such on such meager evidence.

DISTRIBUTION

Known only from Argentina. Map 2.

SPECIMENS EXAMINED

ARGENTINA. 2♀, Mendozoa (lectotype and lectoparatype no. 5.351b, BMNH); 1♀, Estancia La Noria, Río San Javier, Santa Fe, Jan. 2, 1912 (G.E. Bryant; BMNH).

Symbra, new genus

Type-species: *Symbra cordobensis*, new species.

DIAGNOSIS

This genus can be easily recognized from all the other members of the subfamily by its slender, eleven-segmented antenna, the broad, laterally convex scutellum (Fig. 13) and in the female by its relatively long ovipositor (Fig. 14) and all features associated with it.

DESCRIPTION

FEMALE. Head subcircular in front view, malar area conspicuously convex, in side view subrectangular, face distinctly angled near antennal insertions; length of head (measured along meson from apex of clypeus to top of vertex) nearly 0.80 times width; antennal scrobe long and narrow. Antenna long and slender, eleven-segmented; scape long, reaching median ocellus; pedicel and all flagellar segments except first, longer than broad; first flagellar segment broader than long and asymmetrical, dorsal length greater than ventral length; diameter of second segment subequal to first but length more than 4.0 times first; subsequent flagellar segments gradually decreasing in length and diameter; club undivided, subequal to ninth segment. Scutellum width nearly 0.85 times length; lateral margin in dorsal view more or less convex, subapical margins strongly converging.

Anterior lateral margin of gastral tergum 2+3 narrowly rounded where it overlaps sterna 2 and 3+4; tergum 6+7 acutely convex in lateral profile and without deep transverse groove; tergum 8 with visible portion nearly equal to length of remainder of gaster and apex situated posterior to most caudad portion of tergum 6+7; ovipositor sheaths long.

MALE. Unknown but presumably very similar to female as in *Heimbra* males.

DISCUSSION

This genus at present contains only a single species, *Symbra cordobensis*, which has been taken near Dean Funes in Argentina. *Symbra* is undoubtedly very closely related to *Heimbra* as can be seen by the many shared characters listed in the subfamily and species descriptions. This affinity is particularly conspicuous between it and the species of *Heimbra*

from South America as indicated above in the discussion under *Heimbra*.

Symbra cordobensis new species

Figures 13, 14, 21

DIAGNOSIS

Same as for the genus.

DESCRIPTION

FEMALE. Length 4.8 to 4.9 mm. Primarily black but tegula, ventral portion of gaster, and all appendages except antenna reddish-brown.

Head with large, closely spaced, umbilicate punctures over entire surface except clypeus and antennal scrobes; umbilicate punctures smooth and shiny within, each bearing a long, silvery-white hair whose length is about 1.5 times diameter of puncture; interspaces between punctures appearing weakly, finely granulose but still shiny; antennal scrobes with surface conspicuously transversely striate and shiny; clypeus glabrous; antennal scrobes very long, length over 2.5 times maximum distance between lateral carinae near antennal sockets and somewhat longer than eyes; scrobes with lateral carinae strongly diverging along lower half; interantennal lamella large; inner eye margins weakly convex and diverging below. Antennal scape long, extending to median ocellus, length nearly 7.0 times maximum width near base; relative dorsal lengths of pedicel and first three flagellar segments: 7:4.5:17:16.

Punctuation and vestiture of thoracic dorsum similar to that of head except punctures tend to be somewhat larger and possess slightly longer hairs; punctures and hairs smallest on pronotum anteriorly and largest on scutellum posteriorly; pronotum in lateral view with dorsal outline evenly convex; lateral carinae of pronotal collar weakly developed but strongly oblique to posterior margin; scutellum wide, width 0.85 times length; dorsal prominence of scutellum conspicuous and acute in lateral view; mesopleuron smooth and shiny along posterior margin; propodeum dorsally with large, strongly carinate square, diagonally on meson, otherwise scrobiculate with general surface shiny. Legs with coxae and tibiae darkest, tarsi lightest.

Wing veins light brown; marginal vein long (measured from angle in wing margin to base of stigmal vein), nearly twice length of stigmal vein; postmarginal vein apically indistinct, length 1.25–1.50 times length of marginal vein.

Gastral tergum 2+3 laterally umbilically punctate, punctures most distinct anteriorly and least distinct posteriorly while merging into large reticulations on dorsal surface; umbilicate punctures and dorsal reticulations with inner surfaces smooth and shiny; posterior margin of terga 2+3, 4, and 5 appearing weakly, irregularly granulose; tergum 6+7 and most of 8 somewhat more coarsely punctured than preceding two; ventral margin of tergum 8 finely reticulate; dorsum of tergum 2+3 weakly concave medially, appearing flat in lateral view; posterior lateral margin of tergum 2+3 weakly convex in lateral view; tergum 6+7 acutely convex in lateral view, posterior margin at meson well behind anterior margin and

apex of convexity projecting far caudad of posterior margin of tergum 2+3; tergum 6+7 without conspicuous keel on meson or conspicuous transverse groove; exposed portion of tergum 8 very long, more than twice length of hind femur; tergum 8 with lateral ridge entire, not produced posteriorly into ventrally projecting broad spine.

MALE. Unknown but probably like female in most pertinent characters described above.

TYPE DATA

Holotype female and one paratype: 5 mi. N Dean Funes, Cordoba, ARGENTINA, Feb. 8, 1951 (Ross and Michelbacher; CAS); the holotype is in the collection of the California Academy of Sciences, San Francisco, and the paratype is in the Natural History Museum of Los Angeles County. Map 2.

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CONTRIBUTIONS IN SCIENCE

CONTRIBUTIONS TOWARD A REVISION OF THE NEW WORLD
NOMADINE BEES. A PARTITIONING OF THE GENUS
NOMADA (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling



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

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CONTRIBUTIONS TOWARD A REVISION OF THE NEW WORLD NOMADINE BEES. A PARTITIONING OF THE GENUS *NOMADA* (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling¹

ABSTRACT. The higher classification of the New World representatives of the cleptoparasitic bee genus *Nomada* is reexamined. As a result, I propose to divide *Nomada* into three genera: *Nomada* Scopoli, *Centrias* Robertson, and *Hypochrotaenia* Holmberg.

The New World genus *Hypochrotaenia* consists of three subgenera: *Hypochrotaenia* s. str. (=*Nomadosoma* = *Polybiapis*), *Micronomada* (=*Cephen*), and *Aphelonomada* (n. subg.; type-species, *Nomada cruralis* Moure).

No subgenera are recognized within *Centrias* (=*Nomadula*, N. SYN.), an exclusively Nearctic genus.

Within the Holarctic genus *Nomada* six subgenera are recognized: *Nomada* s. str. (=*Heminomada* = *Xanthidium* = *Phor* = *Gnathias*, all N. SYN.), *Holonomada*, *Laminomada*, *Pachynomada*, *Nomadita* (=*Callinomada*, N. SYN.), and *Phelonomada* (n. subg.; type-species, *N. belfragei* (Cresson)).

A key is given for the separation of the genera of Nomadini present in North America.

IN MEMORIAM P.H. TIMBERLAKE 1883–1981

This Contribution is dedicated to the memory of the late P.H. Timberlake in recognition of his many years of invaluable contributions to the systematics of the bees of North America. The present study was begun as a cooperative effort with Tim and it is appropriate that this first part honor an esteemed colleague.

INTRODUCTION

Nomada has hitherto been recognized as a large genus of usually brightly marked, wasp-like anthophorid bees. All species are presumed parasitoids in nests of other bees; females lack all modifications for collecting and transporting pollen. Although most abundant, in numbers of species, in the Holarctic Region, the genus extends as far south as Argentina in the New World. In the Old World there are species in northern Australia, the Solomon Islands and the Philippine Islands, and Cape Province, South Africa.

In general, the sanctity of *Nomada* as a single, very large

genus has never been seriously questioned. A few species that clearly did not belong here were removed to such genera as *Melanomada* (Cockerell, 1903b) and *Hesperonomada* (Linsley, 1939) in the New World and *Acanthonomada* (Schwarz, 1966b) in the Old World. Within the very extensive Old World fauna no subgenera have been recognized. However, *Nomadita* Mocsáry, usually treated as a synonym of *Nomada*, is equivalent to the New World subgenus *Callinomada*. In the New World, Robertson (1903) proposed to divide *Nomada* into seven genera, but has not been followed by later systematists. Most recent work, such as that of Mitchell (1962), has adhered to the concept of a single genus with 11 subgenera, most of them hazily defined.

GENERAL SYSTEMATICS

The vast majority of cleptoparasitic bees belong to the subfamily Nomadinae, a very large and complex assemblage of approximately 45 genera arrayed within 13 tribes. Despite the extreme diversity of the Nomadinae, the group appears to be a monophyletic one (Stephen, Bohart, and Torchio, 1969; Rozen, Eickwort, and Eickwort, 1978; Michener, 1979). The Nomadinae attain their greatest diversity in the New World; six tribes and 24 genera are exclusive to the New World; six tribes and three genera are shared with the Old World. In contrast, only one tribe (Ammobatoidini) is limited to the Old World, as are 13 genera, mostly within the Ammobatini.

Based on studies of the mature larvae, Rozen, Eickwort, and Eickwort (1978), have examined group relationships within the New World tribes. Their results, derived through cladistic analyses, corroborate the distinctness of the various groups, as well as the apparent monophyly, of the subfamily Nomadinae.

Warncke (1977, 1982) proposed to drastically revise the

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Table 1. Host species of *Hypochrotaenia* and *Centrias*.

| Parasitoid | Host | Authority |
|--|--|---|
| <i>Hypochrotaenia</i> , subg. <i>Micronomada</i> : | | |
| <i>cubensis</i> (Cresson) | <i>Exomalopsis globosa</i> (Fabricius) | Raw, 1977 |
| <i>cubensis</i> (Cresson) | <i>E. similis</i> (Cresson) | Raw, 1977 |
| <i>formula</i> (Viereck) | <i>Agapostemon texana</i> Cresson | Eickwort & Abrams, 1980 |
| <i>gutierreziae</i> (Cockerell) | <i>E. crenulata</i> Timberlake | Parker, 1984 |
| <i>suavis</i> (Cresson) | <i>Nomia melanderi</i> Cockerell | Bohart, 1970 |
| species? | <i>E. solani</i> Cockerell | Linsley, 1954 |
| <i>Hypochrotaenia</i> , subg. <i>Hypochrotaenia</i> : | | |
| <i>pilipes</i> (Cresson) | <i>E. globosa</i> (Fabricius) | Raw, 1977 |
| <i>pilipes</i> (Cresson) | <i>E. similis</i> (Cresson) | Raw, 1977 |
| <i>tomentifera</i> (Ducke)? | <i>E. aureopilosa</i> Spinola | Zucchi, 1973 |
| <i>Centrias</i> : | | |
| <i>articulata</i> (F. Smith) | <i>A. radiatus</i> (Say) | Eickwort & Abrams, 1980 |
| <i>articulata</i> (F. Smith) | <i>A. virescens</i> (Fabricius) | Eickwort & Abrams, 1980 |
| <i>crotchii</i> (Cresson) | <i>Andrena prunorum</i> Cockerell | NEW RECORD (pers. obs. & pers. comm. S.L. Buchmann & J. Cane) |

higher classification of the bees. He (1977) recognized only two families: Andrenidae (with subfamilies Colletinae, Halictinae, and Andreninae) and Apidae (with subfamilies Melittinae, Nomadinae, Anthophorinae, Apinae, Ceratinae, and Megachilinae). Some modification was made in 1982: the Apidae acquired an additional subfamily, the Dasypodinae, and the Anthophorinae apparently were merged with the Melittinae. The Nomadinae, in Warncke's concept, include all cleptoparasitic anthophorids and are asserted to be closely allied with the Dasypodinae. Warncke's proposals are unconvincing and are based on character states of a few selected structural apomorphies that clearly evolved independently many times. The proposed classification has the effect of uniting very disparate groups on the basis of superficial similarities. His conclusions are rejected here.

The principal tribe, in terms of both distribution and diversity, is the Nomadini, with 12 genera. Ten of these genera are exclusive to the New World. The genus *Nomada* is Holarctic and one genus (*Acanthonomada* Schwarz, 1966b) is limited to the eastern Mediterranean region. Of the strictly New World genera, six are found only in the Nearctic and three are wholly Neotropic; only *Hypochrotaenia* is present in both regions.

Hypochrotaenia, with three subgenera, ranges from Argentina to southern Canada and its distribution includes the Antilles. The nominate subgenus is largely South American, but does range into the extreme southern United States (the lower Rio Grande Valley of Texas) and throughout the Antilles to Cuba. One subgenus (*Aphelonomada*) is confined to Cuba. The subgenus *Micronomada* is primarily North Amer-

ican but is present in the northern Antilles and in South America to Argentina.

The principal hosts of *Hypochrotaenia* appear to be the Exomalopsini, the pollen-collecting group apparently most closely related to the nomadines. At least some species of *Micronomada* have retained the primitive cleptoparasitism in exomalopsine nests, but others switched to halictid hosts (see Table 1).

The related genus *Centrias* is confined to North America. Some species are inquilines in nests of halictids and others in nests of *Andrena* (Table 1). Like *Nomada*, *Centrias* appears to be a derivative of *Hypochrotaenia* through *Micronomada*.

Nomada is probably derived from *Hypochrotaenia* (*Micronomada*), possibly by way of such groups as *Phelonomada*, *Nomadita*, and *Pachynomada*. Among the New World *Nomada*, known hosts are mostly species of *Andrena*, but apparently do include species of *Halictus* (Table 2). *Phelonomada* may be cleptoparasitic on halictids (*Agapostemon* or *Nomia*). Some Old World species of *Nomada* parasitize other genera of bees (*Halictus*, *Eucera*, *Panurgus*: Perkins, 1919; *Melitta*, *Colletes*: Brauns, 1930), but *Andrena* seems to be the host for most species (Perkins, 1919).

Once cleptoparasitism of *Andrena* "... arose in the Nearctic region, *Nomada* had open to it an enormous trophic and geographic opportunity. The Holarctic distribution of various groups of *Nomada* indicates that the intercontinental dispersal occurred under more mild climates than the present, probably when the Bering Strait area was temperate and perhaps across the North Atlantic in the Paleogene" (Michener, 1979).

Table 2. Host species of Nearctic *Nomada*.

| Parasitoid | Host | Authority |
|----------------------------------|---------------------------------------|---------------------------|
| subg. <i>Nomada</i>: | | |
| <i>annulata</i> F. Smith | <i>Andrena macra</i> Mitchell | Hurd, 1979 |
| <i>crudelis</i> Cresson | <i>A. obscuripennis</i> F. Smith? | Hurd, 1979 |
| <i>imbricata</i> F. Smith | <i>Halictus rubicundus</i> (Christ)? | Hurd, 1979 |
| <i>imbricata</i> F. Smith | <i>A. vicina</i> F. Smith | Packard, 1868 |
| <i>morrisoni</i> Cresson | <i>A. irana</i> Cockerell | Hurd, 1979 |
| <i>obliquella</i> Fowler | <i>A. suavis</i> Timberlake | Linsley & MacSwain, 1959 |
| <i>obliterata</i> Cresson | <i>A. vicina</i> F. Smith | Packard, 1868 |
| <i>obscurella</i> Fowler | <i>A. complexa</i> Viereck | Linsley & MacSwain, 1955a |
| <i>obscurella</i> Fowler | <i>A. caerulea</i> F. Smith | Linsley & MacSwain, 1959 |
| <i>opacella</i> Timberlake | <i>A. caerulea</i> F. Smith | Linsley & MacSwain, 1959 |
| <i>opacella</i> Timberlake | <i>A. suavis</i> Timberlake | Linsley & MacSwain, 1959 |
| <i>rhodalis</i> Cockerell | <i>A. cleodora</i> Viereck | NEW RECORD |
| <i>rubrica</i> Provancher | <i>A. prunorum</i> Cockerell | NEW RECORD |
| <i>vallesina</i> Cockerell | <i>A. irana</i> Cockerell ? | Hicks, 1934 |
| “sp. A” | <i>Halictus ligatus</i> Say | Rozen, 1966 |
| “sp. C” | <i>A. bisalicis</i> Viereck | Rozen, 1966 |
| “species” | <i>A. morrisonella</i> Viereck | Rozen, 1977 |
| subg. <i>Holonomada</i>: | | |
| <i>edwardsii</i> Cresson | <i>A. perimelas</i> Cockerell | Linsley & MacSwain, 1955b |
| subg. <i>Pachynomada</i>: | | |
| undescribed species | <i>A. helianthi</i> Robertson | Parker & Bohart, 1983 |
| undescribed species | <i>A. haynesi</i> Viereck & Cockerell | Parker & Griswold, 1983 |
| subgenus unknown: | | |
| “sp. B” | <i>A. flexa</i> Malloch | Rozen, 1966 |

In preparation for a revisionary study of the New World *Nomada*, I have redefined the various groups recognized by previous authors. It appears now that *Nomada* consists of three major phyletic lines treated here as discrete genera. While maintaining an overall similarity to one another, they are easily separable in several details.

The Neotropical *Hypochrotaenia*, originally described as a genus, was found to be possibly identical to the Nearctic *Micronomada*, and has priority over it. This is a moderately large group, with numerous species in the Neotropics and seems to be exclusively New World in distribution.

The second genus includes the two erstwhile subgenera *Centrias* and *Nomadula*. *Centrias* is a small group and seems to be limited to the Nearctic Region.

All remaining groups belong to the redefined genus *Nomada*, with the previously described subgenera *Gnathias*, *Phor*, *Heminomada*, *Holonomada*, *Laminomada*, *Pachynomada*, and *Nomadita*. This genus accommodates the majority of the Nearctic species and is abundantly represented in the Old World.

In redefining the subgenera I recognize only those based on more than a single characteristic. If subgenera were based on a single, unique feature it would be possible to recognize

many more than is done here, but to no practical purpose. Although they would represent natural species groups, most would consist of only one or a few closely related species.

A given apomorphy, such as a spinose procoxa, may occur sporadically; those species possessing this particular characteristic are not necessarily related. Unless a number of features, and usually not those utilized in species level taxonomy, can be correlated, I am not inclined to accord these groups any formal status. By application of this principle it is ironic that *Gnathias*, one of the few North American subgenera with heretofore unquestioned validity, must be placed in synonymy.

I recognize the following:

- genus *Hypochrotaenia* Holmberg
- subg. *Micronomada* Cockerell & Atkins
 - = *Cephen* Robertson
- subg. *Hypochrotaenia* Holmberg
 - = *Nomadosoma* Rohwer
 - = *Polybiapis* Cockerell NEW SYNONYMY
- subg. *Aphelonomada* new subgenus
- genus *Centrias* Robertson
 - = *Nomadula* Cockerell NEW SYNONYMY

genus *Nomada* Scopoli
 subg. *Nomada* Scopoli
 = *Gnathias* Robertson NEW SYNONYMY
 = *Phor* Robertson NEW SYNONYMY
 = *Heminomada* Cockerell & Atkins NEW SYNONYMY
 = *Xanthidium* Robertson (not Ehrenberg) NEW SYNONYMY
 subg. *Holonomada* Robertson
 subg. *Laminomada* Rodeck
 subg. *Pachynomada* Rodeck
 subg. *Nomadita* Mocsáry
 = *Callinomada* Rodeck NEW SYNONYMY
 subg. *Phelonomada* new subgenus.

The numerous species here assigned to *Hypochrotaenia* share an overall similarity of habitus and this genus is probably monophyletic. Superficially, the species resemble one another in that they are usually blackish, sometimes partially or wholly replaced by ferruginous, and with conspicuous whitish to yellow maculations. The integument is smooth to polished between deep, distinctly separated punctures; many species, however, are very finely and sparsely punctate, especially on the thorax.

Females of *Hypochrotaenia* always lack a paraocular ridge or carina, always present in *Centrias* and *Nomada* (except subgenus *Phelonomada*). In both sexes, the first flagellar segment is at least as long as the second, and the male flagellar segments are always devoid of spines or tubercles. In both sexes, the procoxa has an inner, apical spine or tooth, though this has been lost in a few species. Most *Centrias* and a few *Nomada* also possess a procoxal spine.

Hypochrotaenia is also characterized by the subangulate to angulate anterior margin of the side of the pronotum (Fig. 5), a feature shared with species of *Centrias*. In *Nomada*, the margin of the pronotum is evenly convex (Fig. 64). The characteristic male genital structures, lack of a patterned subgenital brush, digitiform inner dorsal lobe of the gono Coxite, etc. are discussed in the section on terminology; see also Figs. 11–14.

The species comprising the genus *Centrias* are united by one unusual feature: the protuberant upper portion of the metapleuron; the protuberant area is crossed by a sharp ridge or carina (Fig. 65). In some species the ridge is lamelliform and deflected downward. In a few small species the protuberance and ridge are greatly reduced. Although the metapleuron is uniformly simple in *Nomada*, it is slightly produced and submarginate in a few Neotropical *Hypochrotaenia*.

Females of *Centrias* are easily separated from those of *Hypochrotaenia* by the presence of a distinct paraocular carina. The clypeus of *Centrias* species is moderately protuberant and the paraocular area, between the clypeus and the paraocular carina is concave. In species of *Hypochrotaenia*, if the clypeus is somewhat convex, the paraocular area usually is also convex.

In addition to the presence of a metapleural prominence, *Centrias* females are separable from those of *Nomada* by the presence of procoxal spines. Procoxal spines are present in

a few species of *Nomada*, including those in the aberrant subgenus *Phelonomada*; both sexes in this subgenus are unusually robust, with distinct punctures separated by shiny interspaces, the females lack a paraocular carina, both sexes have a simple metapleuron, and males lack flagellar spines and modified subgenital brush. A few rare species of *Nomada* s. str. also have short procoxal denticles but possess none of the other features of *Centrias* in either sex.

Males of *Centrias* rarely have the middle flagellar segments simple; usually, at least segment 3 is spinose, and subsequent segments may be spinose or bispinose. Less often, segments 3–7 may bear tubercles or narrow ridges. In males of most species of *Centrias*, the hairs that comprise the subgenital brush are arranged in characteristic patterns; in both *Hypochrotaenia* and *Nomada* the hairs are suberect to erect and randomly dispersed.

The genus *Nomada*, as here defined, includes those species in which the metapleuron is not protuberant above, the female possesses a distinct paraocular ridge (except in the subgenus *Phelonomada*), the anterior margin of the pronotum is evenly convex, the procoxa has no outer carina and only very rarely bears an inner, apical spine or tooth, the male subgenital brush consists of suberect to erect hairs of about the same length that are randomly distributed over the disc of sternum 7, and the inner dorsal lobe of the gonocoxite is short and broad.

The acquisition of a procoxal spine has apparently occurred several times in *Nomada*, being present in all three species of *Phelonomada*, and two or three species of *Nomada* s. str. that do not appear to be closely related to one another. This apomorphy is an acquisition that is independent of the species of *Hypochrotaenia* and *Centrias*.

It is my view that the above grouping represents three major lineages and that each is probably monophyletic. Whether or not the latter is true remains to be determined by a major reexamination of the characters of the entire subfamily Nomadinae and of the Exomalopsinae, the presumed ancestral group. Pending such a review, the classification proposed here will provide a previously nonexistent framework.

Following the discussion of each genus and subgenus is a listing of the New World species-group names presently assigned to that taxon. Those pertaining to exclusively Neotropical (including the Antilles) forms are marked with an asterisk.

IMMATURE STAGES

The larvae of parasitic anthophorids, as a whole, have been the subject of several papers by Rozen (1966, 1969, 1977), Rozen, Eickwort, and Eickwort (1978), Rozen and McGinley (1974), and Ehrenfeld and Rozen (1977). Michener (1953) described larvae of *N. fowleri*; the same specimens were redescribed by Rozen (1966), as well as those of several additional species, including that of *Hypochrotaenia* (*Micronomada*) *suavis*. The larva of *H. suavis*, as described by Rozen, is very similar to that of *N. fowleri*, and the significance of the few differences noted is uncertain. Rozen (1966) provided

a key to the known postdefecating larvae of Nomadinae, and McGinley (1981) included the Nomadinae in a key to mature apoid larvae.

TERMINOLOGY

For the most part, the morphological terminology utilized in the keys and descriptions is conventional, based on that of Michener (1944). Explanation is necessary for a few characters.

The *paraocular ridge* is present in females of all nomadine genera except *Hypochrotaenia*. In all these genera, the ridge, and its lower end, extends across the front of the malar area between the lower end of the eye and the apicolateral angle of the clypeus (Figs. 19, 25). The paraocular area, immediately adjacent to the ridge, is more or less definitely concave. In *Hypochrotaenia* (and subg. *Phelonomada* of *Nomada*) the paraocular ridge is low and broad along the inner eye margin and disappears altogether at its lower end; the junction of the malar area and the paraocular area is uniformly convex or, rarely, broadly subangulate (Figs. 1, 3).

The relative lengths of the first several segments of the flagellum are sometimes useful in characterizing the various taxa. The first flagellar segment is conspicuously shorter on one side than the other; the *minimum length* of this segment is measured on this shorter side. The *maximum length* of the second segment is measured *on the same side* as minimum length of the first segment.

Several characteristics of the pronotal collar are used in defining the various groups. In some groups, such as *Micronomada*, it may be swollen and with subhemispherical lateral lobes. More commonly it is compressed and subcarinate or ridged across the middle and with distinctly angulate lateral lobes. This character is, however, sufficiently variable that it is unreliable.

On the side of the pronotum there is a more or less sharply defined vertical ridge immediately behind the anterior margin, that extends dorsad onto the neck of the pronotum. Except in *Hypochrotaenia* this *lateral ridge* extends mesad on the pronotal neck, becoming evanescent before attaining the midline; a distinct groove usually separates the lateral ridge from the base of the pronotal collar. In *Hypochrotaenia* the upper end of the lateral ridge commonly turns toward the base of the pronotal collar near the lateral lobe; this is especially clear in *Hypochrotaenia* s. str. in which the lateral ridge may become cariniform.

In the genera *Centrias* and *Hypochrotaenia* the anterior rim of the pronotum, at a point approximately directly anterior to the lower margin of the posterior lobe of the pronotum, is more or less abruptly angulate (Fig. 5). In *Nomada* (except *Nomadita*) the anterior rim is evenly rounded, very rarely weakly subangulate (Fig. 64).

The upper end of the metapleuron is more or less sharply protuberant in *Centrias* (Fig. 65), but not in *Hypochrotaenia* and *Nomada* (Fig. 66). This metapleural prominence is crossed by a sharp cariniform ridge which, posteriorly, joins the lateral arm of the metanotum. In some species this ridge may be broad, lamelliform, and sharply deflected ventrad.

Only in the subgenera *Holonomada* and *Laminomada* of

Nomada does the propodeum exhibit any group characteristic of interest. The side of the propodeum, mesad of the propodeal spiracle, is flat in all except these two subgenera when viewed in oblique profile. In a few species of *Holonomada* this area is sharply elevated, but in others (and in *Laminomada*) it is merely evenly convex.

The last visible sternite of the males of all groups bears numerous hairs that differ, in various ways, from those of the foregoing segments. These hairs comprise the *subgenital brush*. In most *Nomada* the hairs of the subgenital brush are dense, short, stiff and, when viewed in profile, more or less definitely inclined cephalad. In a few species they may be rather long and/or fully erect and/or slightly to strongly curled at the tips. The disc of the segment, in profile, is flat, more or less abruptly rounded distad.

In all but a few species of *Centrias* and *Hypochrotaenia*, the hairs of the subgenital brush are mostly long, fully erect, and distinctly curled; those at the sides are often curled toward the midline and those of the posterior middle curled cephalad so that a "basket" is formed. The profile of the segment may be flat or concave, but the apical margin is thin. In some species of *Centrias* the subgenital brush may be complex, composed of distinct clusters of quite long hairs which may be prostrate for much of their length.

The genitalic capsule of the male offers many characters of value in separating the various groups. In dorsal view, the gonocoxite is rather short and broad and the two segments are not contiguous basad. The area between the two gonocoxites is termed here the *median sinus* and the ratio of length to greatest width is a useful diagnostic feature.

The gonocoxite in *Nomada* (Fig. 30) and *Hypochrotaenia* (Fig. 13), has a more or less distinct inner, *dorsal lobe*; the lobe may be short and apically truncate or oblique (*Nomada*) or it may be elongate, digitiform and rounded distally (*Hypochrotaenia*). Between the dorsal lobe and the *outer lobe* is the *dorsal invagination*; the depth and width are useful characteristics. In *Centrias* (Fig. 24) the dorsal lobe and dorsal invagination are usually obsolescent.

In most *Nomada* the gonostylus is usually short and rather stout; in *Centrias* and *Hypochrotaenia* it is most commonly slender and elongate. A setose *basoventral lobe* is present on the gonostylus of most *Nomada* (Figs. 31, 37, 51), but absent in *Hypochrotaenia* (Fig. 12) and absent or poorly developed in *Centrias* (Fig. 24). In many *Nomada* there is, in addition, a cluster of short, flattened setae on the inner, basal margin of the gonostylus; no such *basal seta-cluster* is present in either *Centrias* or *Hypochrotaenia*.

In most groups of *Nomada* the gonostylus is thickly covered, on its distal portion, with long, often plumose, setae. These setae commonly are attenuated toward the apices and usually the attenuated portions are curled and/or sinuate (Fig. 30). Although setae may be abundant in *Centrias* and *Hypochrotaenia* they never attain the characteristic appearance of those of *Nomada*. More commonly the setae are short and straight and more sparse in these two genera.

The aedeagus is generally similar in all groups, but there are some differences, especially between species groups, in the dorsobasal lobes. The subgenus *Pachynomada* of *No-*

mada is unique in that the aedeagus has a distinct ventral hook (Fig. 49).

SYSTEMATICS

Following is a key to the North American genera of Nomadini. Although Michener (1954) indicated that such tribes as Osirini and Epeolini should be merged with Nomadini, for purposes of this key, Nomadini is as defined by Michener (1944). While the tribal characters given by Michener are not universally applicable, they do work for the North American fauna.

Michener (1944) defined the Nomadini as follows: "The scopa is absent, the basitibial plates are absent, and the jugal lobes of the posterior wings are very small. The pterostigma is rather large, almost always considerably broader than the distance from the inner margin of the prestigma to the costal margin. The marginal cell is conspicuously longer than the distance from its apex to the wing tip and pointed or narrowly rounded [broadly rounded in *Coelioxoides*]. The pygidial plate is present in both sexes. The seventh sternum [i.e., the sixth gastric sternum] of the female is subtruncate to bilobed at the apex, which is provided with a few to many coarse, spine-like setae."

Coelioxoides is a small Neotropical genus that ranges from central Mexico to Brazil. It is provisionally included within the Nomadini but probably belongs in a separate tribe. However, a new tribe in this complex would be premature and a complete reevaluation of all groups within the Nomadinae is needed.

KEY TO NORTH AMERICAN GENERA OF NOMADINI

- 1a. Thorax normal, maximum width about equal to height; median flagellar segments at least as broad as long, rarely broader; integument of head and thorax distinctly punctured, rarely vertex and dorsum of thorax almost impunctate; head and body maculate or not 2
 - 1b. Thorax flattened, maximum width nearly twice height; flagellum short, middle segments broader than long; integument smooth, polished, virtually impunctate; head and body immaculate *Paronomada*
 - 2a. Apex of marginal cell pointed and on wing margin or narrowly rounded and slightly removed from wing margin; third submarginal cell, when present, no larger than first; male with metatibial spurs; mesometapleural suture distinct 3
 - 2b. Apex of marginal cell broadly rounded and well removed from wing margin; third submarginal cell larger than first; male without metatibial spurs; mesometapleural suture absent *Coelioxoides*
 - 3a. Anterior and posterior basal angles of mandible almost equidistant from eye; maxillary palpus not more than half as long as galea, three- to six-segmented; male gonostylus rather long and slender; sixth gastric sternum of female produced posteriorly as a broad, acute or rounded, hairy process; seventh gastric sternum of female with a pair of small, slender apical lobes with a few coarse setae along margin 4
 - 3b. Anterior basal angle of mandible more distant from eye than posterior basal angle; maxillary palpus six-segmented, more than half as long as galea; male gonostylus short and robust (rarely slender); sixth gastric sternum of female truncate or bilobed at apex; seventh gastric sternum of female subtruncate or with a pair of broad, well-separated lobes provided with coarse, spine-like setae 6
- 4a. Apex of marginal cell acute, on wing margin; maxillary palp five- or six-segmented 5
 - 4b. Apex of marginal cell narrowly rounded and slightly bent from wing margin; maxillary palp three- or four-segmented *Triopasites*
 - 5a. Forewing with three submarginal cells; maxillary palp six-segmented; middle coxa as long as distance from summit to base of hind wing *Melanomada*
 - 5b. Forewing with two submarginal cells; maxillary palp five-segmented; middle coxa shorter than distance from summit to base of hind wing *Hesperonomada*
 - 6a. Gastric segments usually more or less conspicuously yellow to white maculate, without transverse pubescent fasciae; marginal cell acutely pointed on wing margin; sixth gastric sternum of female concealed, truncate or weakly bilobed at apex, with a few spine-like setae apicad; first gastric tergum projecting as transparent ventral flaps in dried specimens 7
 - 6b. Gastric segments immaculate, with transverse pubescent fasciae; apex of marginal cell slightly separated from wing margin, narrowly rounded; sixth gastric sternum of female exposed, bilobed, lobes margined with a row of spine-like setae; lateral lobes of first gastric tergum closely appressed to first sternum *Hexepeolus*
 - 7a. Upper end of metapleuron not protuberant and without transverse carina or lamella (Fig. 66); procoxa simple or, if spinose, then first flagellar segment equals or exceeds second or gastric terga are weakly and superficially punctate 8
 - 7b. Upper end of metapleuron protuberant, sharply marginate or lamellate along edge (Fig. 65); procoxa spinose or dentate; first flagellar segment conspicuously shorter than second; gastric terga sharply punctate (rarely punctures weak) *Centrias*
 - 8a. Procoxa seldom spinose. *Female*: Paraocular ridge present (except *Phelonomada*); anterior rim of pronotum narrow and evenly rounded at side, rarely subangulate or angulate (Fig. 64). *Male*: Gonostylus usually with basoventral setose lobe (Figs. 31, 44, 63); inner dorsal lobe of gonocoxite short and broad (Fig. 30), if somewhat elongate, outer lobe is short and broad and median sinus is broader than long *Nomada*
 - 8b. Procoxa usually spinose. *Female*: Paraocular ridge absent; anterior rim of pronotum broad, angulate or subangulate at side (Fig. 5) (rarely not, in which case upper end of lateral ridge turns dorsad onto lobe of collar). *Male*: Gonostylus without basoventral setose lobe (Fig. 12); inner dorsal lobe of gonocoxite digitiform (Figs. 13,

14), but if not, outer lobe very slender and median sinus is longer than broad (Fig. 11) *Hypochrotaenia*

Genus *Hypochrotaenia* Holmberg

DIAGNOSIS. Female without paraocular ridge; anterior rim of pronotum angulate or subangulate at side; procoxa usually spinose; minimum length of first flagellar segment equal to, or exceeding, maximum length of second; inner dorsal lobe of male gonocoxite usually digitiform, never short and broad, invagination deep; gonostylus of male without setose basoventral lobe.

DESCRIPTION. (A) Mandible without preapical tooth. (B) Paraocular ridge of female absent. (C) Minimum length of first flagellar segment equal to, or exceeding, maximum length of second. (D) Gena less than half as wide as eye in profile, posterior margin rounded. (E) Procoxa usually spinose or dentate at apex; outer carina present or absent. (F) Anterior rim of pronotum subangulate to angulate at side; pronotal collar somewhat swollen or narrow and with dorsal crest; lateral ridge at its upper end often turned toward pronotal collar. (G) Metapleuron simple or (rarely) protuberant and margined. (H) Metacoxa rounded above or compressed and sublamellate to lamellate. (I) Gastric terga almost always sharply and closely punctate; impunctate apical margins narrow to broad. **Male.** (J) Hairs of subgenital brush usually fully erect or with apices curled. (K) Inner dorsal lobe of gonocoxite usually digitiform, rarely another shape, but never short and broad; outer lobe elongate; invagination deep; median sinus longer than broad. (L) Gonostylus without setose basoventral lobe or inner, basal seta-cluster.

DISCUSSION. *Hypochrotaenia* was described by Holmberg (1886) for a single South American species. Cockerell (1916b) recognized that *Nomadosoma*, based on a Cuban species, could not be separated from *Hypochrotaenia*. That some Neotropical *Micronomada* should be placed in *Hypochrotaenia* was correctly noted by Rodeck (*in* Cockerell, 1949) and Michener (1954) treated all Panamanian species as members of *Hypochrotaenia*. Michener also enumerated the essential differences between *Hypochrotaenia* and *Micronomada*, both treated as subgenera of *Nomada*.

Polybiapis was described by Cockerell (1916b), as a genus closely allied to *Nomada*, for two Brazilian species: *mimus* Cockerell and *polybioides* (Ducke). A third species, *abnormis* (Ducke), also belongs here. The principal distinction for *Polybiapis* is that there are but two submarginal cells, the transverse cubital vein being absent. This is likely not significant; a few species of *Nomada* also lack this vein but are otherwise normal for their groups. Some species of subgenus *Hypochrotaenia* may, in one or both sexes, lack the second transverse cubital vein. In features other than wing venation, *Polybiapis* is an unremarkable *Hypochrotaenia*.

Some South American species of *Hypochrotaenia* have a metapleural structure very similar to that of *Centrias* and, in some, the protuberance is more or less sharply marginate. Both sexes may be readily separated from *Centrias* by the long first flagellar segment. The females lack a paraocular

ridge and the genitalic structures of the males are very different from those of *Centrias*.

KEY TO SUBGENERA OF *HYPOCHROTAENIA*

- 1a. Labrum broader than long (Fig. 4); procoxa usually spinose; outer carina of procoxa, when present, complete 2
- b. Labrum distinctly longer than broad (Fig. 2); procoxa without distal spine or tooth; outer carina of procoxa present on distal half only (Fig. 7) *Aphelonomada*
- 2a. Outer carina of procoxa present (Fig. 8); metacoxa of female sublamellate to lamellate above; metatibia with long, suberect, coarse spiniform setae, at least in female (Fig. 10) *Hypochrotaenia*
- b. Outer carina of procoxa absent (Fig. 6); metacoxa of female rounded above; metatibia with coarse tubercles, but without spiniform setae, except at apex (Fig. 9) *Micronomada*

Subgenus *Micronomada* Cockerell and Atkins

Figures 3–5, 6, 9, 11–12, 15

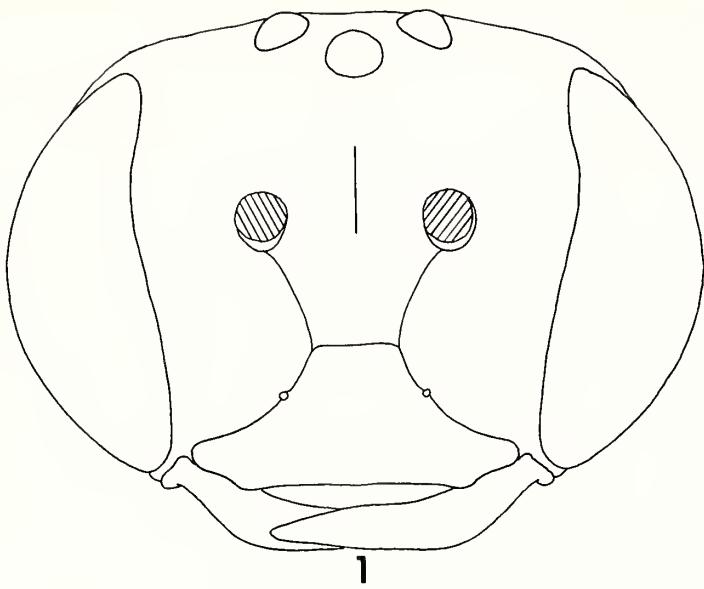
Nomada subg. *Micronomada* Cockerell and Atkins, 1902: 44. Type-species: *Nomada modesta* Cresson, 1863; original designation and monobasic.
Cephen Robertson, 1903:174, 176. Type-species: *Nomada texana* Cresson, 1872; original designation and monobasic.

DIAGNOSIS. Procoxa without outer carina; metacoxa rounded above; lobes of pronotal collar often swollen; metatibia without spiniform setae except at apex; labrum broader than long.

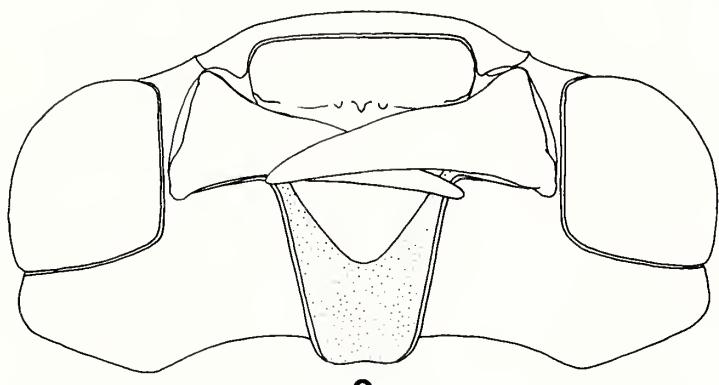
DESCRIPTION. (1) Mandibular apex subacute to blunt. (2) Labrum about one-half wider than long, not extending beyond lower margin of closed mandibles. (3) Clypeus convex to (rarely) flattened. (4) Face, in profile, protuberant below, rarely flattened. (5) Frons and thorax shiny to dull between dense to contiguous punctures over most areas. (6) Pronotal collar narrow to broad, usually rounded and somewhat swollen; lateral ridge directed mesad or, rarely, toward base of collar. (7) Mesoscutum convex to slightly flattened; scutellum flat or convex, with distinct sloping posterior face. (8) Procoxa with apical spine or tubercle, rarely aspinose; outer carina absent. (9) Metacoxa rounded dorsally; metatibia more or less distinctly tuberculate along length, but without distinctly spiniform setae except at apex. (10) Depressed apical margin of second and third gastric terga punctate nearly to margin.

DISCUSSION. The separation between the subgenera *Hypochrotaenia* and *Micronomada* may not prove valid when more species are studied, especially those of the Neotropics. A few with the rounded metacoxae typical of *Micronomada* have a sharp lateral pronotal ridge and the lobes of the pronotal collar are angulate dorsally as in *Hypochrotaenia*. In other features they are more like *Micronomada* and are placed here for the present.

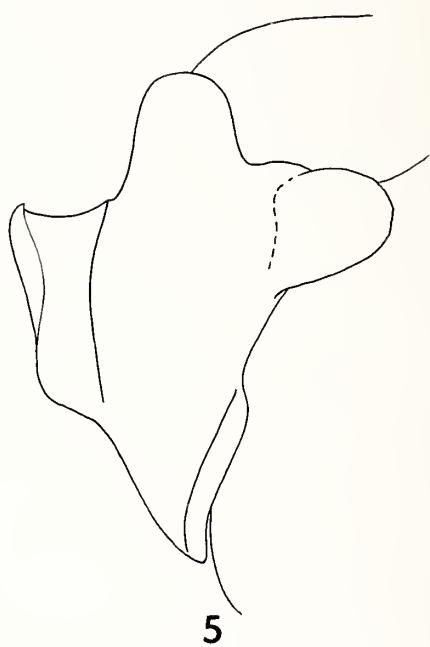
Micronomada is primarily North American. Species fly



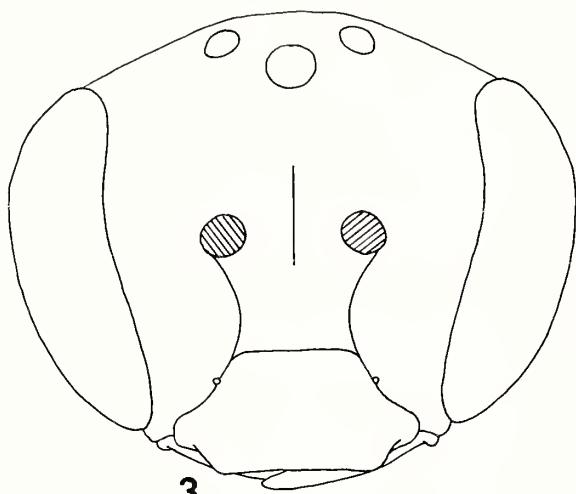
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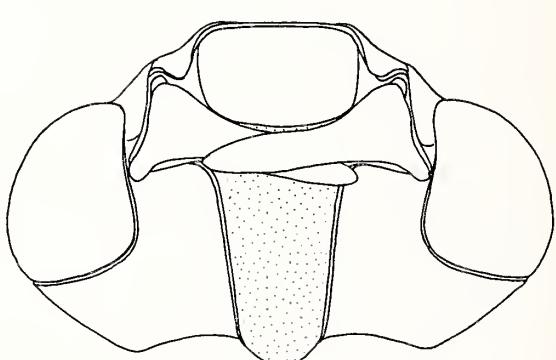
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Figures 1–5. *Hypochrotaenia* spp. 1 and 2, *H. (Aphelonomada) cruralis*, female, frontal and ventral views of head; 3 and 4, *H. (Micronomada) texana*, female, same. 5, *H. (M.) texana*, lateral view of pronotum.

from spring to autumn. Hosts for species of *Micronomada* are, so far as now known, limited to the families Halictidae and Anthophoridae (Table 1).

All names listed below are new combinations in the genus *Hypochrotaenia*.

INCLUDED NAMES

- amorphae* (Swenk, 1913)
arenicola (Swenk, 1913)
convolvuli (Swenk, 1913)
crassula (Cockerell, 1903d)
crucis (Cockerell, 1903a)
cubensis (Cresson, 1865)*
fervida (F. Smith, 1854)
flavipes (Provancher, 1888)
formula (Viereck, 1903)
garciana (Cockerell, 1907c)
gutierreziae (Cockerell, 1896)
heiligbrodtii (Cresson, 1878)
jamaicensis (Cockerell, 1912)*
lamarensis (Cockerell, 1905c)
lippiae (Cockerell, 1903a)
melanoptera (Cockerell, 1921)
mitchelli (Cockerell, 1911a)
modesta (Cresson, 1878)
nitescens (Cockerell, 1905c)
neomexicana (Cockerell, 1903a)
pallidelutea (Swenk, 1915)
pampicola (Holmberg, 1886)*
panamensis (Michener, 1954)*
peninsularis (Cockerell, 1925)
putnami (Cresson, 1876)
ridingsii (Cresson, 1878)
rivertonensis (Cockerell, 1903d)
semisuavis (Cockerell, 1910c)
simplicicoxa (Swenk, 1915)
suavis (Cresson, 1878)
sublippiae (Cockerell, 1907c)
texana (Cresson, 1872)
tiftonensis (Cockerell, 1903d)
trapidoi (Michener, 1954)*
uhleri (Cockerell, 1905c)
vegana (Cockerell, 1903d)
vierecki (Cockerell, 1903a)
wisconsinensis (Graenicher, 1911)

Subgenus *Hypochrotaenia* Holmberg

Figures 8, 10, 13, 17-18

Hypochrotaenia Holmberg, 1886:273. Type-species: *Hypochrotaenia parvula* Holmberg, 1886; original designation and monobasic.

Nomadosoma Rohwer, 1911:24. Type-species: *Pasites pilipes* Cresson, 1865; original designation and monobasic.
Polybiapis Cockerell, 1916b:208. Type-species: *Polybiapis*

mimus Cockerell, 1916b; original designation. NEW SYNONYMY.

DIAGNOSIS. Procoxa with complete outer carina; metacoxa of female sublamellate to lamellate; metatibia of female with coarse, spiniform setae along most of length of outer face.

DESCRIPTION. (1) Mandibular apex blunt, rarely subacute; external surface flattened except on apical one-third. (2) Labrum about one-half broader than long, in repose not extending beyond lower margin of closed mandibles. (3) Clypeus flattened; less commonly weakly convex. (4) Face, in profile, usually distinctly flat. (5) Frons and thorax shiny between punctures ranging from dense to nearly absent (latter condition especially common on mesoscutum). (6) Pronotal collar narrow, subangulate to crested above; upper end of pronotal ridge turned toward lateral lobes of pronotal collar. (7) Mesoscutum, in profile, weakly convex to flat; scutellum weakly convex or flat, usually without discrete posterior face. (8) Procoxa spinose or dentate; outer carina present, complete. (9) Metacoxa sharply compressed and sublamellate to lamellate above (except some males); metatibia with scattered spiniform setae along its length (except some males). (10) Depressed apical margin of second and third gastric terga punctate nearly to apical margin.

DISCUSSION. This is an essentially Neotropical group with many species, most of which seem to be undescribed. At least one species, presently undescribed, enters the United States in southern Texas. Some species of *Micronomada* especially those allied to *H. gutierreziae*, closely resemble *Hypochrotaenia* s. str., particularly in the flattened face and mesoscutum. However, the structure of the pro- and metacoxae and of the metatibiae are as in typical *Micronomada*.

INCLUDED NAMES

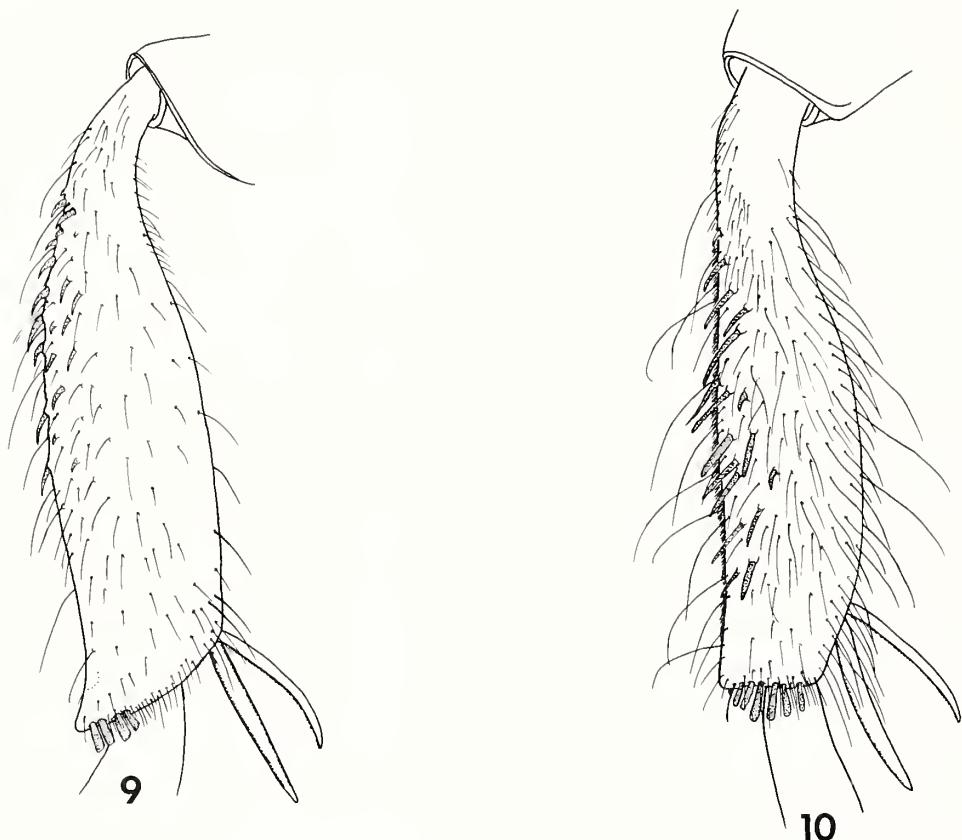
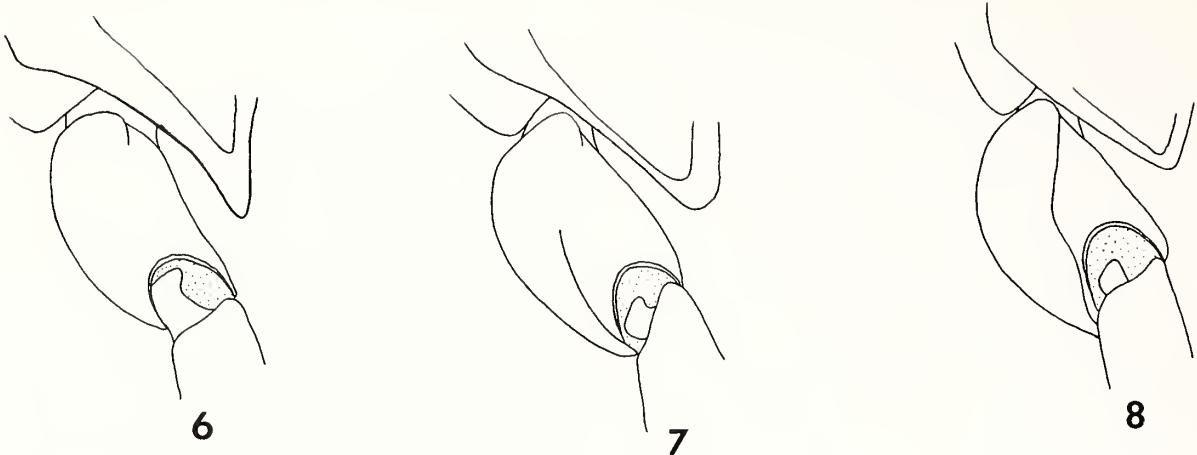
- abnormis* (Ducke, 1912)*
costalis (Brethes, 1909)*
costaricensis (Schrottky, 1920)*
hondurasica (Cockerell, 1949)*
? *krugii* (Cresson, 1878)*
limata (Cresson, 1878)*
mexicana (Cresson, 1878)*
mimus (Cockerell, 1916b)*
nigrescens (Friese, 1921)*
parvula Holmberg, 1886*
pilipes (Cresson, 1872)*
polybioides (Ducke, 1908)*
xanthaspis (Cockerell, 1949)*
xanthopus (Friese, 1921)*
zamoranica (Cockerell, 1949)*

Aphelonomada new subgenus

Figures 1-2, 7, 14, 16

DIAGNOSIS. Labrum longer than broad, its apex subtruncate and extending over base of mouthparts (Fig. 2).

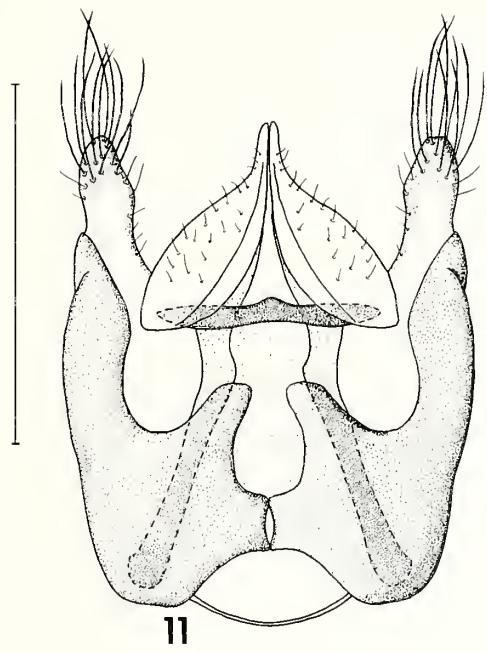
DESCRIPTION. (1) Mandibular apex blunt. (2) Labrum



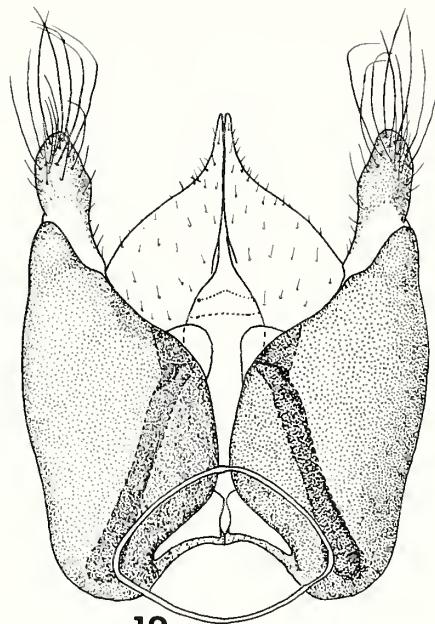
Figures 6–10. *Hypochrotaenia* spp. 6–8, external view of procoxa of *H. (Micronomada) texana*; 7, *H. (Aphelonomada) cruralis*; 8, *H. (H.) mexicana*. 9–10, outer face of female metatibia of: 9, *H. (M.) texana*; 10, *H. (H.) mexicana* (pilosity reduced).

longer than broad, in repose covering half or more of pro-boscidial fossa. (3) Clypeus weakly convex. (4) Face, in profile, flattened. (5) Head and thorax smooth and shiny between sparse to scattered punctures. (6) Pronotal collar narrow, but

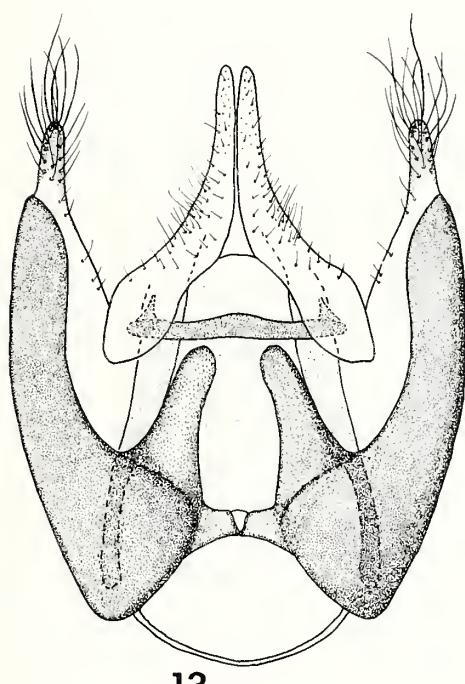
rounded, dorsally. (7) Mesoscutum somewhat flattened; scutellum flat dorsally and with distinct posterior face. (8) Pro-coxa without apical spine or tooth; outer carina present on distal half only. (9) Metacoxa, from above, rounded basad,



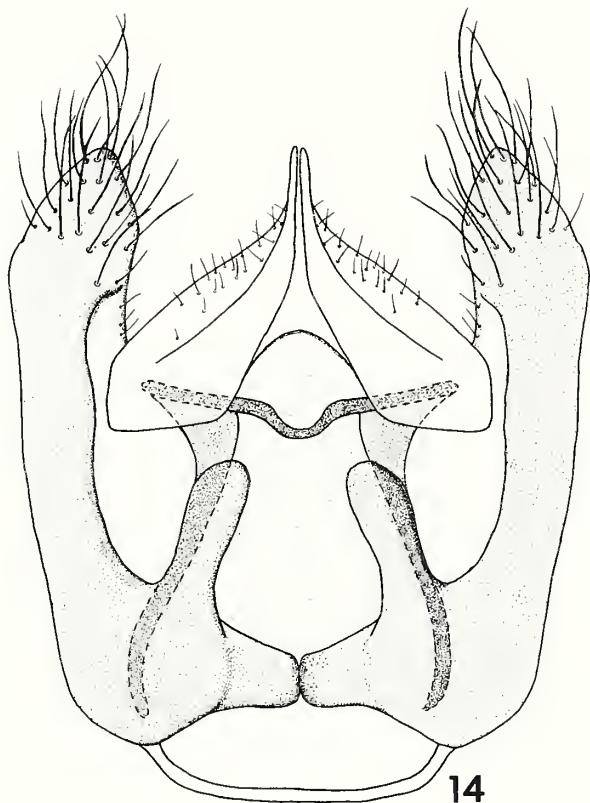
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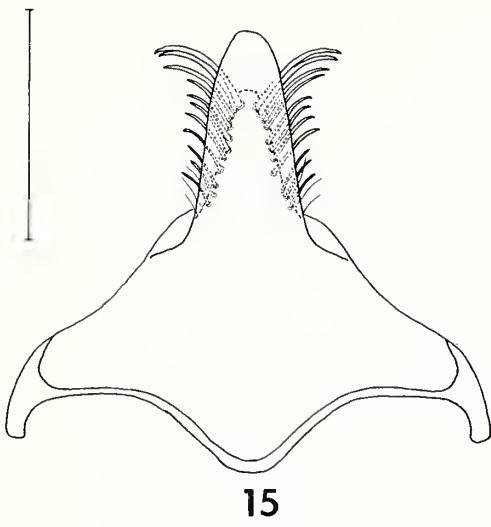


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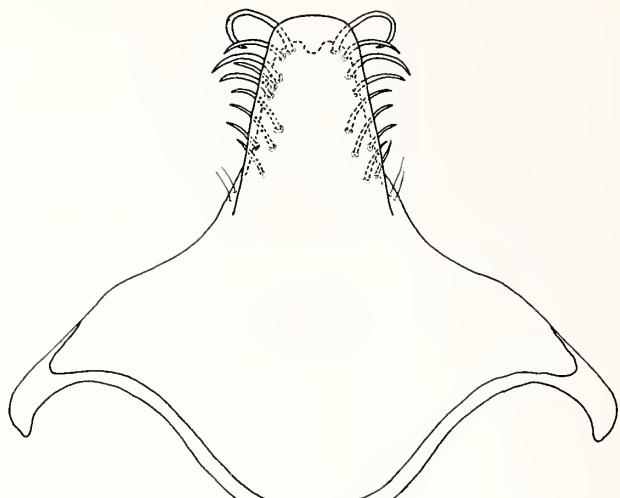


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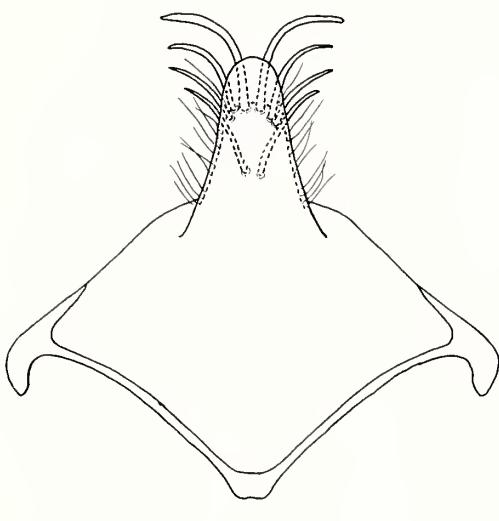
Figures 11–14. *Hypochrotaenia* spp., male genitalia. 11–12, *H. (Micronomada) texana*, dorsal and ventral views; 13, *H. (H.) mexicana*, dorsal view; 14, *H. (Aphelonomada) cruralis*, dorsal view. Scale line = 0.50 mm.



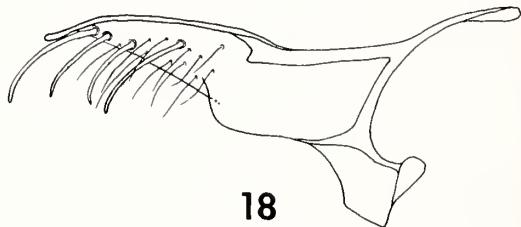
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Figures 15–18. *Hypochrotaenia* spp., male sternum seven. **15,** *H. (Micronomada) texana*; **16,** *H. (Aphelonomada) cruralis*; **17–18,** *H. (H.) mexicana*, ventral and lateral views. Scale line = 0.25 mm.

compressed apicad; metatibia without tubercles or spiniform setae along its length. (10) Depressed apical margin of second and third gastric terga impunctate.

TYPE-SPECIES. *Nomada cruralis* Moure, 1960.

ETYMOLOGY. Gr., *apheles* (smooth or simple) + *Nomada*, because of the smooth, shiny integument.

DISCUSSION. Moure (1960) correctly noted that Cresson's specific epithet for this species was preoccupied in *No-*

mada and he proposed the new name *N. cruralis*; according to the International Code of Zoological Nomenclature, a name that is a primary junior homonym, as is the case here, is permanently rejected (Art. 59a), presumably even when transferred to another genus.

Although the only known species of this subgenus closely resembles those of *Hypochrotaenia* s. str., *Aphelonomada* is distinct. Most notable of the differences is the unusual length

of the labrum, unique among the New World "Nomada." Unique also within the genus *Hypochoptaenia* are the broad impunctate apical margins of the gastric terga which include the entire depressed apical portion of those segments. The metatibia is covered, as is much of the body, with long, rather silky, white hairs; the integument of the outer face is devoid of tubercles and the coarse, spine-like setae typical of *Hypochoptaenia* are absent.

The only known species occurs in Cuba. Nothing is known of the biology of this bee.

INCLUDED NAMES

cruralis Moure, 1960*
tibialis Cresson, 1865*

UNASSIGNED SPECIES OF *HYPOCHROTAENIA*

The following species-group names for Neotropical species evidently all apply to species of *Hypochoptaenia*. But, until the types can be studied, their subgeneric placement is uncertain. Most, if not all, probably belong to *Hypochoptaenia*, s. str. All are new combinations in *Hypochoptaenia*.

bicellularis (Ducke, 1908)*
carcarenensis (Cockerell, 1917)*
ecuadaria (Friese, 1916)*
flavescens (Friese, 1916)*
flaviceps (Cresson, 1865)*
fuliginosa (Friese, 1916)*
infrequens (F. Smith, 1879)*
nitidiceps (Cockerell, 1931)*
rugicollis (Friese, 1916)*
sanguinolenta (Friese, 1916)*
subscopifera (Ducke, 1908)*
tenuicornis (Cockerell, 1949)*
tomentifera (Ducke, 1907)*

Genus *Centrias* Robertson

Figures 19-24, 65

Centrias Robertson, 1903:174, 176. Type-species: *Nomada erigeronis* Robertson, 1897; original designation and monobasic.

Nomada subg. *Nomadula* Cockerell, 1903d:611. Type-species: *Nomada articulata* F. Smith, 1854; original designation.
NEW SYNONYMY.

DIAGNOSIS. Metapleuron protuberant and marginate above; paraocular ridge present in female; procoxa usually spinose; anterior rim of pronotum subangulate to angulate at side; male subgenital brush often complex; inner dorsal lobe of male gonocoxite virtually absent; segment 3 of male flagellum often spinose (Fig. 20).

DESCRIPTION. (A) Mandible without preapical tooth. (B) Paraocular ridge present in female. (C) Minimum length of first flagellar segment distinctly less than maximum length of second; male flagellar segments 3-10 often conspicuously spinose, tuberculate, or sharply ridged beneath. (D) Gena about half as wide as eye in profile, genal margin sharply

angulate to cariniform. (E) Procoxa usually with distal spine or tooth; outer carina absent. (F) Anterior rim of pronotum subangulate to angulate at side; pronotal collar compressed, more or less crested above. (G) Metapleuron protuberant and marginate or lamellate above. (H) Metacoxa rounded above. (I) Gastric terga usually sharply and closely punctate and with narrow impunctate margins, but may be shallowly and obscurely punctate. **Male.** (J) Hairs of subgenital brush erect, long, curled and often in a complex pattern. (K) Inner dorsal lobe of gonocoxite virtually absent, outer lobe short, stout; median sinus broader than long. (L) Gonostylus without setose basoventral lobe and without inner, basal seta-cluster.

DISCUSSION. The generic name *Centrias* was published by Robertson (1903) in June; the name *Nomadula* was published, as a subgenus of *Nomada*, in August of that same year by Cockerell (1903d).

Nomadula was described as a subgenus allied to *Centrias*, the principal justification being that in *Nomadula* the two sexes were dissimilar in appearance, rather than very similar in color and markings as in *Centrias*. Some western species are known in which the two sexes have similar color patterns but are morphologically similar to other species in which this is not true. There is no basis for continued separation of these two names.

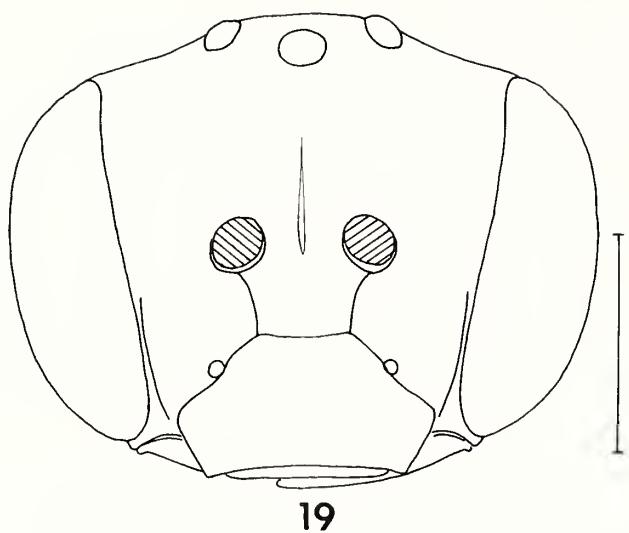
This appears to be a strictly New World genus limited to the Nearctic Region. *Centrias* is probably more nearly related to the genus *Hypochoptaenia* than to *Nomada*. The two genera share a tendency toward spinose procoxae (rare and sporadic in *Nomada*), laterally angulate pronotal rim, sharply punctate gaster and features of male terminalia. The peculiar modification of the metapleuron is unique to *Centrias*, although some South American species of *Hypochoptaenia* have the metapleuron somewhat protuberant above, but the prominence is usually not marginate. Presumably, this feature is independently derived in the two groups. In addition to the metapleural structure, *Centrias* consistently differs from *Hypochoptaenia* in both sexes by the short first flagellar segment. In addition, male *Centrias* commonly have a short, acute spine on at least the third flagellar segment. Females consistently possess a short paraocular ridge.

Some species of *Centrias* fly in spring months; at least one of these is known to be cleptoparasitic in nests of *Andrena*. Other species are active in summer months and are associated with halictids as hosts (Table 1). It is possible that there are two subgenera involved, but the matter will require further study; the names *Centrias* and *Nomadula*, however, both apply to the summer group of species.

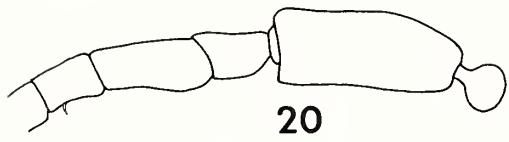
The names listed below are mostly new combinations in *Centrias*.

INCLUDED NAMES

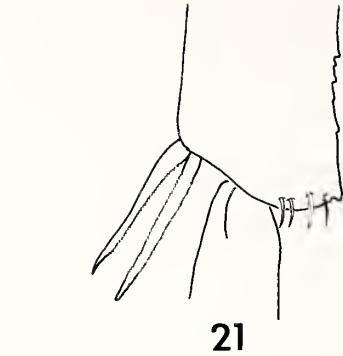
articulata (F. Smith, 1854)
aureopilosa (Swenk, 1913)
australis (Mitchell, 1962)
crotchii (Cresson, 1878)
dacotana (Cockerell, 1903d)
erigeronis (Robertson, 1897)



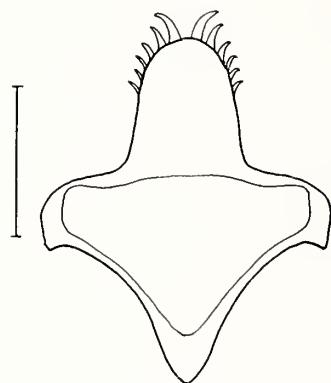
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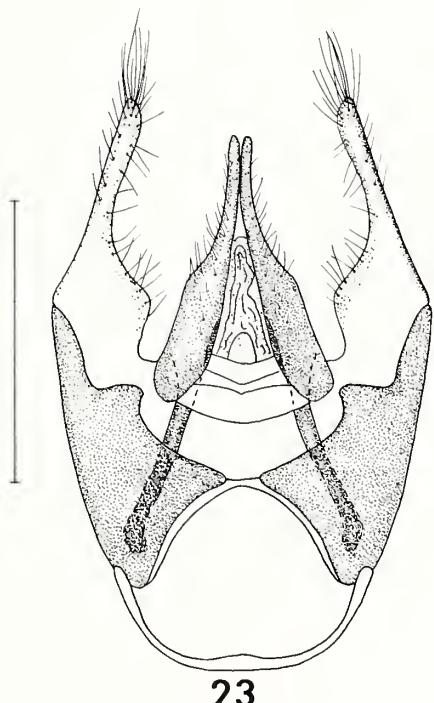
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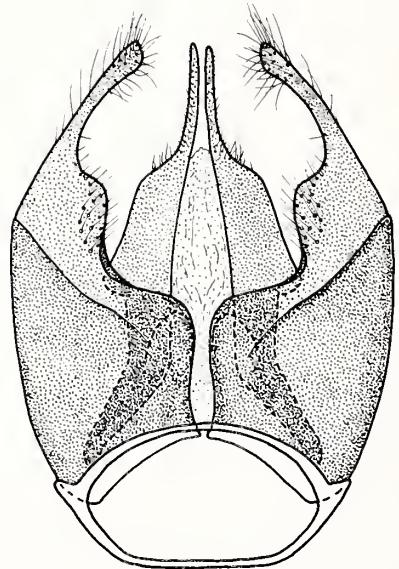
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Figures 19–24. *Centrias articulata*. 19, frontal view of female head (scale line = 1.00 mm); 20, basal segments of male antenna; 21, apex of female metatibia; 22, male sternum seven (scale line = 0.25 mm); 24–25, male genitalia, dorsal and ventral views (scale line = 0.50 mm).

erythrochroa (Cockerell, 1903a)
erythrosipa (Cockerell, 1916c)
frankei (Cockerell, 1929b)
friesiana (Cockerell, 1904)
incerta (Cresson, 1863)
martinella (Cockerell, 1903d)
nigrior (Cockerell, 1903c)
pascoensis (Cockerell, 1903c)
rohweli (Cockerell, 1906a)
rubicunda (Olivier, 1811)
scita (Cresson, 1878)
scitiformis (Cockerell, 1903d)
semiscita (Cockerell, 1904)
seneciophila (Mitchell, 1962)
sophiarum (Cockerell, 1903a)
torrida (F. Smith, 1854)

Genus *Nomada* Scopoli

DIAGNOSIS. Female with paraocular ridge (except subgenus *Phelonomada*); minimum length of first flagellar segment usually less than maximum length of second; procoxa usually without distal spine or tooth; anterior rim of pronotum evenly curved laterally; metapleuron neither protuberant nor marginate above. **Male.** Hairs of subgenital brush usually short, inclined basad; gonostylus usually with setose basoventral process.

DESCRIPTION. (A) Mandible with or without preapical tooth. (B) Paraocular ridge present in female (except subg. *Phelonomada*). (C) Minimum length of first flagellar segment usually less than maximum length of second; male flagellar segments 3–10 often ridged or tuberculate beneath. (D) Gena usually at least half as wide as eye in profile, margin usually angulate to cariniform. (E) Procoxa usually simple at apex; outer carina absent. (F) Anterior rim of pronotum not angulate at side; pronotal collar compressed, especially in middle, often crested above. (G) Metapleuron simple above. (H) Metacoxa rounded above. (I) Gastric terga usually weakly punctate and with broad impunctate margins, but may be closely punctate with narrow margins. **Male.** (J) Hairs of subgenital brush usually short, straight, and inclined toward base. (K) Inner dorsal lobe of gonocoxite usually short and broad, outer lobe usually broad; median sinus usually broader than long. (L) Gonostylus usually with setose basoventral lobe and often with a cluster of short, flattened setae on inner basal margin.

DISCUSSION. With the removal of *Nomadula* and *Hypochrotaenia* as separate genera, *Nomada* assumes a uniformity previously lacking. It is still a very large and complex genus and is primarily northern in distribution. In the New World, no true *Nomada* are known from South America. The Old World forms have not been subjected to a large scale study of the groups and there are no currently named subgenera recognized there, except the Holarctic *Nomadita*.

However, many Old World species can be assigned to existing subgenera described from the Nearctic fauna.

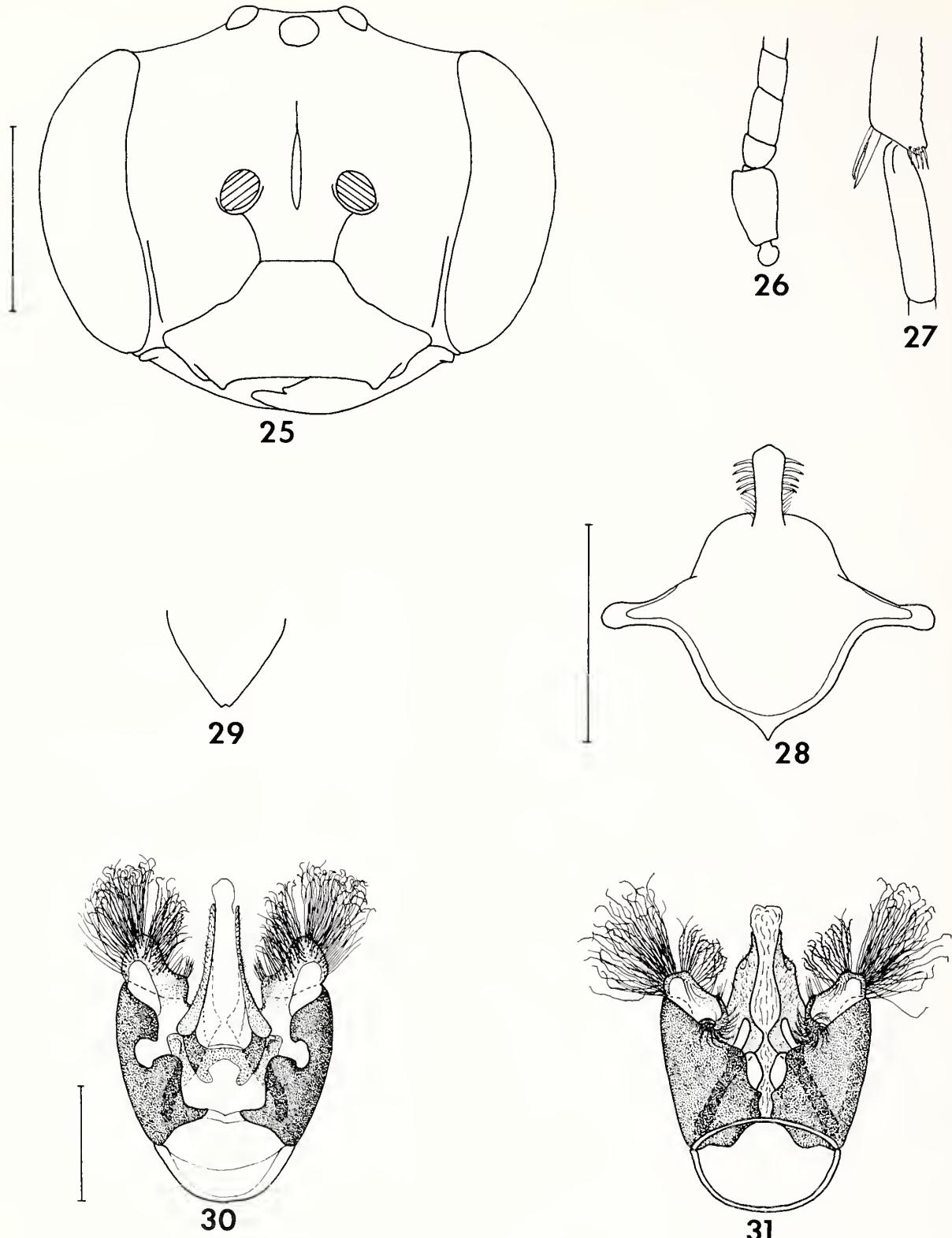
KEY TO SUBGENERA OF *NOMADA*

- 1a. Procoxa usually without spine; if spine present, gastric terga weakly punctate and with broad apical impunctate bands or gena is sharply marginate; inner dorsal lobe of male gonocoxite short and broad, at most as long as broad; paraocular ridge of female present 2
- 1b. Procoxa with short distal spine; gastric terga sharply and closely punctate, with narrow impunctate margins; gena narrow, posterior margin rounded; inner dorsal lobe of male gonocoxite longer than broad, acute; paraocular ridge of female absent *Phelonomada*
- 2a. Minimum length of first flagellar segment equal to, or longer than, maximum length of second; gastric terga closely punctate and with narrow impunctate margins; apex of pygidium broad, without median notch; mandible without preapical tooth 3
- 2b. Minimum length of first flagellar segment less than maximum length of second; if equal, tergal punctures weak, impunctate apical margins broad; apex of pygidium subacute to narrowly rounded, margins straight and strongly convergent distad, with distinct notch, at least in males (rarely entire); preapical mandibular tooth sometimes present *Nomada* s. str.
- 3a. Propodeum not swollen or elevated mesad of spiracle; scape of male stout, often subglobose; metatibia of female with distal setae in a distinct row; erect hairs short and sparse on head and thorax 4
- 3b. Propodeum swollen or elevated mesad of spiracle; scape of male stout-cylindrical; metatibia of female with distal setae in a dense cluster (except one species); erect hairs of head and thorax usually numerous, long, somewhat shaggy 5
- 4a. Posterior margin of gena rounded or weakly angulate; aedeagus of male with ventral hook; metabasitarsus usually somewhat swollen, broadest near middle *Pachynomada*
- 4b. Posterior margin of gena subcarinate; aedeagus of male without ventral hook; metabasitarsus slender, flattened on external face, broadest near base *Nomadita*
- 5a. Labrum with extensive smooth and impunctate areas, at least on basal half; pro- and mesofemur of male greatly flattened and expanded dorso-ventrally; apex of female metatibia with a single, irregular row of 8–11 ferruginous setae *Laminomada*
- 5b. Labrum contiguously punctate; pro- and mesofemur of male neither flattened nor dorso-ventrally expanded; apex of female metatibia with a dense cluster of 15 or more setae *Holonomada*

Subgenus *Nomada* Scopoli

Figures 25–31, 64, 66

Nomada Scopoli, 1770:44. Type-species: *Apis ruficornis* Linné, 1758; designated by Curtis, 1832.
Nomada subg. *Heminomada* Cockerell and Atkins, 1902:42.



Figures 25–31. *Nomada (N.) ruficornis*. 25, frontal view of female head (scale line = 1.00 mm); 26, basal segments of male antenna; 27, apex of female metatibia; 28, male sternum seven (scale line = 0.50 mm); 29, apex of female pygidium; 30–31, male genitalia, dorsal and ventral views (scale line = 1.00 mm).

Type-species: *Nomada oblitterata* Cresson, 1863; original designation and monobasic. NEW SYNONYMY.

Gnathias Robertson, 1903:173. Type-species: *Nomada bella* Cresson, 1863; original designation. NEW SYNONYMY.

Phor Robertson, 1903:173. Type-species: *Phor integra* Robertson, 1903; original designation and monobasic. NEW SYNONYMY.

Xanthidium Robertson, 1903:174 (not Ehrenberg, 1833).

Type-species: *Nomada luteola* Olivier, 1811; original designation. NEW SYNONYMY.

DIAGNOSIS. Minimum length of first flagellar segment less than, rarely equal to, maximum length of second flagellar segment; preapical mandibular tooth sometimes present; procoxa usually not spinose; gastric punctures usually more or less obscure and well separated, apical margin of tergum 2 usually broadly impunctate; apex of pygidium subacute to narrowly rounded, usually with deep median notch in male.

DESCRIPTION. (1) Mandible with or without preapical tooth. (2) First flagellar segment no longer, and usually much shorter, than second; male often with conspicuous ridges or tubercles on segments 3–10. (3) Posterior margin of gena angulate to subcarinate. (4) Procoxa rarely with apical spine or tooth. (5) Propodeum not swollen mesad of spiracle. (6) Tergum 2 more or less sharply punctate on disc, less distinctly so on apical depression, impunctate apical margin usually broad. **Male.** (7) Apex of pygidium usually distinctly notched. (8) Process of sternum 8 usually slender, more or less parallel-sided and with deflected apex. (9) Inner dorsal lobe of gono-coxite almost always short and broad, with invagination between inner and outer lobes broad and deep; median sinus broader than long. (10) Gonostylus with setose basoventral process and often with inner, basal cluster of very short, flattened setae. (11) Aedeagus without ventral hook. **Female.** (12) Paraocular ridge always present. (13) Metatibia usually with a row of 2–8 dark, flattened setae at apex. (14) Apex of pygidium acute to subacute, usually with narrow median notch.

DISCUSSION. As pointed out above, I do not believe that a single characteristic should justify a subgenus. Such is the case with *Gnathias*, here united with the nominate subgenus. There are no other features known which would support recognition of this heterogenous assemblage.

The subgenus *Heminomada* was established for a species with but two submarginal cells in the forewing. Some specimens of *N. oblitterata*, the type-species, may have three submarginal cells on one wing, two on the other or only partial loss of the transverse cubital vein in one or both wings. The equivalence of *Heminomada* with *Xanthidium*, a junior homonym, has long been recognized.

Heminomada has been utilized for those species in which the head and thorax are more or less richly yellow-marked and one or more gastric segments have a complete transverse yellow band. The weakness of this division was recognized by Mitchell (1962), who observed that "... if a species is known in but one sex it may be difficult to place it with confidence in one or the other of these groups." Among the species in western North America, some species would have

the two sexes in different subgenera. I am certain that *Heminomada* may be safely put to rest.

The subgenus *Phor* was established for a single species with a long first flagellar segment and a short procoxal spine. The few other species tentatively placed in *Phor* seem to have little relationship to that species or to each other. Both character states occur sporadically throughout *Nomada* s. str. It is hardly surprising that these would combine in a few species, but a formal name hardly seems necessary.

Nomada is a very large subgenus, including the vast majority of the North American species. Future study may result in further splitting, but not along previous lines.

This subgenus is Holarctic and is largely northern and montane in the Western Hemisphere. Those few species whose hosts are known are mostly cleptoparasites in nests of *Andrena* (Table 2). In addition to the hosts listed in Table 2, Barrows (1978) has implicated *N. luteola*, *N. maculata*, and *N. illinoensis* as possible cleptoparasites of *Andrena* (*Ptilandrena*) *erigeniae* Robertson.

INCLUDED NAMES

- accepta* Cresson, 1878
agnynia Cockerell, 1905c
albofasciata F. Smith, 1879
aldrichi Cockerell, 1910a
alpha Cockerell, 1905c
amoena Cresson, 1863
angelarum Cockerell, 1903c
angulata Swenk, 1913
annulata F. Smith, 1854
apriliina Swenk, 1913
arizonica Cockerell, 1911b
armatella Cockerell, 1903d
ashmeadi Cockerell, 1903c
astori Cockerell, 1903a
atrofrontata Cockerell, 1903c
augustiana Mitchell, 1962
autumnalis Mitchell, 1962
avalonica Cockerell, 1938
azaleae Mitchell, 1962
banksi Cockerell, 1907b
bella Cresson, 1863
bethunei Cockerell, 1903d
beulahensis Cockerell, 1903a
bicincta Howard, 1902!
bicrista Swenk, 1913
bifurcata Cockerell, 1903c
bilobata Swenk, 1913
binotatus Robertson, 1903
bisetosa Swenk, 1913
bishoppi Cockerell, 1911a
bisignata Say, 1824
californiae Cockerell, 1903c
calloxyantha Cockerell, 1921
callura Cockerell, 1911a
capillata Mitchell, 1962
capitalis Mitchell, 1962

- carinicauda* Cockerell, 1921
carolinae Cockerell, 1903d
ceanothi Cockerell, 1907b
citrina Cresson, 1878
civilis Cresson, 1878
clarescens Cockerell, 1921
clarkii Cockerell, 1903a
collinsiana Cockerell, 1905c
coloradella Cockerell, 1905c
coloradensis Cockerell, 1903d
colorata Mitchell, 1962
composita Mitchell, 1962
concinna Cockerell, 1921
contractula Cockerell, 1903d
coquilletti Cockerell, 1903c
cordleyi Cockerell, 1903b
cornelliana Cockerell, 1908c
corvallisensis Cockerell, 1903a
crawfordi Cockerell, 1905c
cressonii Robertson, 1893
crudelis Cresson, 1878
cuneatus Robertson, 1903
custeriana Cockerell, 1911b
cymbalariae Cockerell, 1906a
davidsoni Cockerell, 1903c
debilis Timberlake, 1954
decemnotatus Robertson, 1903
decompunctata Cockerell, 1903c
decepta Mitchell, 1962
dentariae Robertson, 1903
denticulata Robertson, 1902a
depressa Cresson, 1863
depressicauda Cockerell, 1908a
detrita Mitchell, 1962
dialpha Cockerell, 1921
dilucida Cresson, 1878
dreisbachi Mitchell, 1962
eastonensis Cockerell, 1903d
ednae Cockerell, 1907a
electa Cresson, 1863
electella Cockerell, 1903d
elegantula Cockerell, 1903c
elrodi Cockerell, 1903d
erythraea Dalla Torre, 1896!
festiva Cresson, 1863
flagellaris Cockerell, 1903d
flammigera Cockerell, 1906c
flavomarginata Swenk, 1913
florilega Lovell & Cockerell, 1905
fontis Cockerell, 1910b
fowleri Cockerell, 1903a
fragariae Mitchell, 1962
fragilis Cresson, 1878
fuscincta Swenk, 1915
gibbosa Viereck, 1905
gilletti Cockerell, 1905c
gracilis Cresson, 1863
graenicheri Cockerell, 1905a
grayi Cockerell, 1903a
heterosticta Cockerell, 1921
honorata Cockerell, 1922a
hoodiana Cockerell, 1903d
hydropylli Swenk, 1915
idahoensis Swenk, 1913
illinoiensis Robertson, 1900
illinoensis Cockerell, 1911a!
illinoënsis Cockerell, 1921!
imbricata F. Smith, 1854
indusata Mitchell, 1962
inepta Mitchell, 1962
infantula Cockerell, 1907b
infrarubens Cockerell, 1905c
integerima Dalla Torre, 1896!
"integra" Robertson, 1893"
"interrupta" Fowler, 1899"
interruptella Fowler, 1902!
itamera Cockerell, 1910c
jocularis Cresson, 1879
kincaidiana Cockerell, 1903d
kingstonensis Mitchell, 1962
klamathensis C. Fox, 1926
krombeini M. Schwarz, 1966a!
lachrymosa Cockerell, 1921
laramiensis Swenk, 1913
latifrons Cockerell, 1903c
lehighensis Cockerell, 1903d
levida Cresson, 1863
leucozona Rodeck, 1931
lewisi Cockerell, 1903a
libata Cresson, 1863
limbata Dalla Torre, 1896!
louisianae Cockerell, 1903d
luteola Olivier, 1811
luteoloides Robertson, 1895
luteopicta Cockerell, 1905c
maculata Cresson, 1863
maculiventer Swenk, 1915
malonella Cockerell, 1910c
malonina Cockerell, 1910c
marginella Cockerell, 1903c
mckenziei Timberlake & Cockerell, 1937
media Mitchell, 1962
mediana Swenk, 1913
melanosoma Cockerell, 1916c
melliventris Cresson, 1878
mendica Mitchell, 1962
mera Cockerell, 1908c
mesosticta Cockerell, 1939
mimula Cockerell, 1908b
miniata F. Smith, 1854
minima Mitchell, 1962
"minuta" Swenk, 1913"
modocorum Cockerell, 1903b
morrisoni Cresson, 1878
munda Cresson, 1878
nigrociliata Swenk, 1913

- nigrofasciata* Swenk, 1913
 “*obliqua* Fowler, 1899”
obliquella Fowler, 1902!
obliterata Cresson, 1863
 “*obscura* Fowler, 1899”
obscurella Fowler, 1902!
obstusata Swenk, 1915
obtusata Swenk, in Muesebeck et al., 1951!
ochlerata Mitchell, 1962
ochrohirta Swenk, 1913
octomaculata Robertson, 1903
octonotatus Robertson, 1903
odontocera Cockerell, 1916c
opacella Timberlake, 1954
opposita Cresson, 1878
orba Mitchell, 1962
orcusella Cockerell, 1910c
oregonica Cockerell, 1903a
ornithica Cockerell, 1906d
orophila Cockerell, 1921
osborni Cockerell, 1911b
ovata Robertson, 1903
pacata Cresson, 1878
packardiella Cockerell, 1906b
pallidella Cockerell, 1905c
pallidipicta Swenk, 1913
parallela Swenk, 1913
paralpfa Cockerell, 1921
parata Cresson, 1878
parva Robertson, 1900
perbella Viereck, 1905
perivincta Cockerell, 1905c
perplexa Cresson, 1863
perplexans Cockerell, 1910c
physura Cockerell, 1903d
placitensis Cockerell, 1903b
plenus Robertson, 1903
propinqua Swenk, 1913
proxima Cresson, 1863
pseudops Cockerell, 1905a
pulchella F. Smith, 1854
pulsatillae Cockerell, 1906c
pygmaea Cresson, 1863
pyrrha Cockerell, 1916c
quadrimaculatus Robertson, 1903
quadrisignatus Robertson, 1903
rhodalis Cockerell, 1903d
rhodomelas Cockerell, 1903d
rhodosoma Cockerell, 1903c
rhodosomella Cockerell, 1903c
rhodoxantha Cockerell, 1905c
rivalis Cresson, 1878
robertsonella Cockerell, 1903d
rubi Swenk, 1915
rubrella Cockerell, 1905c
 “*rubra* Provancher, 1888”
rubrica Provancher, 1896!
rufula Cockerell, 1903d
- ruidosensis* Cockerell, 1903d
salicola Swenk, 1913
salicis Robertson, 1900
sanctaerucris Cockerell, 1903c
sayi Robertson, 1893
schwarzii Cockerell, 1903d
sedae Cockerell, 1919a
sedi Cockerell, 1920!
semirufula Cockerell, 1905c
semirugosa Cockerell, 1929a
septentrionalis Swenk, 1913
sexmaculatus Robertson, 1903
sexnotatus Robertson, 1903
siccorum Cockerell, 1919a
simplex Robertson, 1902b
siouxensis Swenk, 1913
skinneri Cockerell, 1908a
sobrina Mitchell, 1962
sphaerogaster Cockerell, 1903d
spokanensis Cockerell, 1910c
stevensi Swenk, 1913
subaccepta Cockerell, 1907c
subangusta Cockerell, 1903c
subgracilis Cockerell, 1903c
subnigrocincta Swenk, 1915
subpacata Swenk, 1913
subrubi Swenk, 1915
subrutila Lovell & Cockerell, 1905
subsimilis Cockerell, 1903c
subvicinalis Cockerell, 1903c
suda Cresson, 1878
sulphurata F. Smith, 1854
swenki M. Schwarz, 1966a!
taraxacella Cockerell, 1903d
tintinnabulum Cockerell, 1903c
townesi Mitchell, 1962
trevoriana Cockerell, 1905b
tricurta Swenk, 1915
truttorum Cockerell, 1909b
tyrrellensis Mitchell, 1962
ulsterensis Mitchell, 1962
ultima Cockerell, 1903a
ultimella Cockerell, 1903c
undulaticornis Cockerell, 1906c
utensis Swenk, 1913
unicolor Robertson, 1903
valida F. Smith, 1854
vallesina Cockerell, 1906b
velutina Swenk, 1913
vernonensis Cockerell, 1916a
vexator Cockerell, 1909b
viburni Robertson, 1897
vicina Cresson, 1883
vicinalis Cresson, 1878
volatilis F. Smith, 1879
vulpis Cockerell, 1921
washingtoni Cockerell, 1903d
wootonella Cockerell, 1909b

wyomingensis Swenk, 1913
xantholepis Cockerell, 1911b
xanthoparius Robertson, 1928
xanthophilus Cockerell, 1900
xantheta Cockerell, 1908c
ziziae Swenk, 1915

NOTE. “ ” denotes preoccupied name. ! denotes variant spelling, including emendations and new names.

Subgenus *Holonomomada* Robertson

Figures 32–37

Holonomomada Robertson, 1903:174, 177. Type-species: *Nomada superba* Cresson, 1863; original designation.

DIAGNOSIS. Minimum length of first flagellar segment equal to, or exceeding, maximum length of second; propodeum convex and prominent mesad of spiracle; distal setae of female metatibia slender, ferruginous, forming a dense cluster; apex of pygidium broadly rounded; medium sized to moderately large species.

DESCRIPTION. (1) Mandible without preapical tooth. (2) Minimum length of first flagellar segment as long as, or longer than, maximum length of second. (3) Genal margin abrupt, but not cariniform. (4) Procoxa without distal spine. (5) Propodeum weakly to strongly swollen or protuberant mesad of spiracle. (6) Tergum 2 densely and finely punctate, with very narrow impunctate margin; punctures often obscured by transverse lineation of interspaces. **Male.** (7) Apex of pygidium without median notch. (8) Process of sternum 8 elongate, narrow, broadened distad. (9) Inner dorsal lobe of gonocoxite about as long as broad, invagination between inner and outer lobes moderate to deep; median sinus as long as, or a little longer than, broad. (10) Gonostylus with setose basoventral lobe and with seta-cluster or inner basal margin. (11) Aedeagus without ventral hook. **Female.** (12) Paraocular ridge present. (13) Distal setae of metatibia long, slender, ferruginous, forming dense cluster. (14) Apex of pygidium broadly rounded, without median notch.

DISCUSSION. *Holonomomada* is a small group of primarily western, relatively large and robust species. Previous authors have stressed the propodeal structure as diagnostic of *Holonomomada*. At its greatest development, in such species as *N. superba*, it is certainly obvious. But, in some western species, such as *N. edwardsii* and *N. hemphilli*, the swelling above the spiracle is very subtle. Some species of *Nomada* s. str. approach this condition, but may be separated by the shorter first flagellar segment, the notched pygidium of the males, and the lack of a definite seta-cluster on the metatibia of the females.

Holonomomada is a weak subgenus and it may be necessary to merge it with the nominate subgenus when the fauna of western North America becomes better known. Some western species, now assigned to subgenus *Nomada*, are as large as *Holonomomada*, equally hairy and the notch of the male pygidium is poorly defined. The apparent females, however, do not have the metatibial seta-cluster characteristic of *Holonomomada*.

The only known host for any species of *Holonomomada* is a species of *Andrena* (Table 2). However, it seems possible that the anthophorid, *Synhalonia amsinckiae* Timberlake, may be a host for *N. hemphilli*. This is a presumption based on the coincidence of flight activity and the fact that in the area where I observed both species for more than ten years, no *Andrena* of suitably large size was encountered at the appropriate time of year. It is possibly relevant that a Japanese species of *Holonomomada*, *N. daimio* Matsumura, is known to be a parasitoid in nests of *Tetralonia*, a eucerine genus closely related to *Synhalonia* (H. Nagase, pers. comm.).

Holonomomada was revised by Evans (1972). Eleven species were recognized; three of these were each divided into two subspecies. There are additional species yet to be described.

INCLUDED NAMES

- affabilis* Cresson, 1878
- australior* Cockerell, 1903c
- dallasensis* Cockerell, 1911a
- edwardsii* Cresson, 1878
- excellens* Cockerell, 1903c
- excurrens* Cockerell, 1903c
- grandis* Cresson, 1875
- hemphilli* Cockerell, 1903c
- henningeri* Evans, 1972
- hurdi* Evans, 1972
- intercepta* F. Smith, 1879
- linsleyi* Evans, 1972
- magnifica* Cockerell, 1903d
- malvastri* Swenk, 1913
- nebrascensis* Swenk, 1913
- parkeri* Evans, 1972
- pecosensis* Cockerell, 1903d
- rhodotricha* Cockerell, 1903c
- superba* Cresson, 1863
- vinnula* Cresson, 1879

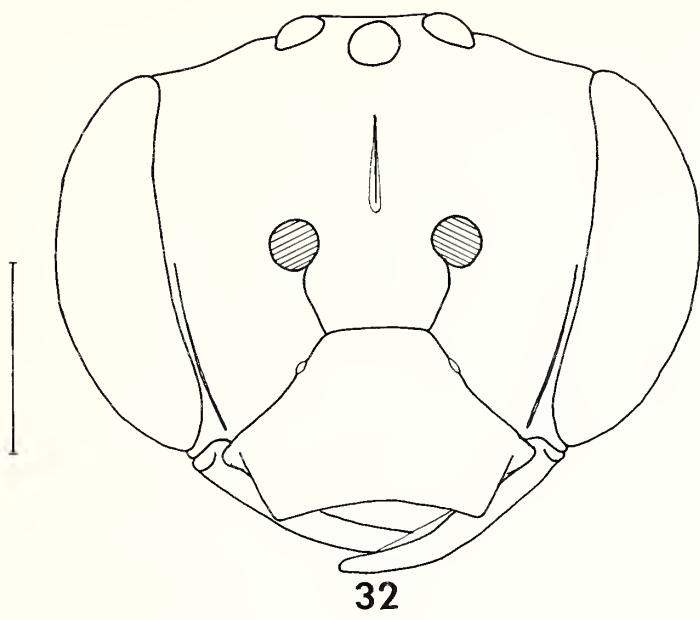
Subgenus *Laminomomada* Rodeck

Figures 38–44

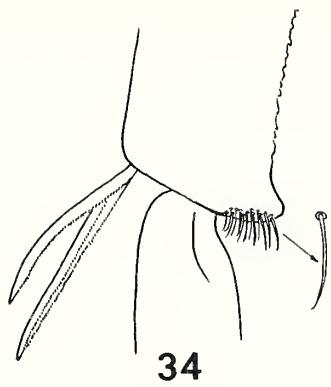
Nomada subg. *Laminomomada* Rodeck, 1947:266. Type-species: *Nomada hesperia* Cockerell, 1903c; original designation.

DIAGNOSIS. Minimum length of first flagellar segment greater than maximum length of second; procoxa with conical distal process; pro- and mesofemur of male expanded; labrum shiny on basal half between distinctly separated punctures; female metatibia with a single irregular row of 8–11 coarse setae at apex.

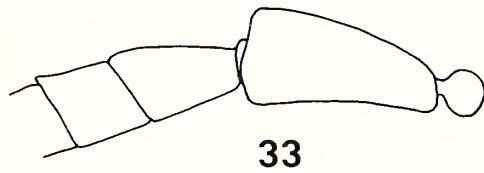
DESCRIPTION. (1) Mandible without preapical tooth. (2) Minimum length of first flagellar segment greater than maximum length of second; segments 3–10 of male without conspicuous ridges or tubercles. (3) Posterior margin of gena subangulate but not cariniform. (4) Procoxa with short, conical process at apex. (5) Propodeum weakly swollen mesad of spiracle. (6) Tergum 2 densely and finely punctate, with very narrow impunctate margin. **Male.** (7) Apex of pygidium



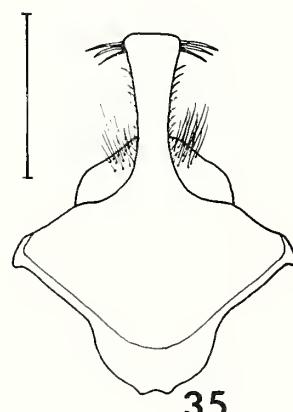
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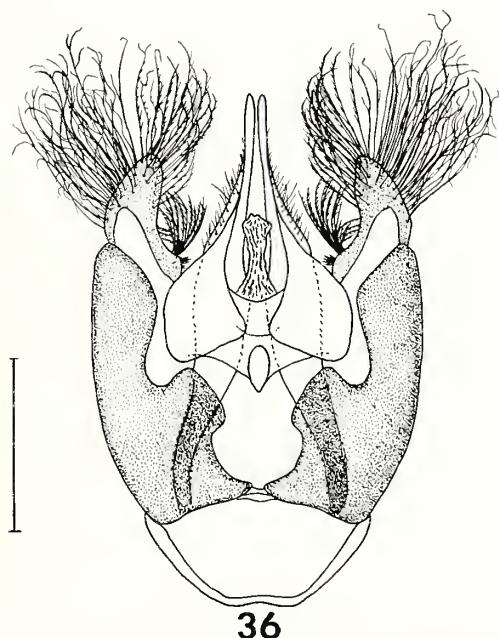
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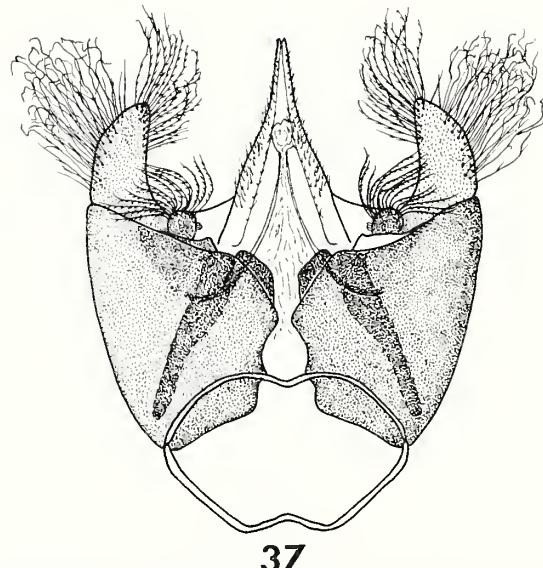
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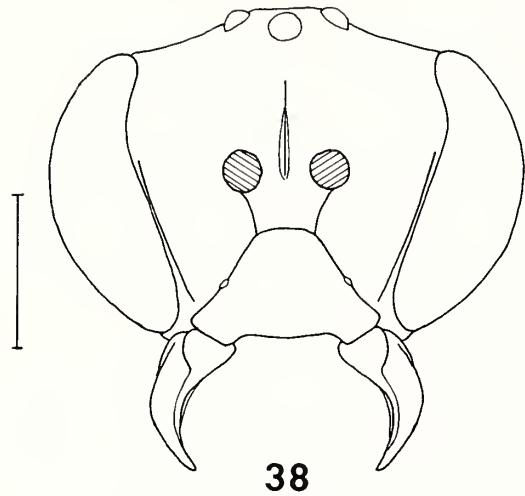


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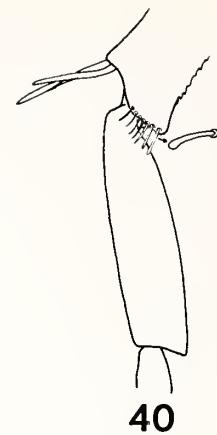
Figures 32–37. *Nomada (Holonomada) superba*. 32, frontal view of female head (scale line = 1.00 mm); 33, basal segments of male antenna; 34, apex of female metatibia; 35, male sternum seven (scale line = 0.50 mm); 36–37, male genitalia, dorsal and ventral (scale line = 0.50 mm).



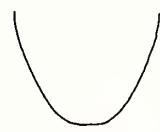
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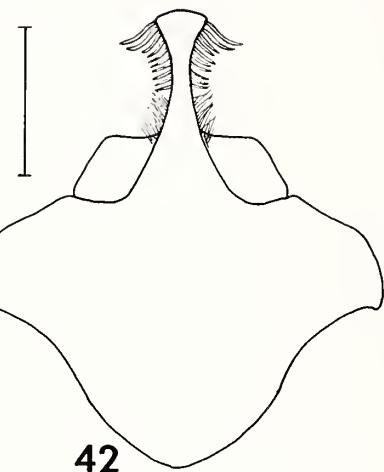
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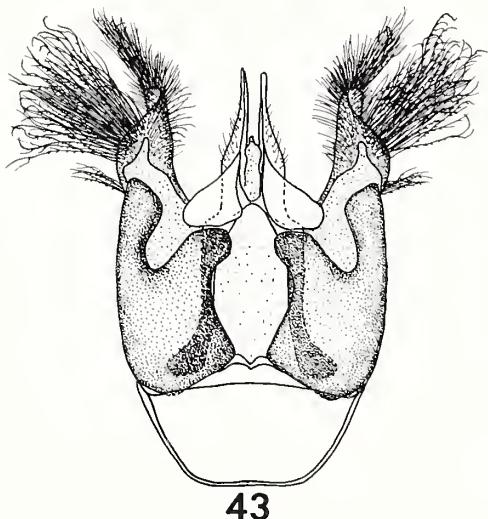
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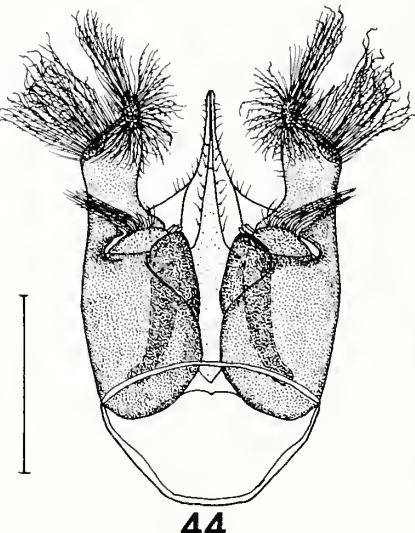
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Figures 38–44. *Nomada (Laminomada) hesperia*. 38, frontal view of female head (scale line = 1.00 mm); 39, basal segments of male antenna; 40, apex of female metatibia; 41, apex of female pygidium; 42, male sternum seven (scale line = 0.50 mm); 43–44, male genitalia, dorsal and ventral (scale line = 0.50 mm).

without median notch. (8) Process of sternum 8 short, slender, broadened distad, apex deflected. (9) Inner dorsal lobe of gonocoxite broad, invagination between inner and outer lobes deep; median sinus longer than broad. (10) Gonostylus with setose basoventral lobe and with seta-cluster on inner basal margin. (11) Aedeagus without ventral hook. **Female.** (12) Paraocular ridge present. (13) Metatibia with a single irregular row of 8–11 long, slender ferruginous setae. (14) Apex of pygidium broadly rounded, without median notch.

DISCUSSION. This subgenus is very close to *Holonomada* and perhaps should be merged with it although there are conspicuous differences, especially in the structure of the pro- and mesofemur and the metabasitarsus of the male. The female is much more like that of such *Holonomada* species as *N. edwardsii* and the differences are those which normally differentiate species.

The single species of *Laminomada* ranges from southeastern Washington to southern California. The flight period is from late March to early June. The host is unknown.

INCLUDED NAMES

- falconis* Rodeck, 1947
- flavopicta* Swenk, 1913
- hesperia* Cockerell, 1903c

Subgenus *Pachynomada* Rodeck

Figures 45–51

Nomada subg. *Pachynomada* Rodeck, 1945:180. Type-species: *Nomada vincta* Say, 1837; original designation.

DIAGNOSIS. Minimum length of first flagellar segment equal to, or exceeding, maximum length of second; genal margin rounded to weakly angulate; female metabasitarsus swollen, broadest near middle; female pygidium broadly U-shaped; male aedeagus with ventral hook.

DESCRIPTION. (1) Mandible without preapical tooth. (2) Minimum length of first flagellar segment at least equal to maximum length of second; male without conspicuous ridges or tubercles on segments 3–10. (3) Posterior margin of gena rounded to weakly angulate. (4) Procoxa without distal spine. (5) Propodeum not swollen mesad of spiracle. (6) Tergum 2 densely and finely punctate, with narrow impunctate apical margin (except *N. vinctrix*). **Male.** (7) Apex of pygidium broad, rounded, sometimes with weak median notch. (8) Process of sternum 8 slender, apex weakly deflected. (9) Inner dorsal lobe of gonocoxite very broad and weak; invagination between inner and outer lobes broad, weak; median sinus longer than broad, margins straight or nearly so. (10) Gonostylus without setose basoventral process or inner basal seta-cluster. (11) Aedeagus with ventral hook. **Female.** (12) Paraocular ridge present. (13) Metatibia with short to very short, well separated apical spines. (14) Apex of pygidium broadly U-shaped, without median notch.

DISCUSSION. To this subgenus are assigned a few uncommon summer and fall species. The species are mostly western. Males are further distinguished from those of other subgenera by the distinctly swollen antennal scape. The

hooked aedeagus is apparently unique. Females are less easily characterized. The metabasitarsus is somewhat swollen and widest near the middle, the pygidium is usually broadly U-shaped and the posterior margins of the gena are rounded or, less commonly, weakly angulate.

This, and the two remaining subgenera, *Nomadita* and *Phelonomada*, share an unusual feature within the genus. In all three the face, adjacent to the inner eye margins, is more or less distinctly convex. In the subgenera *Nomada*, *Holonomada*, and *Laminomada*, the face is concave between the inner eye margins.

There are other parallels between these three subgenera: they are summer or fall flying, are largely western in distribution, have reduced erect pubescence on head and thorax, and all possess a relatively long first flagellar segment.

Thus, *Pachynomada*, *Nomadita*, and *Phelonomada* rather closely resemble many species of *Hypochrotaenia* (*Micronomada*). These similarities prompted Moalif (1979) to opine that *Pachynomada* and *Nomadita* (as *Callinomada*) were probably more closely allied to *Micronomada* than to other groups of *Nomada*. However, the pronotal and genitalic characteristics of these three subgenera are unlike those of *Micronomada*. *Micronomada* females lack the paraocular ridge (true, also, of *Phelonomada*). These parallels are interesting but do seem to be examples of character convergence rather than of phyletic propinquity.

Pachynomada has been revised by Moalif (1979). Eleven species were recognized, four of which are yet undescribed. Two species (*N. morrisoni* and *N. adducta*), formerly placed in *Pachynomada*, were excluded; *N. morrisoni* is here assigned to subgenus *Nomada* and *N. adducta* is tentatively placed in *Nomadita*.

An undescribed species has been reported to be cleptoparasitic in nests of *Andrena* (*Callandrena*) *helianthi* by Parker and Bohart (1983). The same species of *Pachynomada* has also been seen leaving a nest of *A. (C.) haynesi* (Parker and Griswold, 1983).

INCLUDED NAMES

- asteris* Swenk, 1913
- aztecorum* Cockerell, 1903a
- besseyi* Swenk, 1913
- heterochroa* Cockerell, 1921
- pratensis* Cockerell, 1919b
- suffosa* Cockerell, 1922b
- vinctrix* Cockerell, 1911a
- vincita* Say, 1837
- vitticollis* Cresson, 1878
- zebrata* Cresson, 1878

Subgenus *Nomadita* Mocsáry

Figures 52–57

Nomadita Mocsáry, 1894:37. Type-species: *Nomadita montana* Mocsáry, 1894; monobasic.

Nomada subg. *Callinomada* Rodeck, 1945:181. Type-species:

Nomada antonita Cockerell, 1909a; original designation.
NEW SYNONYMY.

DIAGNOSIS. Minimum length of first flagellar segment equal to, or exceeding, maximum length of second; propodeum not swollen mesad of spiracle; genal margin subcarinate; male sternum 8 rather broad, margins tapering distally; female metabasitarsus broadest near base; propodeum bare or nearly so, with little or no erect hair.

DESCRIPTION. (1) Mandible without preapical tooth. (2) Minimum length of first flagellar segment equal to, or greater than, maximum length of second; male without conspicuous ridges or tubercles on segments 3–10. (3) Posterior margin of gena usually subcarinate. (4) Procoxa simple or with distal process. (5) Propodeum not swollen mesad of spiracle. (6) Tergum 2 finely and densely punctate, apical impunctate margin very narrow. **Male.** (7) Apex of pygidium rounded, entire or with broad, shallow emargination. (8) Process of sternum 8 broad at base, margins convergent distad. (9) Inner dorsal lobe of gonocoxite poorly defined, subacute; invagination between inner and outer lobes broad, shallow; median sinus longer than broad. (10) Gonostylus without setose basoventral lobe or inner, basal cluster of short, flattened setae. (11) Aedeagus without ventral hook. **Female.** (12) Paraocular ridge present. (13) Metatibia with 4–6 short, acute, flattened spines at apex. (14) Apex of pygidium broadly rounded to subacute.

DISCUSSION. The North American components of *Nomadita* have in the past been placed in *Callinomada*. Comparison of these with such European species as *N. montana* (Mocsáry), *N. roberjeotiana* Panzer, and *N. rufipes* Fabricius, convinces me that *Callinomada* is not essentially different from *Nomadita*. The pygidium of the females of the North American species is more broadly rounded than in the European species, but the two groups are otherwise sufficiently similar that their separation seems pointless.

Although externally very similar to species of *Pachynomada*, those of *Nomadita* differ sharply in characters of the male genitalia and associated structures. Both sexes differ from *Pachynomada* in smaller size, slender metabasitarsi, and the sharply angulate to subcarinate posterior genal margin. The broad, distally tapering sternum 8 of the male is apparently unique in *Nomada*, but similar to that of *Hypo-*

pochrotaenia. All other features place *Nomadita* with *Nomada* rather than *Hypochorotaenia*.

The few species of *Nomadita* appear to be uncommon. They are summer and autumnal fliers and mostly western. The hosts are unknown but may be an autumnal group of *Andrena*, possibly of the subgenus *Cnemidandrena*.

The North American species were revised (as *Callinomada*) by Rodeck (1949). One species was added by Mitchell (1962).

INCLUDED NAMES

- ? *adducta* Cresson, 1878
antonita Cockerell, 1909a
aquilarum Cockerell, 1903a
cockerelli Graenicher, 1911
dacotensis Swenk, 1913
mutans Cockerell, 1910c
omahaensis Swenk, 1915
placida Cresson, 1863
rodecki Mitchell, 1962
snowii Cresson, 1878
vereunda Cresson, 1879

Phelonomada new subgenus

Figures 58–63

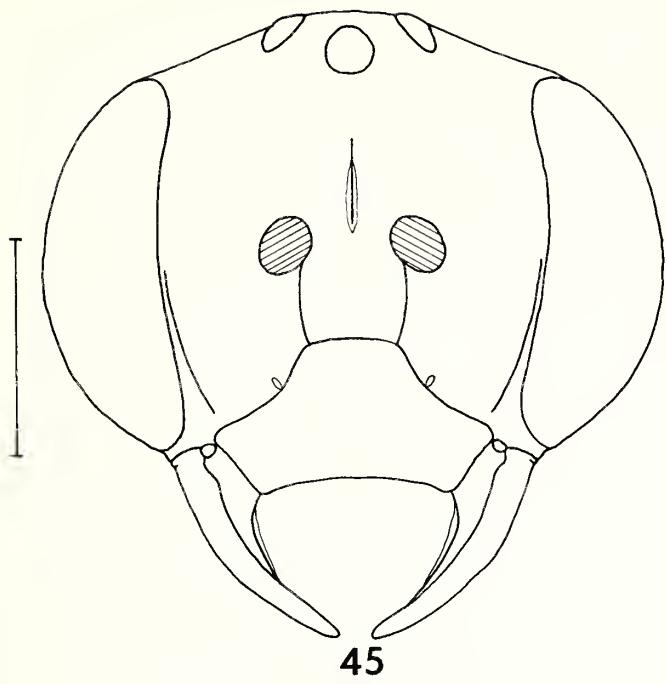
DIAGNOSIS. Minimum length of first flagellar segment equal to maximum length of second; procoxa with short distal spine; gastric terga sharply, closely punctate and with narrow impunctate apical margin; female without paraocular ridge; inner dorsal lobe of male gonocoxite elongate, triangular.

DESCRIPTION. (1) Mandible without preapical tooth. (2) Minimum length of first flagellar segment equal to maximum length of second; segments 3–10 of male without conspicuous ridges or tubercles. (3) Gena narrow, posterior margin rounded. (4) Procoxa with short distal spine. (5) Propodeum not swollen mesad of spiracle. (6) Tergum 2 sharply, closely punctate on disc and apical depression, impunctate apical margin narrow. **Male.** (7) Apex of pygidium entire or with weak median notch. (8) Process of sternum 8 slender, more or less parallel-sided and with deflected apex. (9) Inner dorsal lobe of gonocoxite elongate, apex acute; invagination between inner and outer lobes broad, deep; me-

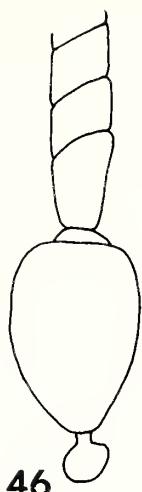
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Figures 45–51. *Nomada (Pachynomada) vincta*. 45, frontal view of female head (scale line = 1.00 mm); 46, basal segments of male antenna; 47, apex of female metatibia; 48, male sternum seven (scale line = 0.25 mm); 49–51, male genitalia, lateral, dorsal, and ventral (scale line = 0.50 mm).

Figures 52–57. *Nomada (Nomadita) montana*. 57, frontal view of female head (scale line = 1.00 mm); 53, basal segments of male antenna; 54, apex of female metatibia; 55, male sternum seven (scale line = 0.25 mm); 56–57, male genitalia, dorsal and ventral (scale line = 0.50 mm).

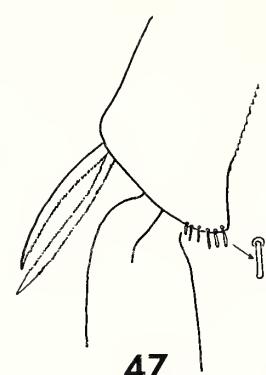
Figures 58–63. *Nomada (Phelonomada) belfragei*. 58, frontal view of female head (scale line = 1.00 mm); 59, basal segments of male antenna; 60, apex of female metatibia; 61, male sternum seven (scale line = 0.25 mm); 62–63, male genitalia, dorsal and ventral (scale line = 0.50 mm).



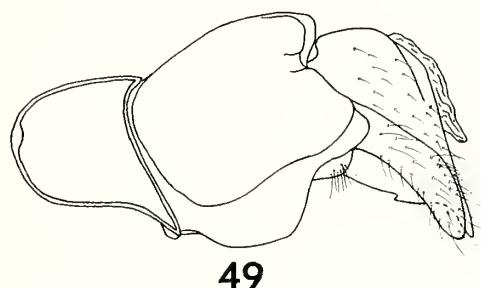
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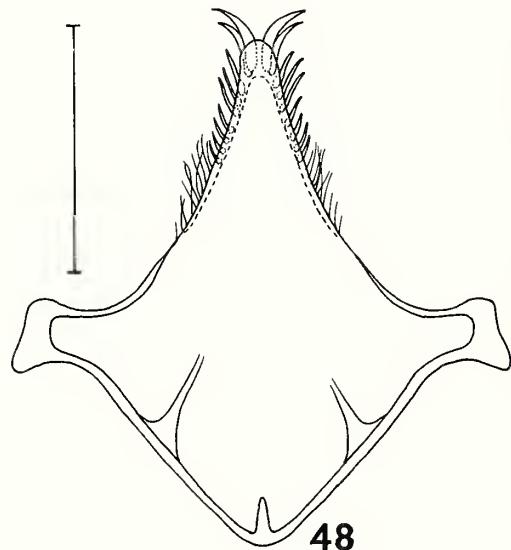
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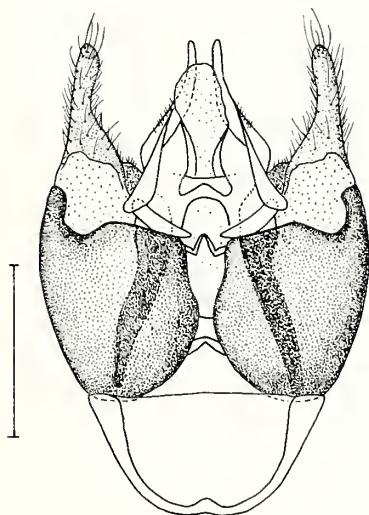
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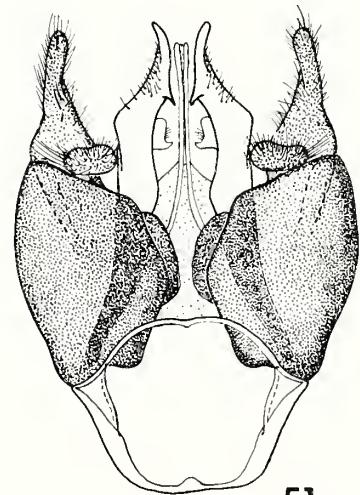
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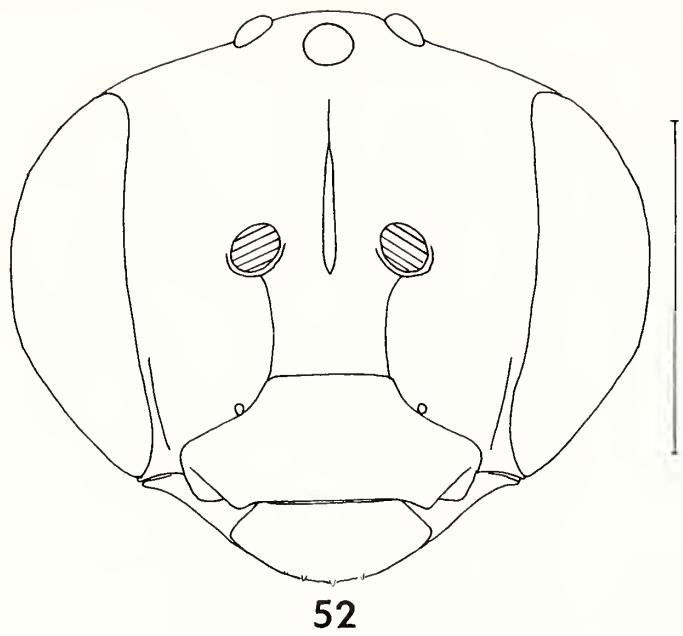
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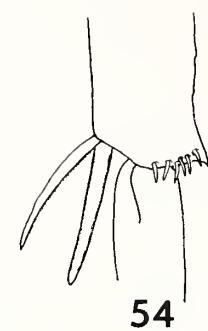
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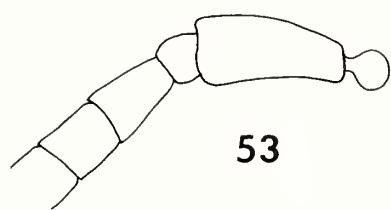
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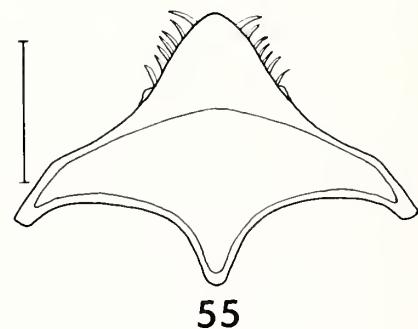
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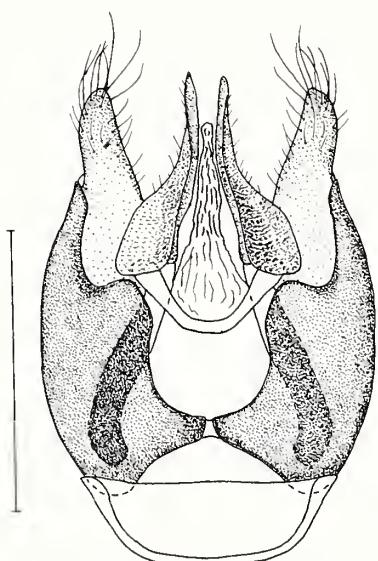
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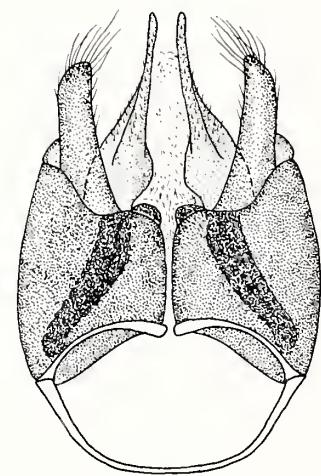
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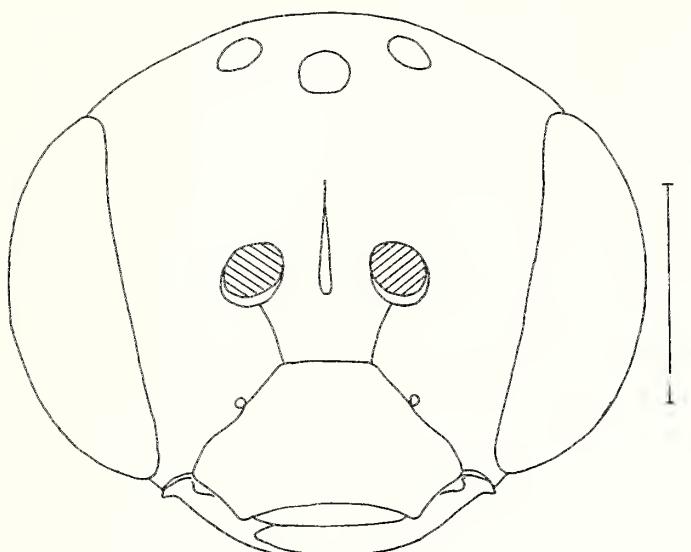
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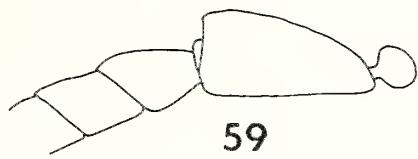
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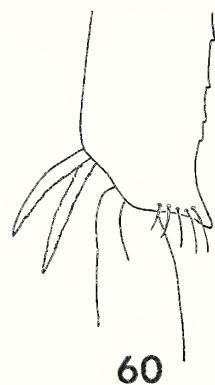
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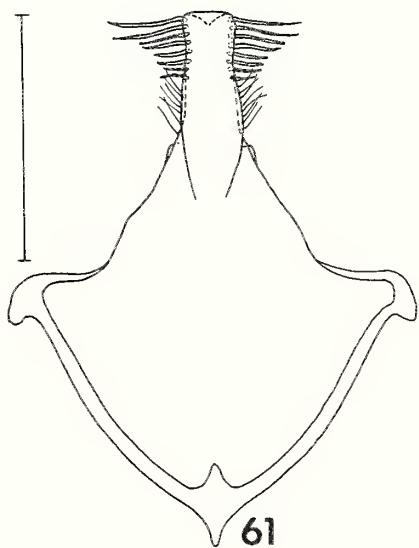
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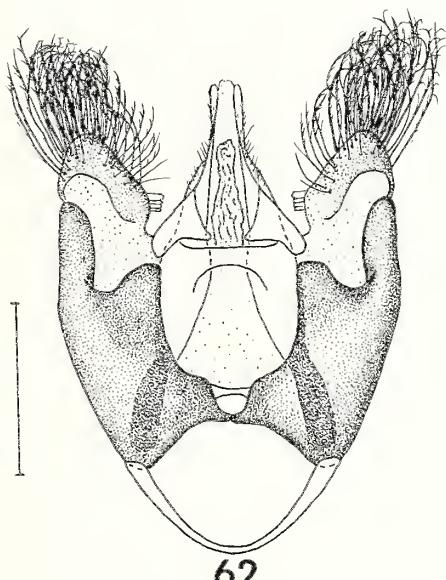
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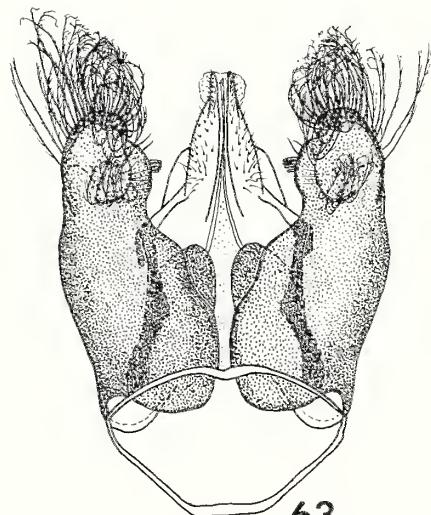
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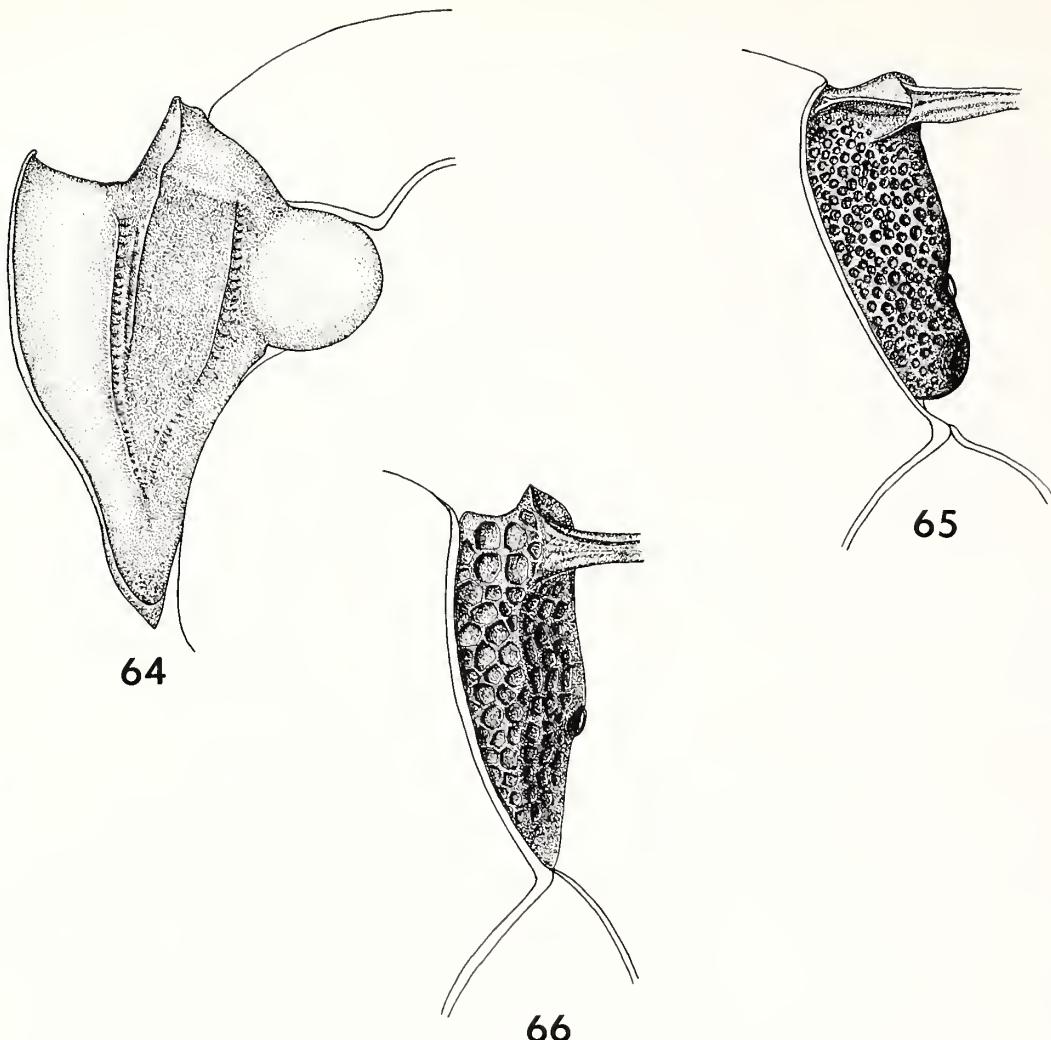
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Figures 64–66. Thoracic structures of: 64, *Nomada* (*N.*) sp., pronotum; 65, *Centrias articulata*, metapleuron; 66, *Nomada* (*N.*) sp., metapleuron.

dian sinus broader than long. (10) Gonostylus with weak setose basoventral lobe and with inner, basal cluster of very short, flattened setae. (11) Aedeagus without ventral hook. **Female.** (12) Paraocular ridge absent. (13) Metatibia with a row of 4–5 slender, pale, well-separated setae at apex. (14) Apex of pygidium narrowly rounded, entire.

TYPE SPECIES. *Nomada belfragei* Cresson, 1878.

ETYMOLOGY. Gr., *phelos* (false or deceitful) + *Nomada*.

DISCUSSION. Superficially, the forms placed here very closely resemble species of *Hypochrotaenia*, subg. *Micronomada*, with which they have usually been associated. The male terminalia and the structure of the pronotum, however, ally *Phelonomada* with *Nomada*. This is the only group of *Nomada* in which the females lack the paraocular ridge.

The few species of *Phelonomada* fly in late spring (April and May) and range from Kansas to central Texas. Hosts are unknown, but probably will be found to be halictids, either *Agapostemon* or *Nomia*.

INCLUDED NAMES

- belfragei* Cresson, 1878
- engelmanniae* Cockerell, 1911a
- wheeleri* Cockerell, 1903d
- xanthogaster* Cockerell, 1911a

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Charles L. Hogue and Ted Georgian

DESCRIPTION OF A NEW SPECIES OF THE SHORE FLY GENUS
DIEDROPS (DIPTERA: EPHYDRIDAE) FROM COLOMBIA

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**RECENT DISCOVERIES IN THE *BLEPHARICERA TENUIPES* GROUP,
INCLUDING DESCRIPTIONS OF TWO NEW SPECIES FROM
APPALACHIA (DIPTERA: BLEPHARICERIDAE)**

Charles L. Hogue and Ted Georgian

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DIEDROPS (DIPTERA: EPHYDRIDAE) FROM COLOMBIA**

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RECENT DISCOVERIES IN THE *BLEPHARICERA TENUIPES* GROUP, INCLUDING DESCRIPTIONS OF TWO NEW SPECIES FROM APPALACHIA (DIPTERA: BLEPHARICERIDAE)

Charles L. Hogue¹ and Ted Georgian²

ABSTRACT. Two new species of *Blepharicera* (*B. appalachiae* and *coweetae*) are described in the *Blepharicera tenuipes* group. Both occur in the southern half of the Appalachian Mountains in eastern North America, the former of wide distribution, the latter restricted to a small portion of the upper Little Tennessee drainage. A key to all the known stages in the *B. tenuipes* group is provided along with new information on ecology, distribution, and phylogeny (for which the sister *Blepharicera micheneri* group is newly recognized).

INTRODUCTION

At the time of his review of the net-winged midges of eastern North America, Hogue (1978) preferred not to make definite identifications of the immatures of any species because of the uncertainty of stage associations until better material could be acquired. He was also unable to distinguish more than one pupal type. The recent availability of numerous specimens, including some valuable individual rearings, collected in the vicinity of the United States Forest Service's Coweeta Hydrologic Laboratory (Macon County, North Carolina) by Georgian and associates, has now made it possible to separate pupae of five of the eastern species. Using integumentary characters of this intermediate stage, we can also identify several of the larvae by inspection of prepupal larvae and pharate adults.

These integumentary characters include the patterns and detailed structures of the papillae and cuticular ornamentation of the abdominal tergites. Streams in the Coweeta locality produce two very distinctive pupal types, the adults of which show small, but consistent features that distinguish them from existing species. They are considered new species and are described here.

Other discoveries in the *Blepharicera tenuipes* group also are presented. Complete synonymies are reserved for a monographic treatment of the Blephariceridae of North America soon to be published (Hogue, in press).

MATERIALS AND METHODS

MATERIALS

Most of the new material used for this study was collected by T. Georgian and D.H. Ross, and placed in the University

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of Georgia Entomological Museum and the Entomology Section of the Natural History Museum of Los Angeles County. However, some paratypes are deposited in the U.S. National Museum of Natural History. See the Acknowledgment section for explanations of abbreviations used for sources of other specimens.

A number of larvae and adults of *B. appalachiae* were considered by Hogue (1978) as a variant of *B. tenuipes* (Walker, 1848). These specimens have been reevaluated and some identifications modified. All those that are now determined as belonging to the new species are listed here; the others cited in that paper as "Atypical adults" (p. 23) and "Larva E" (p. 30) are still of uncertain identity.

TERMINOLOGY

The terminology used in this paper is mostly that established in Hogue's (1978, 1981) earlier treatments of blepharicerid anatomy. One important change is the application of the name "lateral tine" to the prong-like, tubular rods lateral to and paralleling the aedeagal filaments and which have been called "parameres" in most previous works on the family. The tines appear to be secondary developments of the ventral plate (whose presence is probably plesiomorphic for the family) as proposed by Stuckenbergh (1958:101). They are represented either by (1) no more than mere pigmented straps, or (2) as columnar projections without a lumen. The first case occurs in *Blepharicera micheneri* and its close relatives in western North America; the second is the condition in *Paltostoma*, as seen in Hogue's (1979) figures of Costa Rican species. Blepharicerid tines are possibly homologous to similar structures given the same name in the terminalia of tabanids by Bonhag (1951:161, 198).

The neutral term "gonites" is used here for the large, wide plates subtending and sometimes surrounding the base of the

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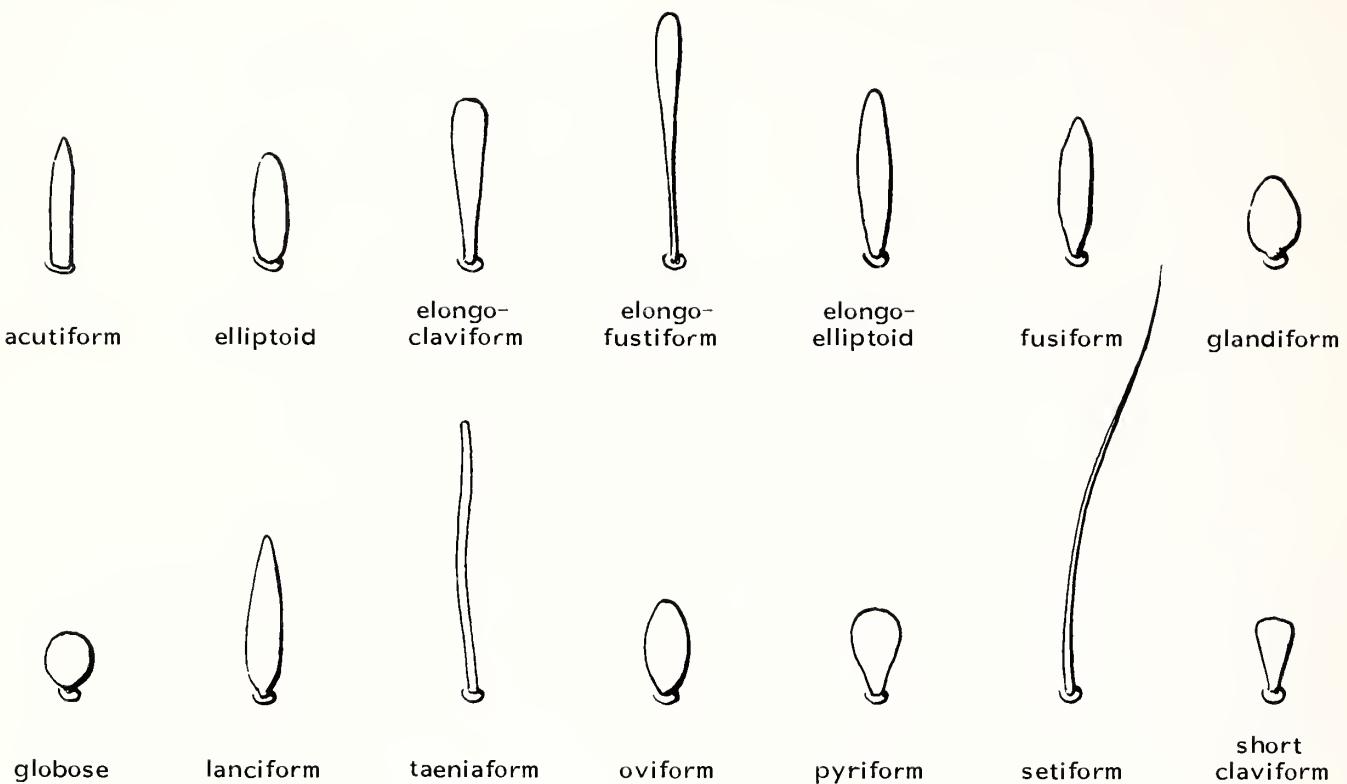


Figure 1. Various forms taken by the modified, dorsal secondary sensilla of the larvae of the *Blepharicera tenuipes* group. Names as used in descriptions.

aedeagus that have been also called "parameres" by authors (McAlpine, 1981:51f). According to G.C.D. Griffiths (pers. comm.), the latter term should be reserved presently for quite distinct organs in other insect orders and not applied to the Diptera until controversies in homologies can be settled.

Leg segment proportions are expressed "progressively," that is, each segment is compared to its proximal neighbor rather than to one standard segment (customarily the most basal segment).

The various forms taken by the modified (generally short, peg-like), dorsal secondary sensilla of the larvae are described with adjectives whose precise definition can be appreciated by the shapes labelled in Figure 1 (only those displayed by species included in this paper are given). See Hogue (1978) for designations of primary setae.

MEASUREMENTS

All measurements are made from topotypic material, unless otherwise noted, and cited in millimeters. The first value represents the mean of the number of specimens indicated by N; values following in parentheses are range extremes. Larval body length is taken only on prepupal specimens (i.e., those showing some trace of pupal branchiae). Adult proboscis length is approximate, measured from a point level with the venter of the eyes to the apex of the labella. The

formula for expressing comparative sizes of male vs. female pupae is $(L)(W)$ male/ $(L)(W)$ female. Meristic counts of sensilla are cited for one side of bilateral structures as absolute values "(20)" or ranges "(15-20)"; where it is necessary to cite different values for each side, a double parenthetic notation is used "(5)(15)".

Blepharicera tenuipes Group

PHYLOGENY

With the addition of the two new species described in this paper the *Blepharicera tenuipes* group contains eight species, all restricted in geographic occurrence to the eastern United States (Appalachians, northward to Hudson's Bay and Labrador, westward to eastern Minnesota). We consider them very closely related and all descended from a single ancestor, as did Hogue (1978).

It has not yet been possible to arrive at a clear phylogeny of the species within the group, because of their homogeneity and incongruous variation in many characters. These blepharicerids are so alike morphologically that relatively few synapomorphies can be distinguished, except one found in the male terminalia. Also, a reticulate pattern of the following synapomorphies emerges when they are applied toward construction of a cladogram:

1. Inner margin of the Xth tergite lobe convexly expanded medially. A simple, straight inner margin is the plesiomorphic condition.

2. A slight to well-developed apicomедial, dorsal carina present on the tegmen. The plesiomorphic tegmen is flat apically.

3. Apex of lateral tine with a conspicuous recurved hook. A simple apex is plesiomorphic but other autapomorphies are common.

4. Apex of tegmen strongly emarginate on either side of median carina. The plesiomorphies entire to weakly emarginate, may actually be reduction apomorphies correlated with small size in those species with this condition. The deep emargination nevertheless is a strongly positive apomorphy.

5. Median aedeagal filament decidedly heavier than laterals.

6. Many integumentary papillae of pupal tergites occurring in diads. These papillae are normally more or less evenly spaced on the sclerites.

Most of the species are closely related to and similar to *tenuipes*, judging from the common shape of the Xth tergite lobe (quadrate with distinct triangular apical sublobe). This configuration may be considered plesiomorphic to the type found in *williamsae* Alexander, 1953, *capitata* Loew, 1863, and *similans* Johannsen, 1929, that have a greatly expanded medial margin, and therefore not a reliable state for indicating relationships. Among these latter three species, the heavy (synapomorphic) median aedeagal filament would seem to indicate a close relationship between the first two, but the very different *similans* could have closer affinities with the *tenuipes* cohort than with the other two species because of its somewhat more similar Xth tergite lobe. Among the species clearly similar to *tenuipes*, *cherokeea* Hogue, 1978, and *diminutiva* Hogue, 1978, segregate by their smallness, a dubious synapomorphy when reduction in size can occur often in this midge family. Complicating the picture still more is the presence of a fairly strong apical carina on the tegmen in *williamsae* which relates it toward *tenuipes* and its close relatives, but away from *capitata*. Among the latter, *appalachiae* and *tenuipes* seem closely related on the basis of the common occurrence of irregular diad formations in the patterns of integumentary papillae on the pupae.

Therefore, at this stage of knowledge of the *Blepharicera tenuipes* group, we refrain from attempting a cladogram. More analysis of characters is needed before a clear selection of phylogenetically significant states can be ascertained. The possibility of hybridization between species may also have affected their evolution. Ultimately, it may be necessary to resort to chromosomal or biochemical analyses to detect interrelationships.

ZOOGEOGRAPHY

Zwick (1984) proposed a preliminary phylogeny of the genus *Blepharicera*. He considered the species of the western United States (with the exception of *B. ostensackeni*, here called the “*Blepharicera micheneri* group”), the sister group to the *B. tenuipes* group. The ancestral stock of both groups probably

arrived in North America from Asia because most *Blepharicera* reside there. The single European species belongs to a distinct group. This hypothesis conflicts with Hogue’s earlier (1978:1–2) supposition of a fundamental division between the two stocks. He suggested that the former arrived in North America from the northwest, while the latter dispersed separately, and probably earlier, over an eastern connection with the Palaearctic Region.

Zwick’s arguments are convincing. The problem remains, however, of connecting the two lines paleogeographically, i.e., to answer the question, by what route did the *B. tenuipes* group reach eastern North America from the northwest? Also, what disruptive events forced the separation of the two groups?

Only a northern path across the Canadian Shield would seem a plausible answer to the first question, because a southern highland corridor was present no later than the Permian. It is unlikely that the *Blepharicerini* would have evolved before that time. Invasion of North America and movement eastward could have been associated with the mid-Cenozoic spread of the temperate deciduous forests, as supposed by Ross (1956) for various mountain caddisflies, such as the “*Rhyacophila Siberica* Group” (and “*Wormaldia Anilla* Group,” and subgenus *Doloclanae*—p. 181–182), with distributions identical to or concordant with the *Blepharicera* in question. Baumann (1975) also noted similar patterns in some rheophilic stoneflies (*Podmosta*). A newly discovered montane genus of limnephilid caddisfly bears very strong affinities to western forms and is believed to have dispersed across the northern deciduous forest and undergone subsequent speciation in the Appalachians (Hury and Wallace, 1984). The absence of *Blephariceridae* from the Ouachita and Ozark mountains, remnants of that intervening orogenic zone, and which surely would preserve some vestige of any past blepharicerid fauna, also provides evidence, albeit negative, in favor of the northern alternative.

The absence of a continuous east–west mountain chain along which these generally monticolous midges could have dispersed does not preclude the hypothesis of a northern route. *Blepharicera tenuipes* extends over low postglacial terrain in southeastern Canada, indicating the ability of these insects to colonize rapidly well-watered land with little relief. The distance between the most southern extreme of the Wisconsin ice sheet across Appalachia and the northernmost recorded Recent occurrence of the species is approximately 1500 km. The ice sheet began retreating from its terminal position about 15,000 years ago (Davis, 1983), giving the flies a dispersal rate of at least 0.1 km per year. To traverse the distance from the Rocky Mountains to the Appalachian Mountains (3500 km) would require about 35,000 years, an easy march, geologically speaking.

Increasingly arid conditions in the late Cenozoic undoubtedly forced the division of the eastern and western groups.

In North America, the greatest variety of species is concentrated in the southern Appalachian Highlands, particularly in the Blue Ridge area, an acknowledged important center of speciation and a refugium from glaciation (see the various papers listed in Holt, 1969). Although *Blephariceridae* are poorly vagile insects, three species (*B. tenuipes*, *sim-*

ilans, and *capitata*) dispersed considerable distances northward in the postglacial era. This seems to show that the adults can move across drainage boundaries fairly easily. Stream capture, while a common phenomenon in the geologic history of the area and significant for the dispersal of strictly aquatic organisms, is not their only means of colonization of new watersheds. However, *diminutiva* may have entered the Savannah drainage from the Little Tennessee when Steko Creek diverted the southern portion of the latter (south of Rabun Gap, Georgia) (Ross, 1971:32). The restricted distributions of *cherokeae* and *coweetae* to the Little Tennessee (Ohio drainage) and northward indicates their probable origin subsequent to this stream-capture event.

TAXONOMY

The *Blepharicera tenuipes* group was defined by Hogue (1978: 6–8) on the basis of the adult flies. A more complete description and definition will appear in Hogue (in press). Zwick (1984) demonstrated some new diagnostic features, in particular some correlated states in the mesosomal complex of the male terminalia, namely, the short, heavy lateral tines, small apodeme of the sperm pump, and anteriorly expanded gonite from which arises a large muscle narrowly inserting at the base of the aedeagal tine and lateral to which the outer aedeagal filament passes. In the *B. micheneri* group this muscle passes lateral to all the aedeagal filaments, which are much reduced in size. The former arrangement is an autapomorphy for the group.

Identification of larvae in the group is somewhat problematical. The following keys only apply to typical specimens in the mature, fourth instar. Atypical larvae may show a considerable variety of conditions of the shape and distribution of the dorsal, secondary sensilla which are the primary identifying characters. There are many intermediates and non-conformants (species appearing to be out of their range or associated with stages of distinct species) and these cannot be assigned with certainty to any species. Therefore, many of the larval records cited by Hogue (1978) are suspect. Only detailed biological work with these Diptera can hope to shed light on the causes and significance of larval variability. Introgression among the closely related members of the group is suspected.

KEY TO ADULT MALES

(Based on the terminalia; slide mounts normally required to see structures)

- 1a. Medial aedeagal filament distinctly longer than laterals and with asymmetrical, hooked apex. Apex of lateral tine incurved, asymmetrically bifurcate. Outer corner of Xth tergite lobe slightly obtusely angulate, inner margin shallowly convex *similans*
- 1b. Medial aedeagal filament about same length as laterals and with simple apex. Apex of lateral tine not bifurcate. Shape of Xth tergite lobe varied 2

- 2a. Medial aedeagal filament distinctly thicker than laterals. Inner margin of Xth tergite lobe convexly expanded 3
- 2b. Medial aedeagal filament similar to laterals. Inner margin of Xth tergite lobe straight 4
- 3a. Inner wall of lateral tine incurved, apex acute and extending well beyond aperture. Inner margin of Xth tergite lobe expanded angularly to or beyond midline. Larger species, wing length 4.9–6.6 mm *williamsae*
- 3b. Inner wall of lateral tine very slightly produced, truncate, with a minute, pointed, dorsal projection, aperture terminal. Inner margin of Xth tergite lobe expanded evenly and moderately, far short of midline. Smaller species, wing length 4.8–5.3 mm *capitata*
- 4a. Apex of tegmen deeply incised on either side of strong, medial dorsal carina. Tip of lateral tine complex, with dorsally recurved, stout hook (Figs. 5, 9) 5
- 4b. Apex of tegmen weakly incised or entire on either side of weak, medial dorsal carina. Tip of lateral tine simple 7
- 5a. Interlobular space (between Xth tergite lobes) U-shaped (Fig. 8) 6
- 5b. Interlobular space V-shaped (Fig. 8) *coweetae*
- 6a. Posteromedial triangular sublobe of Xth tergite lobe situated midway along posterior margin *tenuipes*
- 6b. Posteromedial triangular sublobe of Xth tergite lobe displaced nearly to inner corner (Fig. 4) *appalachiae*
- 7a. Posteromedial triangular sublobe of Xth tergite lobe conspicuous, well produced; outer corner of lobe obtusely rounded *cherokeae*
- 7b. Posteromedial triangular sublobe of Xth tergite lobe minute and barely produced; outer corner of lobe acutely rounded *diminutiva*

KEY TO ADULT FEMALES

(Slide mounts required to see details of terminalia; wing lengths given for confirmation)

- 1a. Two spermathecae, medial reduced to a narrow cylindrical rod. Wing length 5.4–7.3 mm *similans*
- 1b. Three spermathecae 2
- 2a. Ducts of lateral spermathecae sclerotized for a short distance before genital aperture. Wing length 5.2–6.4 mm *capitata*
- 2b. Ducts of spermathecae membranous throughout 3
- 3a. Scutum with a contrasting, light brown, quadrate area anterior to scutellum. VIIth sternite lobe of terminalia devoid of setae. Spermathecae spherical. Large species; wing length usually 7.2 mm or greater *williamsae*
- 3b. Scutum generally unicolorous. VIIth sternite lobe of terminalia usually with several setae, at least one. Smaller species; wing length 7.1 mm or less 4
- 4a. VIIth sternite lobes of terminalia contiguous, medial depression V-shaped. Very small species; wing length about 5.1 mm *diminutiva*
- 4b. VIIth sternite lobes of terminalia disjunct, medial depression U-shaped. Larger species; wing length 5.5 mm or greater 5

Note: Remaining species very difficult to distinguish. Following continuation of key is for typical specimens only. Wing lengths overlap.

- 5a. Accessory gland narrow throughout, apparently (one specimen available) sclerotized and pigmented anteriorly *cherokeae*
- b. Accessory gland widened at some point, unpigmented throughout 6
- 6a. Accessory gland very wide posteriorly, twice narrowed anteriorly. Lobe of hypogynial plate apically truncate *tenuipes*
- b. Accessory gland moderately wide posteriorly, narrowing once anteriorly. Lobe of hypogynial plate variously shaped 7
- 7a. Anterior portion of accessory gland straight, parallel-sided. Lobe of hypogynial plate broadly rounded apically *appalachiae*
- b. Anterior portion of accessory gland dilated. Lobe of hypogynial plate narrowly rounded *coweetae*

KEY TO PUPAE

(Pupae of *capitata*, *diminutiva*, and *cherokeae* unknown)

- 1a. Integument of abdominal tergites with a fine, reticulate pattern (Figs. 20, 25); surface dull. Larger (length usually 5.5 mm or greater) *williamsae*
- b. Integument of abdominal tergites homogeneous or otherwise sculptured, no reticulate pattern; surface shiny. Smaller (length usually less than 5.5 mm) 2
- 2a. Integument of abdominal tergites showing minute wavy furrows between and connecting the papillae. Papillae minutely spinulate (Figs. 18, 22) *coweetae*
- b. Integument of abdominal tergites between papillae uninterrupted by cuticular furrows or lines. Papillae smooth 3
- 3a. Papillae, especially in region lateral to muscle scars of abdominal tergites clustered, unevenly distributed, often arranged in pairs or diads (Figs. 12, 17, 21, 24) 4
- b. Papillae all more or less evenly spaced (Figs. 19, 23) *similans*
- 4a. Frequent papillary diads in medial zone of abdominal tergites (between muscle scars) as well as lateral (Figs. 17, 21) *appalachiae*
- b. Papillae of median zone of abdominal tergites all more or less evenly spaced (Figs. 12, 24) *tenuipes*

KEY TO LARVAE

(Larvae of *capitata*, *cherokeae*, and *diminutiva* unknown.)

Larva "F" (Hogue, 1978) apparently an aberration of other species; see below)

- 1a. Dorsal secondary sensilla mostly setiform (Fig. 13) (taeniaform to elongo-fustiform³ in many specimens) *appalachiae*

3. Latin: *fustis* = cudgel + *forma* = shape.

- b. Dorsal secondary sensilla mostly modified (capitate to claviform) present dorsally 2
- 2a. Modified sensilla large, globose, apically spinulate, clustered in vicinity of st and tp primary sensillae and anteromedially on segment (Fig. 15) *similans*
- b. Modified sensilla small to medium, mostly elongate forms, apically smooth, clustered or diffusely arranged 3
- 3a. Modified sensilla short claviform to pyriform, arranged generally in transverse anterior and posterior clusters, the latter including primary sensillum st (Figs. 10, 11) *tenuipes*
- b. Modified sensilla more or less generally distributed over segment (may be in broad transverse patterns but never clustered) 4
- 4a. Modified sensilla lanciform to fusiform, arranged in 3 broad transverse fields medially (Fig. 16). Dorsum longitudinally dark pigmented medially, light laterally *williamsae*
- b. Modified sensilla pyriform, glandiform or oviform, diffusely distributed (Fig. 14). Dorsal pigmentation uniform *coweetae*

DESCRIPTIONS OF NEW SPECIES

Blepharicera appalachiae, new species

Figures 2-5, 13, 17, 21, 26

Blepharicera tenuipes "Atypical (southern type)" of Hogue, 1978:21, fig. 24.

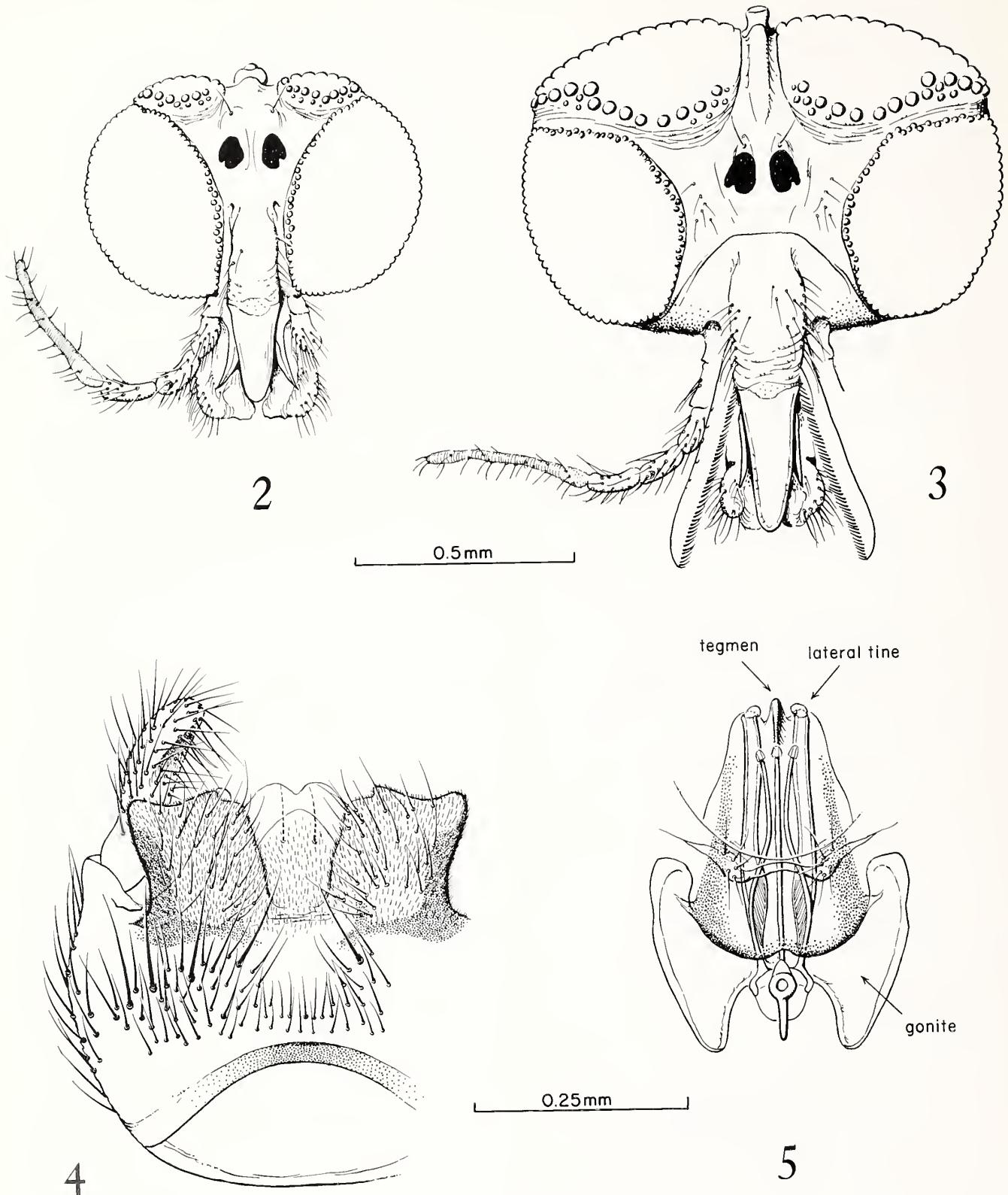
Larva "E" (partim) Hogue, 1978:29-30.

Larva "C" Hogue, 1978:28-29, fig. 35.

DIAGNOSIS. In the male terminalia, while all structures are otherwise virtually identical to those of *B. tenuipes* and other members of the *B. tenuipes* group, the posterior margin of the Xth tergite lobe is uniquely shaped: the outer corner is acutely rounded, followed medially by a deep concavity and central sublobe strongly displaced toward the inner corner. The secondary sensilla on the larval dorsum are typically setiform rather than peg-like or otherwise modified, as in *tenuipes* and other members of the group. (A few modified sensilla may intrude in some specimens.) The arrangement of the dorsal papillae distinguishes the pupa. The papillae are very irregularly arranged, neighboring pairs often coalescing into diads over the entire surface of the abdominal tergites, but more so in the outer areas lateral to the main muscle scars.

DESCRIPTION. Adult a small, sturdily built, well-sclerotized blepharicerid. Very similar to *B. tenuipes* and *cweetae*.

Male (Figs. 2, 4-5). *Coloration.* Generally dull gray-brown, pruinose. Mesoscutum concolorous, dull gray. (With illumination at some angles, lateral portions become translucent, reddish-brown, medial area longitudinally brown to blackish.) Corners of posterior pronotum and scutellum contrasting light brown, pleurites similar to scutum. Wing membrane completely hyaline. *Size.* A medium-sized *Blepharicera*.



Figures 2–5. *Blepharicera appalachiae*, new species. 2. Male head. 3. Female head. 4. Male terminalia, external structures (dorsal view). 5. Male terminalia, phallic structures (dorsal view).

Measurements (from non-topotypical material) (N = 10):
Wing length 5.3 (5.0–6.0). Leg segment lengths:

| | foreleg | midleg | hindleg |
|----------|------------------|------------------|------------------|
| femur | 3.2 (3.1–3.7) | 3.4 (3.2–3.9) | 4.6 (4.3–5.1) |
| tibia | 3.0 (2.9–3.3) | 2.9 (2.8–3.3) | 4.3 (4.0–4.8) |
| tarsus 1 | 1.6 (1.5–1.8) | 1.5 (1.4–1.7) | 1.7 (1.5–1.9) |
| 2 | 0.80 (0.76–0.89) | 0.74 (0.66–0.81) | 0.53 (0.46–0.62) |
| 3 | 0.55 (0.51–0.64) | 0.52 (0.48–0.57) | 0.35 (0.29–0.42) |
| 4 | 0.29 (0.27–0.36) | 0.29 (0.27–0.34) | 0.24 (0.22–0.29) |
| 5 | 0.29 (0.27–0.32) | 0.29 (0.27–0.34) | 0.28 (0.25–0.33) |

Head (Fig. 2). Structure: Normal type, subholoptic. Suprafrontal carina a rounded convexity. Clypeus elongate, L/W = 2.0. Eyes approximate dorsally, interocular distance equal to combined diameters of 5 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi narrow), much smaller (0.4×) than lower in area, 10–11 rows of ommatidia along mid-meridian; upper ommatidia slightly larger (1.4×) than lower in diameter. Proboscis short, free portion about 0.4× head width; mandibles completely absent; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.3–3.4. Antenna 15-segmented, flagellar segments elongate throughout, ultimate longer (1.4×) than penultimate, apical 3 segment proportions 1.0–1.0–1.4. Sensilla: Setiform groups on head capsule as follows: clypeals several (10), medium, only a few, small setae medially, more numerous and longer along distolateral margins. A single, medium strong seta over antennal socket; facial groups otherwise absent. Postocellars few (2–3), small, lateral. Medioccipitals absent. Supracervicals very numerous (30), tiny. Occipitals separated from and larger than postgenals, numerous (30), long. Postgenals numerous (17–26), smaller toward center of group.

Thorax and appendages. Structure: Wing venation typical for *Blepharicera*. Tibial spurs 0-0-1. Progressive leg-segment proportions: foreleg 0.9–0.6–0.5–0.7–0.6–0.9; midleg 0.8–0.5–0.5–0.7–0.6–1.0; hindleg 0.9–0.4–0.3–0.7–0.7–1.1. Sensilla: Macrotrichia on wing veins as follows: complete ventrally on R₄ and dorsally on R₅; apicodorsally only on M₁, M₂, and CuA1. Setiform groups on thoracic sclerites as follows: anterior pronotals apparently absent. Humeral callus with 4–5 small setae. Acrostical series short. Dorsocentral series apparently absent. Supraalar few (6–7), restricted to posterior and medial portions of sclerite. Prescutellars several (6). Scutellars medium-sized, forming a dense group on outer corner, numerous, similar, more widely spaced setae dispersed toward the midline. Metapleurals absent. Suprametapleurals few (3–4), small.

Terminalia (Figs. 4–5). Structure: Abdominal segment VIII greatly reduced, mostly membranous; tergite consisting of a short, medial, ligulate sclerite, sternite and pleurites undifferentiated. Epandrium simple, emarginate posteromedially. Xth tergite lobes well developed, prominent, parallel; interlobular depression deep, U-shaped; individual lobe shape quadrate, apex trilobate: outer sublobe acutely rounded; middle sublobe small, displaced toward inner corner, also slightly angled inwardly; inner sublobe right-angled; inner margin

straight, paralleling outer and extending directly to base of lobe; distal margin of lobe between outer and middle lobes slightly concave; inner arm poorly sclerotized, elongate, apex lobate, disjunct from same member opposite. Fused gonocoxites and hypandrium well sclerotized, forming capsule about as wide as long; posterolateral corners of gonocoxite strongly produced. Outer gonostylus large (length about 0.7× mid-line length of hypandrium), an entire, subrectangular, lobe with concave inner margin. Inner gonostylus a narrow, porrect, smooth, simple, digitiform projection. Phallic complex straight, supinate, not recurved. Aedeagal filaments equal, with slightly flared apices, outer filaments strongly bowed outward near bases; lateral tine longer than rods, broad throughout, tapering slightly to complex apex; latter with dorsal hook on inner wall; canal wide toward the base and containing numerous long spiculae, arising from inner wall and directed toward the apex; aperture subapical. Sperm pump and piston poorly developed, former without internal spines, latter with conspicuous, tubular ejaculatory atrium attached to apodeme; apodeme a small, ventral, vertical flange. Subanal pouch wide, bowl-shaped; tegmen broad, apex trilobate: deeply incised on either side of strong, vertical, medial carina. Gonite large, broad, ovate; gonocoxal lobe poorly developed, posterior lobe elongate, anterior lobe expansive, ventral bridge complete beneath basiphallus. Sensilla: Epandrium with numerous, short to long setiforms generally, these shorter toward the anterior. Xth tergite lobe with medium setiforms generally and evenly spaced over central portion dorsally these longer toward the apex; inner arm with few to several (5–8), small setiforms near apex. Fused gonocoxites and hypandrium ventrally with numerous, medium setiforms, these spaced generally only over posterior half. Outer gonostylus with very numerous, medium setiforms generally and evenly spaced over outer surface and marginally, absent from middle of inner face. Epiproct with few (4–6) alveoliforms in dorsolateral group. Hypoproct with few (3–4) long setiforms apically.

Female (Fig. 3). Coloration and measurements from non-topotypic material. **Coloration.** As in male, paired medial longitudinal lines present under some illumination. **Size.** A medium-sized *Blepharicera*. Measurements (N = 6): Wing length 6.7 (6.2–7.6). Leg segment lengths:

| | foreleg | midleg | hindleg |
|----------|------------------|------------------|------------------|
| femur | 3.8 (3.6–4.2) | 3.8 (3.4–4.2) | 5.3 (4.9–5.8) |
| tibia | 3.2 (2.9–3.5) | 3.2 (2.9–3.5) | 4.8 (4.4–5.3) |
| tarsus 1 | 1.6 (1.5–1.7) | 1.5 (1.4–1.7) | 2.1 (1.9–2.3) |
| 2 | 0.78 (0.72–0.82) | 0.77 (0.71–0.81) | 0.72 (0.65–0.78) |
| 3 | 0.49 (0.44–0.54) | 0.51 (0.46–0.55) | 0.45 (0.38–0.52) |
| 4 | 0.34 (0.29–0.38) | 0.32 (0.28–0.37) | 0.32 (0.28–0.38) |
| 5 | 0.40 (0.37–0.42) | 0.40 (0.36–0.44) | 0.40 (0.36–0.44) |

Head (Fig. 3). Structure: Normal type, subholoptic. Suprafronts narrow, with a long, strongly convex carina. Clypeus elongate L/W = 2.5. Eyes approximate dorsally, interocular distance equal to combined diameters of 1–2 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi very broad, anterior portion strongly striate), approximately equal to lower in area, somewhat flattened

dorsally, 15–16 rows of ommatidia along mid-meridian; upper ommatidia much larger ($2.3 \times$) than lower in diameter. Parietal sclerite broad, trapezoidal in outline shape. Proboscis short, free portion about $0.6 \times$ head width; mandibles present and complete; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–2.4. Antenna 15-segmented, flagellar segments narrowly elongate throughout, ultimate longer ($2.0 \times$) than penultimate, apical 3 segment proportions 1.0–0.9–1.7. Sensilla: Setiform groups on head capsule as follows: clypeals numerous (23–24), medium, only a few small setae medially, these more numerous and longer along distolateral margins. A single, moderately strong seta over antennal socket. Parietal setae several (5–7 usually, rarely more, 14–16). Postocellars few (2–3), small, lateral. Medioccipitals absent. Supracervicals numerous (23–25), tiny. Occipitals separated from and larger than postgenals, numerous (18), long. Postgenals numerous (14–15), smaller toward center of group.

Thorax and appendages. Structure: Wing venation as in male. Tibial spurs 0–0–2 (inner twice length of outer). Hind basitarsus short. Progressive leg segment proportions: foreleg 0.8–0.5–0.5–0.6–0.7–1.2; midleg 0.8–0.5–0.5–0.7–0.6–1.3; hindleg 0.9–0.4–0.4–0.6–0.7–1.3. Sensilla: Macrotrichia of wing veins and setiform groups on thoracic sclerites as in male.

Terminalia. Structure: Posterior margin of VIIth sternite lobe broadly bilobate, medial depression shallow; sclerotization in base of latter rectangular (much wider than long). Hypogynial plate subquadrate, base slightly wider than apex; with weak transverse creases across base; apex broadly rounded (outer angle not distant from level of tip). Accessory gland elongate, posterior sides subparallel (not dilated anteriorly). Spermathecae 3 in number, equal in size and shape, ovoid; necks very short; ducts completely unsclerotized. Sensilla: Medial group of VIIth sternite with several to numerous (7–20, usually more than 15), small setae; posterior lobe with several (7–10), medium setae dispersed generally. Short, stout apicodorsal setae of hypogynial lobe several to numerous (9–20). Epiproct with 2 apical setae. Alveoliforms of hypoproc few (4–6).

Pupa (Figs. 17, 21). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral third), scutellar, and abdominal tergites densely papillose. Individual papillae smooth, rounded, oval convexities. Pattern disperse, papillae unevenly spaced, often arranged in pairs or diads (some confluent), both in central area of abdominal tergites and areas lateral to muscle scars. Cuticle between papillae uniform in structure. *Coloration.* Surface reflection shiny; pigmentation more or less even throughout. *Size.* Medium. Measurements, male (N = 48): body length 4.1 (3.5–4.7), width 2.5 (1.9–2.7); female (N = 26): body length 4.7 (3.9–5.2), width 2.9 (2.3–3.2); male about $0.7 \times$ size of female. *Structure.* Outline shape almost ovoid, L/W male = 1.7, female = 1.6; cross section convex, sides declivous all around. Dorsal sclerites: abdominal tergite margins symmetrically convex, of II and

III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about $0.3 \times$ length), apex straight. Apices of leg cases in male ceterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost ceterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seulate in outline.

Larva (Fig. 13). *Integument.* Dorsally with distinct, but fine, linear and zigzagging corrugations, these absent ventrally. *Coloration.* Trunk evenly pigmented, medium-brown, sclerotized portions dark brown to black. *Size.* Medium for the group. Measurements (N = 20): body length 5.9 (4.7–7.1), head capsule width 1.24 (1.14–1.41), antennal segment lengths, basal 0.12 (0.11–0.15), apical 0.18 (0.17–0.21). *General shape.* Cylindrical. *Head.* Antenna short, 2-segmented, intersegmental membrane wide; segment proportions 1.0–1.45. *Trunk.* Structure: Anterior division spheroid. Lateral margins of abdominal segments inclinous, truncate (pseudopods extending well beyond); dorsopseudopodal lobes small and poorly developed. Anal division trilobate: lateroterminal lobe acutely rounded; pleuron straight, medioterminal lobe truncate posteriorly; terminal incision shallow, widely V-shaped. Sensilla: Primary trunk sensilla: tP submedial, taeniaform, tM–T submedial, small, taeniaform, tI–VII submedial, taeniaform, stP lateromedial, taeniaform, stM–T lateromedial, elongo-elliptoid, stI lateromedial, elongo-fustiform, stII–VII lateromedial, large, setiform. Inner tpP far-lateromedial, disjunct from stP, setiform, inner tPI–VII far-mediolateral, disjunct from and anterior to stI–VII, large, setiform. Outer tPI–VII near and slightly lateroposterior to inner tp, smaller, setiform. pdpodI–VII indiscernible. Inner and outer dpodM–T proximate, those of M sublateral, of T mediolateral, setiform, dpodI–VII on minute, anterolateral tubercle (= dorsopseudopodal lobe), setiform, inner and outer dpodVIII contiguous, at apex of lateroterminal lobe, setiform. ssP slightly lateral to ssM–T, decidedly larger than latter. Dorsal secondary trunk sensilla: numerous, more or less generally distributed, usually all setiform with a few taeniaform to elongo-fustiform types intermingled. Terminal setae 3–3, marginal.

VARIATION. Larval specimens are common in which a few or most of the central dorsal sensilla are modified (elongo-fustiform, elongo-pyriform to subclaviform, larval type "C," of Hogue, 1978:fig. 35). These are probably referable to *appalachiae* and some are confirmable as that species by the presence of pharate pupal structure observable beneath the cuticle. It might be theorized that these represent individuals in which introgression is occurring from other regional species which normally have modified setae (*williamsae*, *cweetae*). Further analysis of large samples and reared material are needed to explain these chaetotactic variations.

SPECIMENS EXAMINED. Types. HOLOTYPE male

(extracted from pupal skin), in alcohol with skin (terminalia and head dissected and mounted on slides nos. CLH 84-35 and 84-94, respectively): NORTH CAROLINA, Macon County. Ceweeta Hydrologic Laboratory, Lower Shope Fork, 9 May 1981, T. Georgian (LACM).

ALLOTYPE female (extracted from pupal skin), in alcohol with skin (terminalia dissected and mounted on slide no. CLH 84-33): same locality and collector as holotype, 28 May 1982 (LACM).

Eight PARATYPE males and females (extracted from pupal skins) on slides and in alcohol, with skins: same locality and collector as holotype, 9 May 1981, 28 May 1982 (LACM, UGAM, USNM).

Additional specimens. GEORGIA, Rabun County. Betty's Creek: 23 March 1984, T. Georgian (37 larvae); 7 April 1984, T. Georgian (22 larvae, 6 pupae).

MARYLAND, Frederick County. Little Catoctin Creek, 1 mi. N Harmony, 30 May 1958, P.H. Freytag (1 pupa: OSU). 0.5 mi. E Yellow Springs, 31 May 1958, P.H. Freytag (1 larva, 8 pupae: OSU). Cunningham Falls State Park, Little Hunting Creek, 17 May 1984, R.W. Baumann and C.R. Nelson (2 larvae, 10 pupae: BYU).

NORTH CAROLINA, Macon County. Clear Creek, 3200 ft., Highlands, 2 July 1958, J.G. Franclemont (2 females: CU). Highlands, 3000–5000 ft., May 1936, R.C. Shannon (3 males: USNM). Ceweeta Hydrologic Laboratory, Lower Shope Fork, 2300 ft., T. Georgian: 9 May 1981 (23 larvae, 5 pupae); 24 April 1982 (34 larvae, 29 pupae); 28 May 1982 (10 pupae); April 1984 (11 larvae). Dryman's Fork, 2100 ft., T. Georgian: 1 April 1980 (9 larvae); 21 April 1980 (25 larvae, 5 pupae); 21 April 1980 (3 larvae, 2 pupae). Swain County. Deep Creek, Great Smoky Mountains National Park, Bryson City, Deep Creek Campground, 21 May 1970, G.B. Wiggins and T. Yamamoto (1 pupa, 2 males: ROM).

TENNESSEE, Sevier County. Great Smoky Mountains National Park, Greenbrier Cove, 2000 ft., 22 May 1938, Williams (1 male: USNM). Great Smoky Mountains National Park, 18 May 1957, J.R. Vockeroth (1 male: CNC).

VIRGINIA, Bath County. Blowing Springs Camp, 8 mi. W Warm Springs, 18–20 May 1963, C.M. and O.S. Flint (2 males, 1 female: USNM). Wilson Creek, Route 629, 12 May 1979, C.R. Parker (3 males, 1 female: BCK). Giles County. Stoney Creek, 1800–2000 ft., 26 May 1962, J.R. Vockeroth (1 larva, 33 pupae: CNC). Sinking Creek, 29 May 1941, A. Stone (1 pupa: USNM). Madison County. Shenandoah National Park, White Oak Creek, 24 June 1951, B.D. Burks (4 larvae, 5 pupae: USNM). Nelson County. Crabtree Creek, Crabtree Falls, Highway 56, 28 May 1984, R.W. Baumann and C.R. Nelson (2 males, 1 female: BYU). Page County. Luray, 21–24 June 1933, A. Melander (2 males, 3 females: USNM). Patrick County. Confluence of Little Rock Castle Creek and Rock Castle Creek, Route 605, 31 May 1980, B. Kondratieff (1 male, 2 females: BCK). Rockbridge County. Pedlar River, below Panther Falls, 28 May 1984, R.W. Baumann and C.R. Nelson (9 males, 4 pupae: BYU). Shenandoah County. Passage Creek, Camp Roosevelt, 21 May 1973, S. Fiance (3 larvae: USNM). Smyth County. N Fork Holston

River, Route 42, junction Route 633, 9 May 1981, B. Kondratieff (1 male: BCK). Washington County. S Fork Holston River, Highway 58, near Damascus, 27 May 1984, R. Baumann and C.R. Nelson (2 pupae: BYU).

ETYMOLOGY. The name is considered a noun in the genitive case and refers to the southern Appalachian Mountains where the species is of wide occurrence.

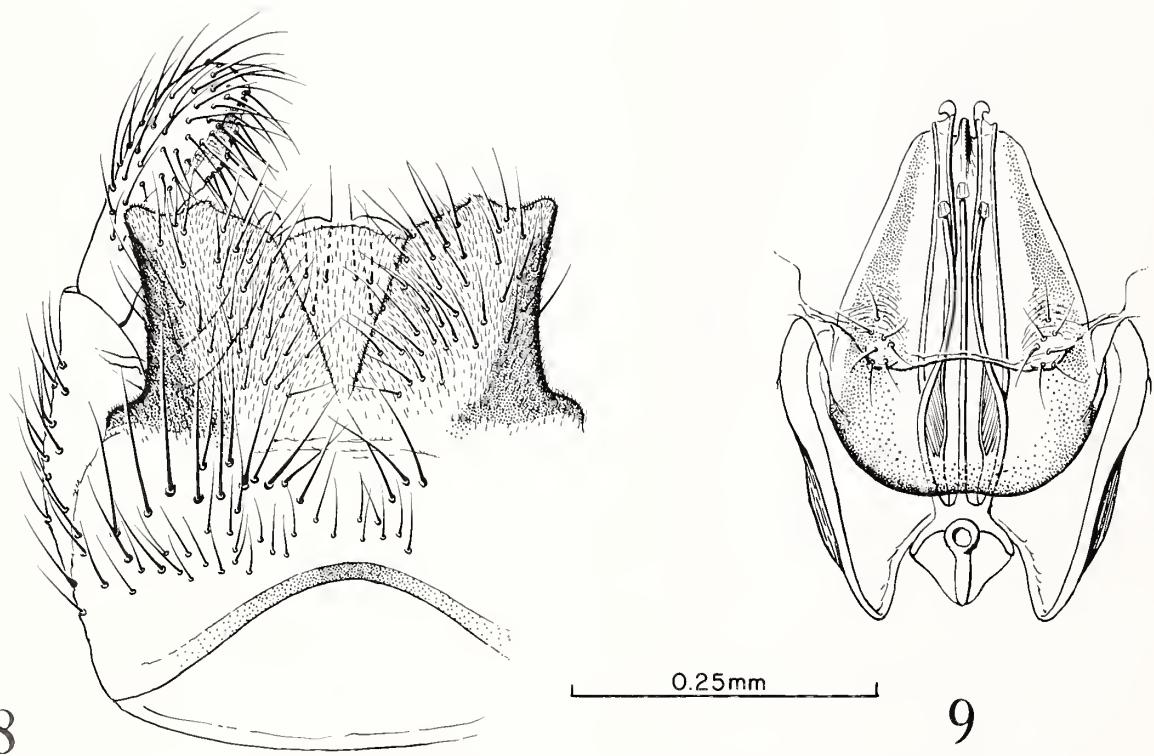
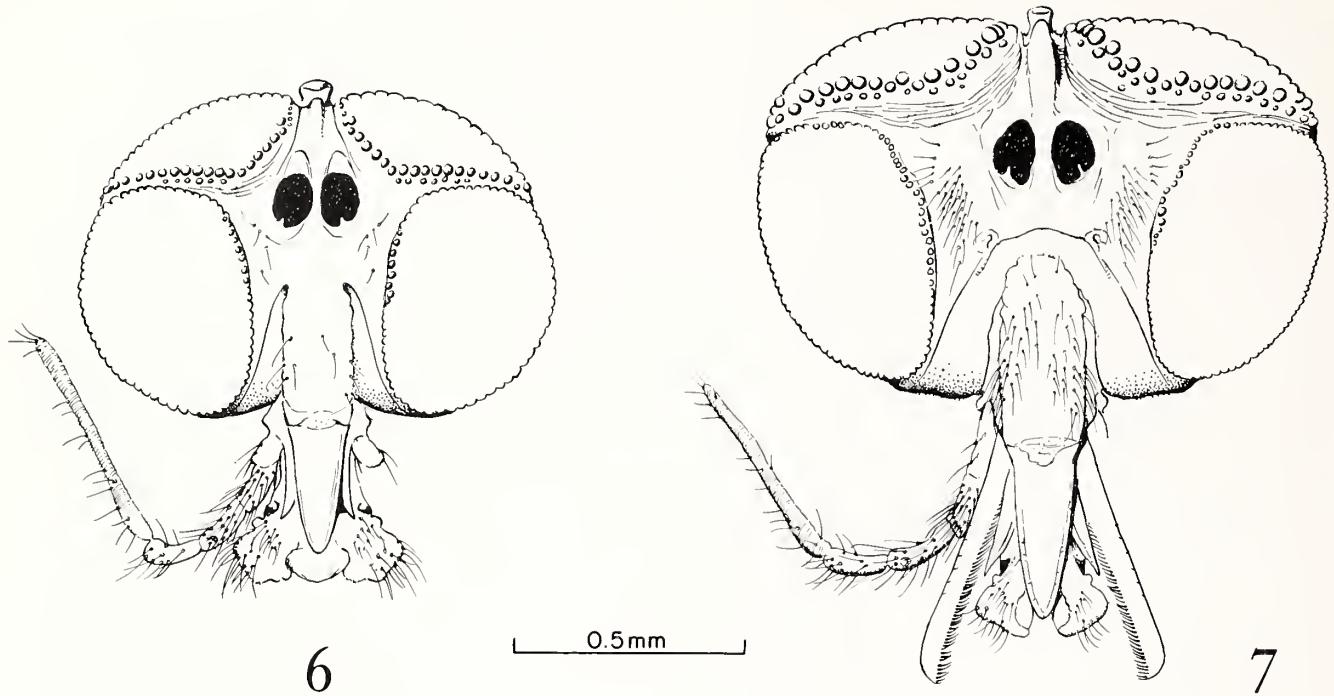
DISTRIBUTION. *Blepharicera appalachiae* is widespread in most major drainages throughout the central and southern Appalachian Mountains (Fig. 26). It is replaced largely by *tenuipes* to the north, except for a zone of overlap in Maryland and Virginia (to Giles County). Its distribution southward ends in northern Georgia (Rabun County), but it has not been found in the Savannah River drainage, although it is present less than 17 km away in the southernmost portion of the Little Tennessee system.

ECOLOGICAL NOTES. The larval ecology of *B. appalachiae* is similar to that of other members of the family (cf. Hogue, 1981). The stream at the type locality is a fourth-order mountain stream with average width 5.5 m, average velocity 50 cm/sec, and a bed predominantly of schist and quartzite boulders averaging 21 cm in greatest dimension. At least three other blepharicerid species (*B. ceweetae*, *similans*, and *williamsae*) are also present. Some habitat segregation based on rock size and water depth has been observed (Georgian, unpubl. data), but individuals of more than one species have been collected from single rocks. The four larval instars can be identified by measuring the width of the dorsal head sclerite, permitting analysis of life cycles (Georgian and Wallace, 1983). Of the four species present at the Ceweeta Hydrologic Laboratory, *B. williamsae* is the most abundant and the earliest to appear. Larvae are first seen in early winter (first instars December–March, mature larvae February–April or early May); they pupate in early spring (April–May). *B. appalachiae* and *ceweetae* complete their larval development from early April through the end of May, and are much less abundant than *williamsae*. The last species to become evident in the annual cycle is *B. similans*, noticeable larvae appearing in early May, with pupae present throughout the summer until mid-September. The rate of growth and timing of life cycles changes with elevation (and is presumably controlled by correlated temperatures). At a site near the type locality only 490 m higher (Ceweeta Hydrologic Laboratory, Watershed #27, 1158 m), mature larvae and pupae of *B. williamsae* were found and other species were absent as late as the first of June.

Blepharicera ceweetae, new species

Figures 6–9, 14, 18, 22, 26

DIAGNOSIS. *B. ceweetae* differs from other members of the *B. tenuipes* group in the unique shape of the Xth tergite lobe: outer corner acutely rounded, followed medially by a shallow concavity and central sublobe displaced toward the midline; the inner margin is straight but angled toward the midline so that the interlobular depression is V-shaped. The larva is most similar to that of *B. tenuipes* but is smaller,



Figures 6–9. *Blepharicera cowetae*, new species. 6. Male head. 7. Female head. 8. Male terminalia, external structures (dorsal view). 9. Male terminalia, phallic structures (dorsal view).

evenly pigmented, and has disperse, longer, predominantly fustiform dorsal sensilla whereas this stage of that species is much larger, usually with longitudinal light bands in the otherwise dark pigmentation and has short claviform dorsal sensilla in series. The pupa displays a unique pattern of light lines in the generally darkly pigmented integument, composed of numerous, very fine, closely set, longitudinal, narrowly wavy, transparent furrows and short, transverse "hyphens," the former appearing maeroseopically as strong striae.

DESCRIPTION. Adult a small, sturdily built, well-sclerotized blepharicerid. Very similar to *B. tenuipes* and *appalachiae*.

Male (Figs. 6, 8–9). Only a single, freshly emerged, alcohol-preserved specimen (holotype) available for coloration and measurements; character values of latter may be insufficient due to incomplete development. Other structural characters from pharate adults dissected from pupae. *Coloration.* Generally dull gray-brown, pruinose. Mesoscutum unicolorous, dull gray, corners of posterior pronotum and scutellum contrasting light brown, latter becoming darker toward the sides; pleurites similar to scutum but paler. Wing membrane completely hyaline. *Size.* A medium-sized *Blepharicera*. Measurements (N = 1): Wing length 6.1. Leg segment lengths:

| | foreleg | midleg | hindleg |
|----------|---------|--------|---------|
| femur | 3.6 | 3.9 | 5.2 |
| tibia | 3.2 | 3.0 | 4.7 |
| tarsus 1 | 1.8 | 1.6 | 1.8 |
| 2 | 0.91 | 0.83 | 0.66 |
| 3 | 0.64 | 0.60 | 0.44 |
| 4 | 0.33 | 0.32 | 0.28 |
| 5 | 0.32 | 0.33 | 0.32 |

Head (Fig. 6). Structure: Normal type, subholoptie. Suprafrons narrow, with long, moderately convex carina. Clypeus elongate, L/W = 2.0. Eyes approximate dorsally, interocular distance equal to combined diameters of 2.8 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi narrow), approximately equal to lower in area, 19–20 rows of ommatidia along mid-meridian; upper ommatidia slightly larger (1.5×) than lower in diameter. Proboscis short, free portion about 0.4× head width; mandibles completely absent; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–3.0. Antenna 15-segmented, flagellar segments elongate throughout, ultimate longer (1.4×) than penultimate, apical 3 segment proportions 1.0–0.9–1.25. Sensilla: Setiform groups on head capsule as follows: clypeals several (9–10), medium, only a few, small setae medially, more numerous and longer along distolateral margins. No single, medium strong seta over antennal socket; parietal setae few (1–2). Postocellars few (2–5), small, lateral. Medioccipitals absent. Supracervicals very numerous (30), tiny. Occipitals separated from and larger than postgenals, numerous (26–30) and long; upper series of longer and heavier setae than lower. Postgenals numerous (12–26), small toward center of group.

Thorax and appendages. Structure: Typical wing venation for *Blepharicera*. Tibial spurs 0–0–1. Progressive leg-segment proportions: foreleg 0.9–0.6–0.5–0.7–0.5–1.0; midleg 0.8–0.5–

0.5–0.7–0.5–1.0; hindleg 0.9–0.4–0.4–0.7–0.6–1.1. Sensilla: Macrotrichia on wing veins as follows: complete ventrally on R₄ and dorsally on R₅; apicodorsally only on M₁, M₂, and CuA1. Setiform groups on thoracic sclerites as follows: anterior pronotals absent. Humeral callus with 3 very small setae. Acrostical series short, divergent anteriorly. Dorsocentral series complete. Supraalar few (5), restricted to posterior and medial portions of sclerite. Prescutellars absent. Scutellars medium-sized, forming a dense group on outer corner; numerous similar, widely spaced setae dispersed toward the midline. Metapleurals present, few (2–6). Suprmetapleurals 2–3, minute.

Terminalia (Figs. 8–9). Structure: Abdominal segment VIII greatly reduced, mostly membranous; tergite consisting only of a short, medial, ligulate sclerite; pleurites and sternite undifferentiated. Epandrium simple, emarginate postero-medially. Xth lobes well developed, prominent, slightly divergent; interlobular depression deep, V-shaped; individual lobe quadrate, apex trilobate: outer sublobe acutely rounded, middle subsublobe small, central, angled inwardly, inner sublobe obtusely angled; inner margin straight, extending medially and directly to base of opposite margin; distal margin of lobe between outer and middle lobes slightly concave; inner arm poorly sclerotized, elongate, apex lobate, disjunct from same member opposite. Fused gonocoxites and hypandrium well sclerotized, forming capsule about as wide as long; posterolateral corners of gonocoxite strongly produced. Outer gonostylus moderately large (length about 0.7× midline length of hypandrium), an entire, subrectangular, lobe with concave inner margin. Inner gonostylus a narrow, porrect, smooth, simple, digitiform projection. Phallic complex straight, supinate, not recurved. Aedeagal filaments equal, with slightly flared apices, outer filaments strongly bowed near bases; lateral tine longer than rods, broad throughout, tapering slightly to complex apex; latter with dorsal hook on inner wall; canal wide toward the base and containing numerous long spiculae arising from inner wall and directed toward the apex; aperture subapical. Sperm pump and piston poorly developed, former without internal spines, latter with conspicuous, tubular, dorsal ejaculatory atrium attached to apodeme; apodeme a small, ventral, vertical flange. Subanal pouch wide, bowl-shaped; tegmen broad, apex trilobate, i.e., deeply incised on either side of strong, vertical, medial carina. Gonite large, broad, ovate; gonocoxal lobe poorly developed, posterior lobe elongate, anterior lobe expansive, ventral bridge complete beneath basiphallus. Sensilla: Epandrium with very numerous, short (toward anterior) to long (toward posterior) setiforms generally. Xth tergite lobe with medium setiforms generally and evenly spaced over central portion dorsally, longer toward apex; inner arm with few to several (5–8), small setiforms near the apex. Fused gonocoxites and hypandrium ventrally with numerous, medium setiforms generally spaced only over posterior half. Outer gonostylus with very numerous, medium setiforms generally and evenly spaced over outer surface and marginally, absent from middle of inner face. Epiproct with few (4–8) alveoliforms in dorsolateral group. Hypoproct with few (2) long setiforms apically.

Female (Fig. 7). Only a single, freshly emerged, alcohol-preserved specimen (allotype) available for coloration and measurements. Structural characters from pharate adults dissected from pupae. *Coloration.* Apparently as in male. *Size.* A medium-sized *Blepharicera*. Measurements (N = 1): Wing length 6.3. Leg segment lengths:

| | foreleg | midleg | hindleg |
|----------|---------|--------|---------|
| femur | 3.7 | 3.6 | 5.2 |
| tibia | 3.1 | 2.9 | 4.3 |
| tarsus 1 | 1.4 | 1.4 | 1.9 |
| 2 | 0.67 | 0.66 | 0.64 |
| 3 | 0.42 | 0.41 | 0.38 |
| 4 | 0.30 | 0.29 | 0.32 |
| 5 | 0.44 | 0.43 | 0.38 |

Head (Fig. 7). Structure: Normal type, subholoptic. Suprafrontal narrow, with a long, strongly convex carina. Clypeus elongate L/W = 2.3. Eyes approximate dorsally, interocular distance equal to combined diameters of 1–2 upper ommatidia; upper division well differentiated from lower (callis oculi very broad, anterior portion strongly striate), approximately equal to lower in area, somewhat flattened dorsally, 17 rows of ommatidia along mid-meridian; upper ommatidia larger (2.5×) than lower in diameter. Parietal sclerite broad, trapezoidal in outline. Proboscis short, free portion about 0.4× head width; mandibles present and complete; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–3.4. Antenna 15-segmented, flagellar segments narrowly elongate throughout, ultimate longer (1.8×) than penultimate, apical 3 segment proportions 1.0–0.9–1.7. Sensilla: Setiform groups on head capsule as follows: clypeals numerous to very numerous (26–45), general basally, more numerous and longer along distolateral margins. Seta over antennal socket. Parietal setae numerous to very numerous (18–38). Postocellars few (3–5), small, lateral. Medioccipitals absent. Supracervicals numerous (20), tiny. Occipitals separated from and larger than postgenitals, numerous (32), long, uppers longer and heavier than lowers. Postgenitals numerous (28–30), smaller toward center of group.

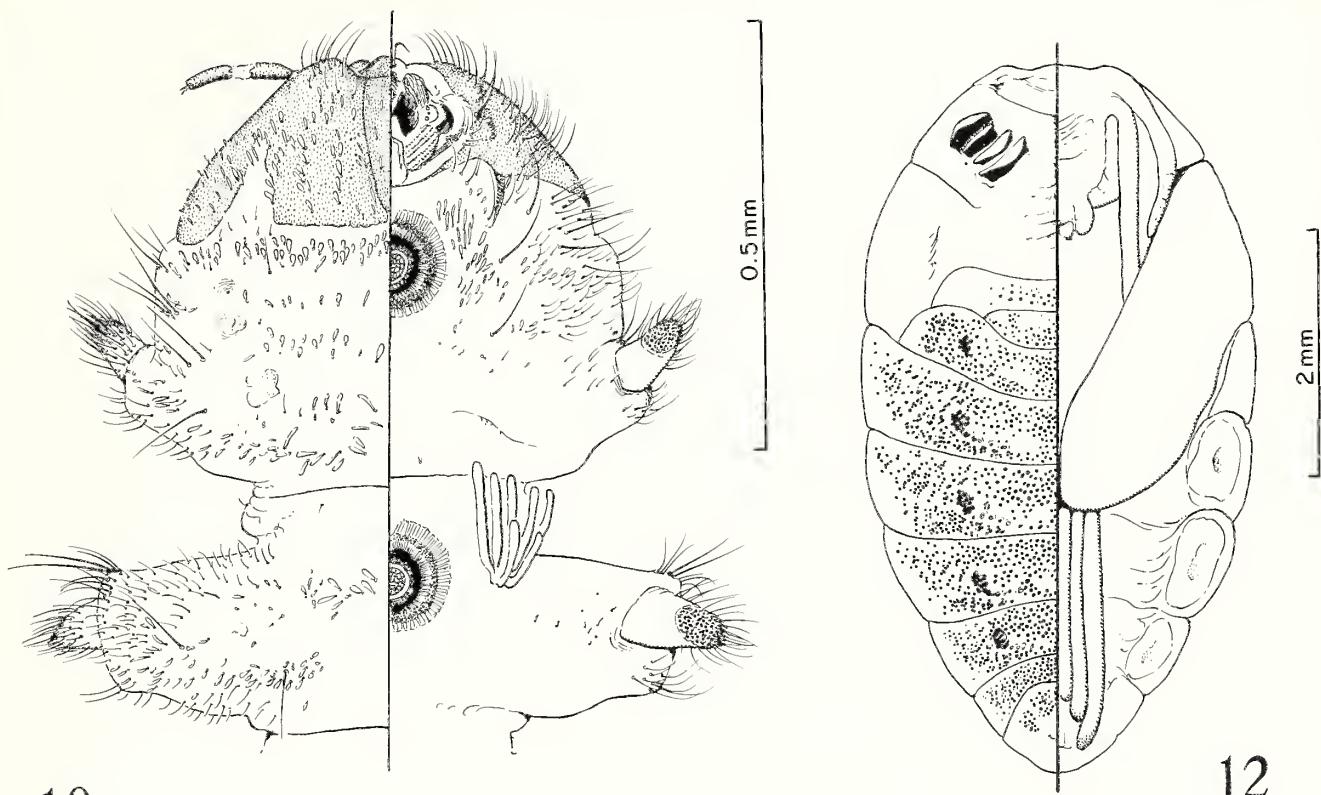
Thorax and appendages. Structure: Wing venation as in male. Tibial spurs 0–0–2 (inner twice length of outer). Hind basitarsus short. Progressive leg segment proportions: foreleg 0.8–0.5–0.5–0.6–0.7–1.5; midleg 0.8–0.5–0.5–0.6–0.7–1.5; hindleg 0.8–0.4–0.3–0.6–0.8–1.2. Sensilla: Macrotrichia of wing veins and setiform groups on thoracic sclerites as in male.

Terminalia. Structure: Posterior margin of VIIIth sternite lobe broadly bilobate, medial depression shallow; sclerotization in base of latter rectangular (much wider than long). Hypogynial plate subhexagonal, base slightly wider than apex; with weak transverse creases across base; apex acutely rounded (outer angle far from level of tip). Accessory gland elongate, decidedly dilated anteriorly. Spermathecae 3 in number, equal in size and shape, ovoid; necks very short to absent; ducts completely unsclerotized. Sensilla: Medial group of VIIIth sternite with few (3) or numerous (12–18) small setae; posterior lobe with few to numerous (2–12), medium-sized

setae restricted to outer one-third. Short, stout apicodorsal setae of hypogynial lobe usually numerous (12–19). Epiproct with 1–2 apical setae. Alveoliforms of hypoproct few (3–6).

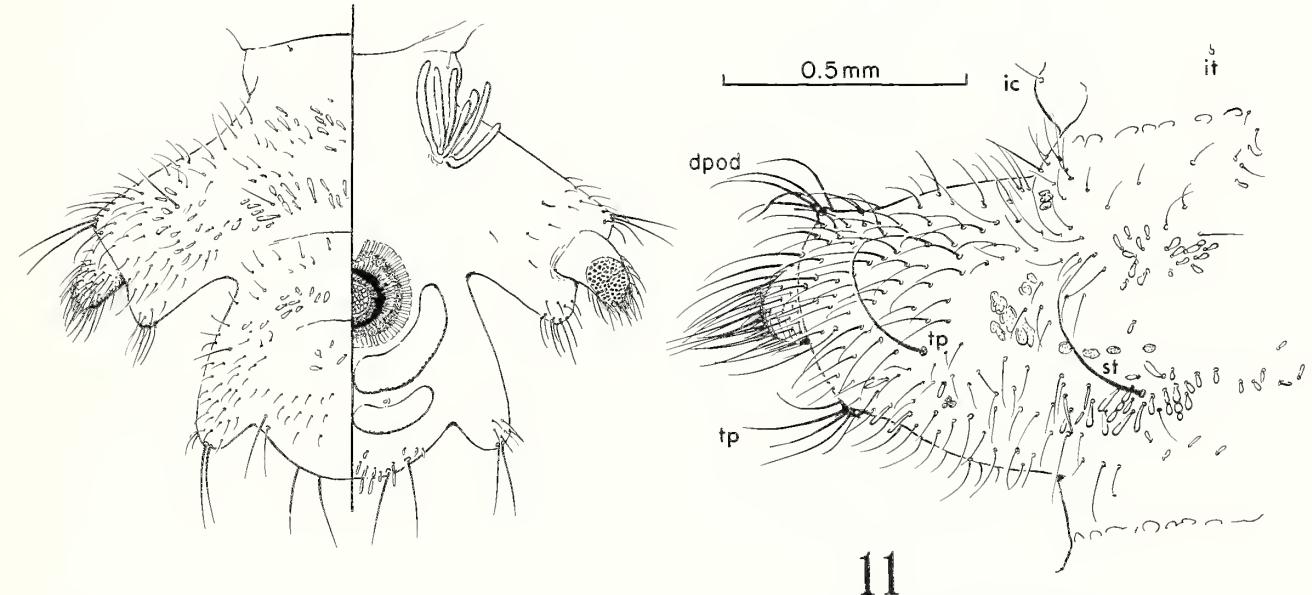
Pupa (Figs. 18, 22). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral one-third), scutellar, and abdominal tergites densely papillose. Individual papillae finely spiculate, rounded, oval convexities. Pattern on abdominal tergites disperse, papillae more or less evenly spaced, slightly more dense toward the middle of sclerites, absent laterally. Cuticular structure between papillae irregular, thin and grooved areas (corresponding to pigmentary pattern as described below). *Coloration.* Surface reflection shiny; dark pigmentation broken by numerous, very fine, close-set, longitudinal, narrowly wavy, transparent furrows or lines and short, transverse “hyphens” between, the former appearing macroscopically as strong striae. *Size.* Medium. Measurements, male (N = 27): body length 4.5 (3.8–5.0), width 2.5 (1.9–2.8); female (N = 27): body length 5.2 (4.7–5.7), width 2.8 (2.5–3.1); male about 0.8× size of female. *Structure.* Outline shape elongate, L/W male = 1.8, female = 1.9; cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments convex, of II and III slightly wider than thorax, of IV often projecting slightly. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male co-terminal; in female tip of hindleg most extended, foreleg and midleg much less, these almost coterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two plates slightly smaller and thinner than outers, slightly spreading; individual plates angularly seculate in outline.

Larva (Fig. 14). Similar to *tenuipes*. *Integument.* Dorsally with distinct, but fine, mostly linear, corrugations, these absent ventrally. *Coloration.* Trunk evenly pigmented, medium brown, sclerotized portions dark brown to black. *Size.* Medium for the group. Measurements (N = 4): Body length (N = 3), 5.4 (5.3–5.6), antennal segment lengths, basal 0.16 (0.13–0.17), apical 0.19 (0.18–0.20). *General shape.* Cylindrical. *Head.* Antenna short, 2-segmented, intersegmental membrane wide; segment proportions 1.0–1.2. *Trunk.* Structure: Anterior division spheroid. Lateral margins of abdominal segments inclinous, truncate (pseudopods extending well beyond); dorsopseudopodal lobes small and poorly developed. Anal division trilobate: lateroterminal lobe acutely rounded; pleuron slightly convex, medioterminal lobe convex posteriorly, evenly rounded; terminal incision deep, V-shaped. Sensilla: Primary trunk sensilla: tP submedial, elongo-elliptoid, tM–T submedial, small, taeniaform, tI–VII submedial, lanciform, obscured by multiplication. stP lateromedial, taeniaform to setiform, stM–T lateromedial, elongo-elliptoid, stI lateromedial, acutiform, stII–VII lateromedial, setiform. Inner tpP far-lateromedial, disjunct from stP, setiform.



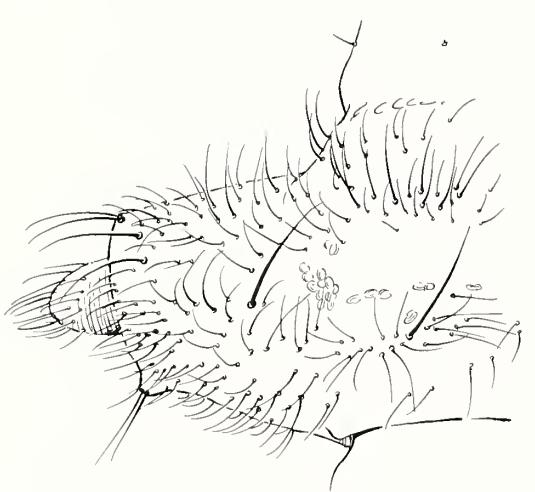
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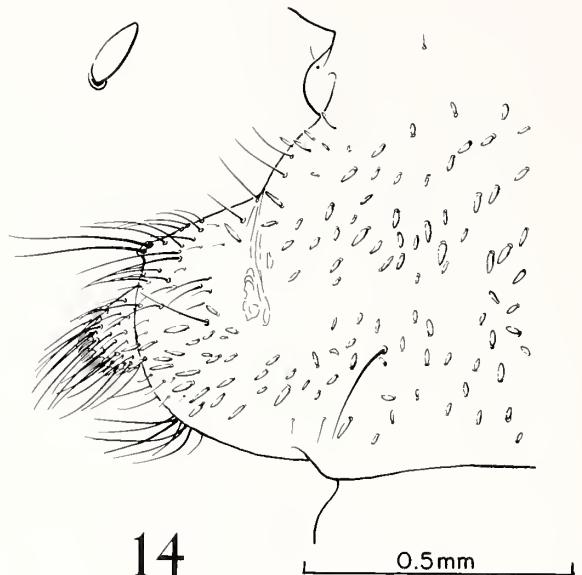
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Figures 10–12. *B. tenuipes*. 10. Larva (dorsum left, venter right). 11. Detail of dorsum of second abdominal segment of larva. 12. Pupa (dorsum left, venter right).



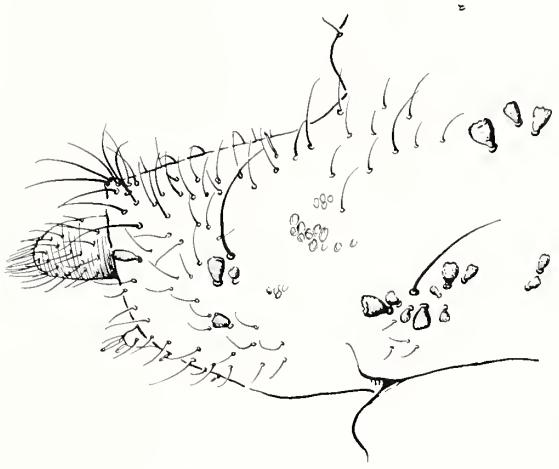
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0.5 mm



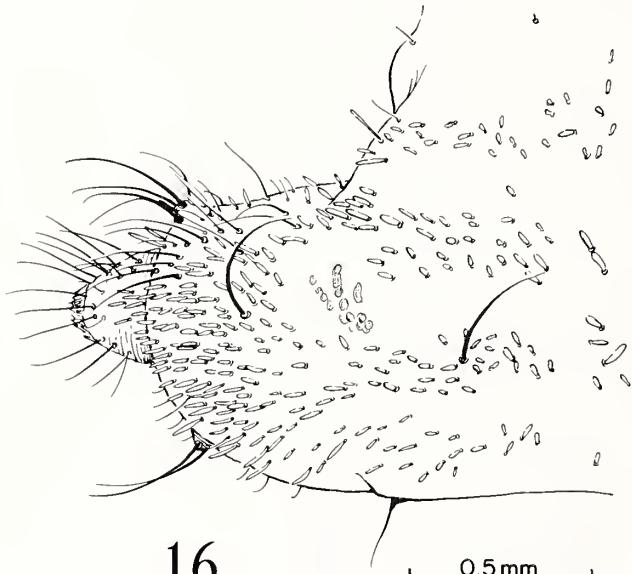
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15

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16

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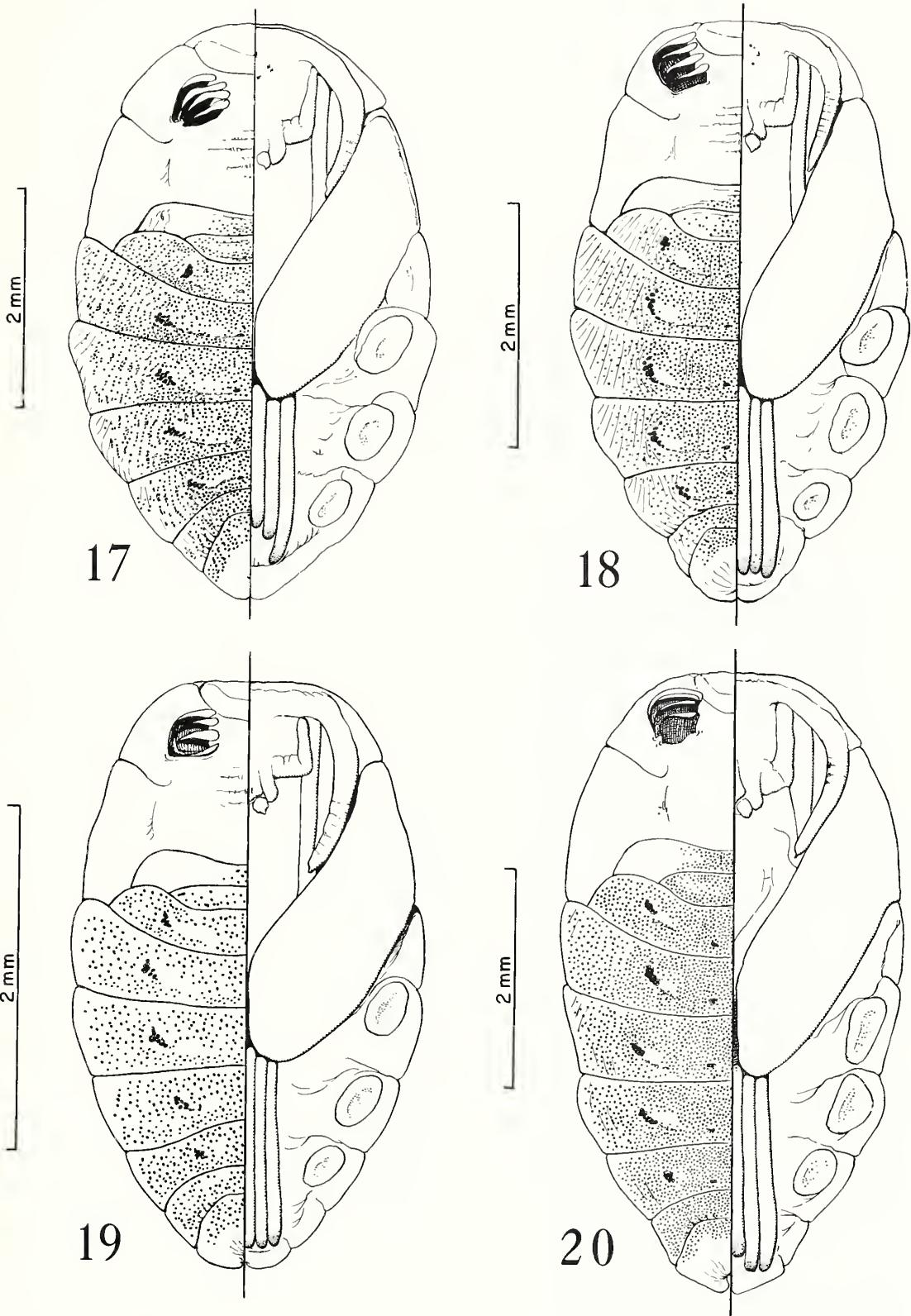
Figures 13–16. Larvae, left dorsal aspects of abdominal segments II. **13.** *B. appalachiae*. **14.** *B. ceweetae*. **15.** *B. similans*. **16.** *B. williamsae*.

form, inner tpi–VII far-mediolateral, disjunct from and anterior to sti–VII, setiform. Outer tpi–VII near and slightly posterior to inner tp, lanciform to elongo-elliptoid. pdpodI–VII indiscernible. Inner and outer dpodM–T proximate, those of M sublateral, of T mediolateral, setiform, dpodI–VII on minute, anterolateral tubercle (= dorsopseudopodal lobe), setiform, inner and outer dpodVIII contiguous, at apex of lateroterminal lobe, setiform. ssP slightly lateral to ssM–T, decidedly larger than latter. Dorsal secondary trunk sensilla: numerous, more or less disperse but tending to be in two broad, transverse series medially, these merging laterally. Almost all elongo-elliptoid to elongo-claviform or lanciform,

these short medially, becoming fairly long laterally; a few long setiforms intermingled laterally. Terminal setae 3–3, marginal.

SPECIMENS EXAMINED. Types. HOLOTYPE male (emerged from pupa), in alcohol with pupal skin (terminalia not dissected): NORTH CAROLINA, Macon County. Co-weeta Hydrologic Laboratory, Lower Shope Fork, T. Georgian. Individually reared: collected 7 April 1984 as mature larva; pupated 13 April; emerged 5 May 1984 (LACM).

ALLOTYPE female (emerged from pupa), in alcohol with pupal skin (terminalia dissected and mounted on slide CLH 84-71). GEORGIA, Rabun County. Betty's Creek, T. Geor-



Figures 17–20. Pupae, dorsal/ventral aspects. **17.** *B. appalachiae*. **18.** *B. ceweetae*. **19.** *B. similans*. **20.** *B. williamsae*.

gian. Individually reared: collected 7 April 1984 as mature larva; pupated 16 April 1984; emerged 12 May 1984 (LACM).

Ten PARATYPE males, 5 PARATYPE females (extracted from pupal skins), variously dissected and mounted on slides no. CLH (males) 81-8, 84-1, 84-2, 84-39, 84-43, 84-44, 84-45, 84-46, 84-83a-d, 84-84a-d, (females) 84-47, 84-48, 84-49, 84-50, and 84-51. Same locality as holotype, 9 May 1981, T. Georgian (LACM, UGAM, USNM).

Additional specimens. NORTH CAROLINA, Macon County. Coweeta Hydrologic Laboratory, Lower Shope Fork, 2300 ft., 9 May 1981 (66 pupae); 24 April 1982 (9 larvae, 15 pupae). Dryman's Fork, 2100 ft., 21 April 1980 (26 pupae).

ETYMOLOGY. This species is named for Coweeta Creek in whose tributaries it was first found. "Coweeta" is treated as a noun in the genitive case. It is a Cherokee word associated with a major tribal settlement in the area, near Franklin, North Carolina. It has more recently been used by the U.S. Forest Service for its Coweeta Hydrologic Laboratory, also the type locality of the insect.

DISTRIBUTION. *B. ceweetae* is known to date only from a roughly circular area about 17 km in diameter in the southern Appalachians, including the type locality and two other streams (Dryman's Fork, Macon County, North Carolina and Betty's Creek, Rabun County, Georgia), all within the Little Tennessee River drainage (Fig. 26).

ECOLOGICAL NOTES. The species is uncommon at the known sites of occurrence and little is known concerning its biology (See Ecological Notes under *B. appalachiae*).

LARVAE AND PUPAE OF OTHER SPECIES

Detailed descriptions of the larvae of the other species are being published by Hogue (in press). The following will verify the provisional identifications made by Hogue (1978), to which reference can be made for brief descriptions and illustrations. Minimal diagnostic features only are repeated here for clarification (see also the keys above). Diagnostic features consist primarily of the shape and distribution of the modified dorsal sensilla. The pupae are described in full and figured.

The immatures of *B. cheroeka*, *diminutiva*, and *capitata* are still unknown.

Blepharicera similans Johannsen, 1929

Figures 15, 19, 23

Larva "B," Hogue, 1978:27, fig. 33.

The dorsal modified sensilla are large, of various sizes, dentate and basically short capitate to almost spherical in shape. They are arranged generally in two transverse rows, a longer series between the large subtergal setiform sensilla and a

shorter anteromedial row; a few also are associated with the large, inner, tergopleural setiform sensilla.

Pupa (Figs. 19, 23). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, without papillae. Metascutal (medially only), scutellar, and abdominal tergites moderately densely papillate. Individual papillae smooth, rounded, oval convexities. Pattern on abdominal tergites disperse, papillae more or less evenly spaced, slightly more dense medially, absent far laterally. Cuticle between papillae uniform in structure. *Coloration.* Surface reflection shiny; pigmentation even. *Size.* Medium. Measurements (northern material, specimens from North Carolina, Shope Creek distinctly smaller, 0.7), male (N = 10): body length 4.1 (3.8–4.5), width 2.4 (2.2–2.8); female (N = 10): body length 5.0 (4.4–5.3), width 2.9 (2.5–3.3); male about 0.7 × size of female. *Structure.* Outline shape almost ovoid, L/W male = 1.4, female = 1.4. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments symmetrically convex, those of II and III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3 × length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, midleg less, hindleg less than either; mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seulate in outline.

Blepharicera tenuipes (Walker, 1848)

Figures 10–12, 24

Larva "A" Hogue, 1978:27, fig. 30.

The dorsal modified sensilla are short, elongo-claviform. They are arranged in two irregular transverse rows, a longer posteromedial series including the subtergal sensilla, and a shorter anteromedial row. Laterally the sensilla are mostly setiform (Figs. 10–11).

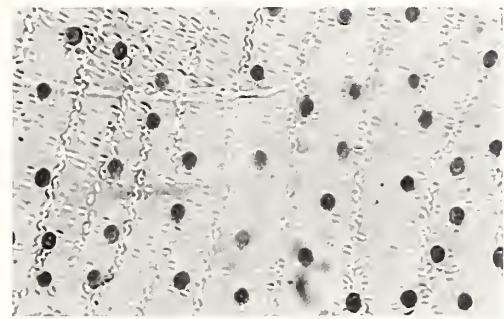
Pupa (Figs. 12, 24). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral one-third), scutellar, and abdominal tergites moderately densely papillate. Individual papillae smooth, rounded, oval convexities. Pattern disperse, unevenly spaced, papillae often arranged in pairs but not in fused diads, mainly in areas of abdominal tergites lateral to muscle scars, more or less evenly spaced in medial area between scars; slightly more dense medially, absent laterally.

Figures 21–25. Pupae, *Blepharicera tenuipes* group. Photomicrographs of tergites of abdominal segment II, showing arrangements of integumentary papillae. Dorsomedial third of sclerite at right, detail of area lateral to major muscle scar at left. 21. *B. appalachiae*. 22. *B. ceweetae*. 23. *B. similans*. 24. *B. tenuipes*. 25. *B. williamsae*.

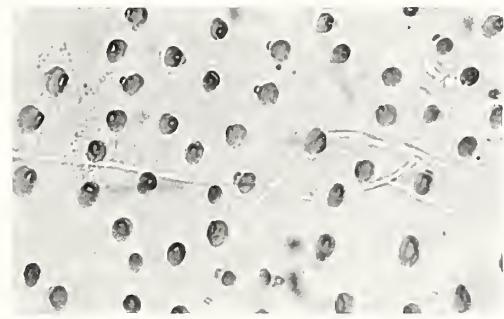
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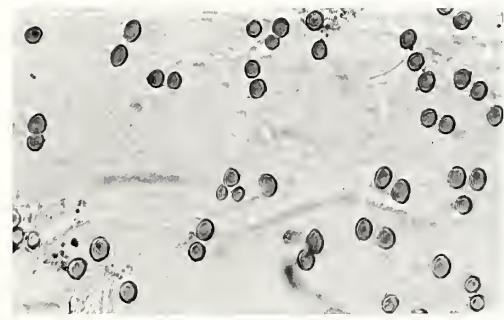
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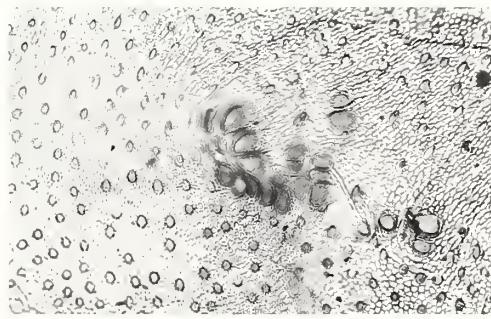
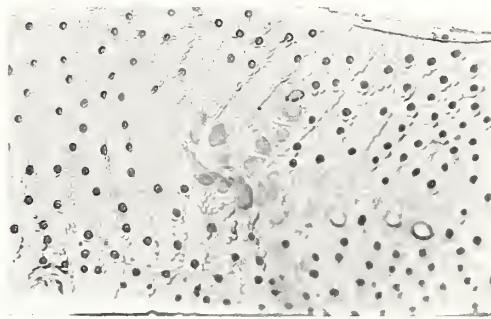
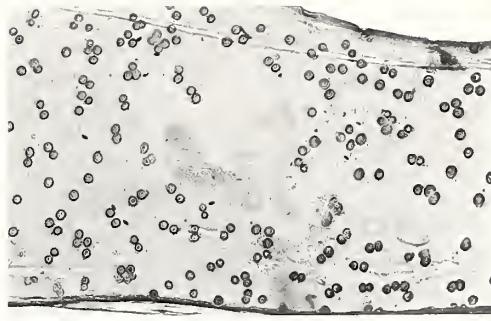
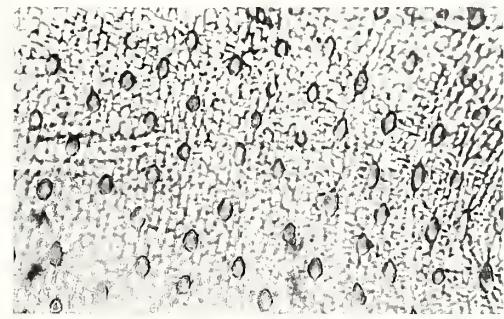




Figure 26. Drainage systems of eastern United States and Canada showing distribution of the *Blepharicera appalachiae* (solid circles) and *ceweetae* (open circle). Shaded area represents range of *Blepharicera tenuipes*. Location of Coweeta Hydrologic Laboratory area indicated by open circle.

Cuticle between papillae uniform in structure. *Coloration*. Surface reflection shiny; pigmentation even. *Size*. Medium. Measurements, male (N = 12): body length 4.6 (4.1–4.9), width 2.5 (2.3–2.8); female (N = 14): body length 5.5 (5.3–5.8), width 3.2 (3.0–3.5); male about 0.6× size of female. *Structure*. Outline shape almost ovoid, L/W male = 1.8, female = 1.8. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments symmetrically convex, of II and III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male ceterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost ceterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seculate in outline.

Blepharicera williamsae Alexander, 1953

Figures 20, 25

Larva "D" Hogue, 1978:29, fig. 31.

The larva of this species is extraordinarily large for the *B. tenuipes* group (mean body length 8.6 mm, range extremes 7.2–10.5 mm). The integument is also pigmented unevenly, i.e., dark dorsomedially, light cream laterally, presenting a longitudinally striped appearance. The dorsal modified sensilla are short, ovoid, elliptoid or pyriform and more or less densely distributed evenly over the entire dorsal surface (slightly more dense laterally) (Fig. 16).

Pupa (Figs. 20, 25). *Integument*. Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral half), scutellar, and abdominal tergites densely papillose. Individual papillae finely spiculate, small, rounded, oval convexities; pattern on abdominal tergites general, papillae more or less evenly but closely spaced, slightly more dense medially, absent marginally. Cuticle between papillae finely reticulate. *Coloration*. Surface reflection dull; pigmentation irrorate, in concordance with reticulate structure. *Size*. Medium. Measurements, male (N = 10): body length 5.5 (5.1–5.9), width 3.1 (2.8–3.4); female (N = 10): body length 6.7 (6.1–7.5), width 3.7 (3.4–4.1); male about 0.8× size of female. *Structure*. Outline shape almost ovoid, L/W male = 1.8, female = 1.8. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments asymmetrically convex, of II and III slightly wider than thorax, of IV projecting slightly. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male ceterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost ceterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just

short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seculate in outline.

Larva F Hogue, 1978

Larva "F" Hogue, 1978:30, figs. 34, 36.

The existence of very distinctive larvae with gross, dorsal, conical protuberances in the center of the abdominal segments with which no equally distinct adults can be associated is a puzzling phenomenon. Such larvae appear among normal larvae of other species in the *tenuipes* group (*tenuipes*, *appalachiae*), suggesting that they are variants expressing a developmental anomaly. This is the conclusion of Zwick (pers. comm.), who also finds the same condition among larvae of European *Blepharicera* and species of *Liponeura*. There is a tendency in some larval individuals and even populations for a centripetal crowding and multiplication of secondary sensilla on the disc of abdominal segments, indicating hyperactive epidermal cell growth in the region which might be expressed maximally by hypertrophy of the entire integument. Larva F, therefore, should not be considered a distinct species until more knowledge can be acquired regarding the morphological significance of this type of larva.

ACKNOWLEDGMENTS

Dr. Wayne Swank kindly provided access to streams at the U.S. Forest Service's Coweeta Hydrologic Laboratory. Equipment for rearings was made available by Dr. J.B. Wallace of the Department of Entomology, University of Georgia. A. Huryn and J. O'Hop gave invaluable assistance in the field.

For the use of material we wish to acknowledge the following repositories and institutions, including our own (listed alphabetically by the abbreviation cited under Specimens Examined for each of the species), and thank their respective curators who kindly arranged loans and provided information:

| | |
|------|---|
| BCK | personal collection, Boris Kondratieff, New Ellenton, South Carolina. |
| BYU | Bean Life Science Museum, Brigham Young University, Richard W. Baumann. |
| CNC | Canadian National Collection, B.V. Peterson. |
| CU | Cornell University, L.L. Pechuman. |
| LACM | Natural History Museum of Los Angeles County. |
| UGAM | University of Georgia Entomological Museum. |
| OSU | Ohio State University, Paul H. Freytag. |
| ROM | Royal Ontario Museum, Glenn B. Wiggins. |
| USNM | U.S. National Museum of Natural History, Alan Stone. |

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Submitted 9 October 1985; accepted 30 April 1986.

DESCRIPTION OF A NEW SPECIES OF THE SHORE FLY GENUS *DIEDROPS* (DIPTERA: EPHYDRIDAE) FROM COLOMBIA

Wayne N. Mathis¹ and Charles L. Hogue²

ABSTRACT. Adults and immatures of *Diedrops roldanorum*, new species, were recently collected in Colombia (Tolima: 3 km west of Boquerón). This species, including the puparium (the first for the tribe Dagini), is described, and a revised key to the species and a revised diagnosis of the genus is provided.

RESUMEN. Adultos y inmaduros de *Diedrops roldanorum*, especie nueva, fueron colectados recientemente en Colombia (Tolima: 3 km oeste de Boquerón). Se describe esta especie, incluyendo la puparia (la primera para la tribu Dagini), y se provee una clave revisada para las especies y una diagnosis revisada del género.

INTRODUCTION

For the past decade the genus *Diedrops* has received considerable attention, beginning with its description (Mathis and Wirth, 1976). Since then the genus was reviewed, as part of a generic review of the tribe Dagini (Mathis, 1982), and later it received further study in the form of a new species description with additional notes on the genus (Mathis, 1984). Each of these contributions resulted directly from fieldwork, especially the collection of new specimens, which also provides the impetus for the present study.

Over 20 years ago, while collecting rheophilic Diptera in Costa Rica, C.L. Hogue collected immatures of a *Diedrops* species for the first time. Although the specimens were then determined to be a shore fly (family Ephydriidae), neither the species nor the genus was recognizable from the material. Hogue sent the specimens to W.N. Mathis, who likewise did not recognize the genus or species. Further study of these insects was then held in abeyance, pending collection of additional material, especially adults.

Subsequent to his original collection, Hogue found immatures, principally puparia, at several other sites in Mexico, Costa Rica, Peru, and Colombia. One site (near Boquerón) in the last country yielded extremely large numbers of immatures, but adults eluded capture despite several attempts to find them. Finally in June of 1984, Hogue returned to this locality in Colombia and succeeded in finding additional

immatures and, more importantly, in rearing 60 adults from some 800 puparia he collected. This paper presents our study of this material in the form of a new species description, including that of the puparium, a revised key, and a slightly revised characterization of the genus. The genus *Diedrops* now includes four species, although differences in puparia from the several disjunct populations indicate that additional species exist. These populations need further sampling and rearing of adults from mature puparia to establish the full range of species diversity in the genus. Puparia usually occur in very large numbers and, if carefully removed in quantity to damp absorbent paper in an enclosed container, they will yield adults suitable for taxonomic study.

Perspective for this paper is provided in the papers referred to previously, and further details concerning generic placement, etc., can be found in them. For convenience and continuity, the descriptive format adopted here essentially follows that of Mathis (1982, 1984).

Four head ratios and two venational ratios used in the species' descriptions are defined here for the convenience of the reader. *Frontal ratio*: frontal height (from the anterior margin of the frons to a line between the posterior pair of ocelli)/frontal width (at the level of the anterior ocellus); *facial-head ratio*: facial width between the eyes (narrowest measurement)/overall head width (greatest measurement); *eye-to-cheek ratio*: genal height (immediately below the eye)/eye height; *eye-to-face ratio*: face length (in profile from anterior margin of eye to anterior margin of face)/eye width (greatest length along plane of eye); *costal vein ratio*: the straight line distance between R_{2+3} and R_{4+5} /distance between R_1 and R_{2+3} ; *M vein ratio*: the straight line distance along M basad of crossvein dm-cu/distances apicad of crossvein dm-cu.

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Figures 1a-c. Type locality of *Diedrops roldanorum* new species. **a.** General area. Puparia most abundant below and to right of lower strike zone of waterfall. **b.** Close-up of puparia on dry portions of rock faces. **c.** Slanted sedimentary beds where puparia concentrated.

SYSTEMATICS

Genus *Diedrops* Mathis and Wirth

Diedrops Mathis and Wirth, 1976:126 [type species: *Diedrops aerigma* Mathis and Wirth, by original designation].—Mathis, 1977:555 [generic key]; 1982:6–10 [review].—Mathis, 1984:349–353 [discussion, key, new species description].

DIAGNOSIS. Head. Ocellar bristles lacking; lateroclinate fronto-orbital bristles 2, sometimes weakly developed; mesofrons in depression; arista moderately long, although not twice length of 1st flagellomere, minute hairs on at least basal $\frac{2}{3}$, sometimes to apex, but generally becoming bare apically; 1st flagellomere nearly twice length of 2nd antennal segment; face shield-like, shallowly and evenly protrudent over entire

height; facial setae uniformly sparse and subequal in size except those along oral margin, the latter setae longer, especially laterally; lacking facial series of setae extended from midfacial height to posteroventral angles of face; genal bristle present and conspicuous.

Thorax. Prescutellar acrostichal bristles 1 pair; scutellar bristles variable as to comparative length; postpronotum bare of setulae; anterior notopleural bristle only slightly smaller than posterior one; level of insertion of posterior notopleural bristle, especially as compared to anterior bristle, variable; proepisternum with scattered setulae; katepisternal bristle conspicuously weaker than anepisternal bristle; apex of vein R_{2+3} approximate to vein R_{4+5} , distance between these at apex less than $\frac{1}{2}$ that between veins R_{4+5} and M; coloration of halter, especially knob, variable; armature of forefemur variable.

Abdomen. Male abdomen and terminalia as follows: 5th sternum divided, each sternite with setulae more densely clustered toward posteromedian angle. Epandrium shield-like, cerci and cercal cavity occupying dorsal $\frac{1}{2}$ to $\frac{2}{3}$, ventral margin emarginate, setulose; gonite at least 3 times higher than wide, with posterodorsal gonal arch, latter with ventro-median process; aedeagal apodeme comparatively large, J-shaped, ventral portion wider; aedeagus 2–3 times longer than wide, in lateral view, variously shaped depending on species.

DISCUSSION. In a recent review of the tribe Dagini, Mathis (1982) hypothesized that the lineage giving rise to the genus *Diedrops* belonged to an unresolved trichotomy; the other two lineages are those from which *Psilephydra* and *Dagus* + *Physemops* arose. With the addition of a third and fourth species to *Diedrops*, one character used previously by Mathis was determined to be invalid (Mathis, 1984). Within the tribe Dagini, Mathis stated (1982:5) that only in specimens of the *Dagus* + *Physemops* lineage was the posterior notopleural bristle inserted more dorsad compared to that of the anterior bristle. In the new species of *Diedrops*, however, the posterior bristle is also distinctly elevated. In the other two species of *Diedrops*, *D. aenigma* and *D. hitchcocki*, the posterior bristle is inserted at a very slight elevation from the level of the anterior bristle. But in specimens of *D. steineri* the posterior bristle is distinctly inserted at an elevated level, similar to specimens of *Dagus* or *Physemops*. We are still of the opinion that an elevated insertion is an apomorphic character state, and consequently, that *Diedrops* is closely related to the *Dagus* + *Physemops* lineage. Repositioning *Diedrops* resolves the trichotomy with *Psilephydra* and *Dagus* + *Physemops* (*Psilephydra* is now the sister group to the remaining lineages of the tribe) but the relationships between *Diedrops*, *Dagus*, and *Physemops* remain unresolved, although each genus in this trichotomy is well characterized.

BIONOMICS. All the immatures of this genus have been taken from small to medium-sized mountain streams, specifically from smooth rocks in the impact and splash areas at the bases of small waterfalls. In Costa Rica puparia were being pounded by water falling from some 2–3 m height and were thus under intense hydraulic pressure. In other places Hogue has found puparia at the base of smaller falls, and at the type locality the main concentration of the population is centered directly below and immediately beside the strike area of a narrow fall of approximately 10 m, on sloping, fine sandstone beds (Fig. 1a–c). The collections there were made during regressive, dry season stream states, when water volume was low. Nevertheless, these stages are definitely capable of surviving very swift current conditions and should be added to the guild of torrenticolous dipterous groups such as the Blephariceridae, Deuterophlebiidae, *Maruina* (Psychodidae), etc. They exhibit some of the same morphological adaptations, although not all to the extreme degrees of these examples: compact and streamlined (flattened in the case of the puparium) shape; erect external respiratory organs; suction disc venter (larva) and adhesive perimeter (puparium); slightly lobulate segmentation; papillose (puparium) and spinulate (larva) integument; and thickened, tough body wall.

Only *Diedrops* and one other species [*Scatella (Apulvillus) cheesmanae*; Craig, pers. comm.] exhibit these conditions among the Ephydriidae, a family with early stages more normally developing in quieter, sometimes saline water.

DISTRIBUTION. The addition of the new locality data, noted previously, does not extend the known distributional limits (southern Mexico to Peru) for the genus, but does provide several localities in between, especially in Costa Rica and Colombia.

KEY TO SPECIES OF *DIEDDROPS*

- 1a. Face distinctly bicolored, with a vertical, wide, brown, median stripe about the width of the distance between the eyes, otherwise face silvery gray to whitish; fore- and midfemora of male with row of prominent, robust setae along posteroventral surface (Panamá)
..... *D. steineri* Mathis
- b. Face unicolorous, silvery gray; leg setation of sexes similar, weak, lacking row of robust setae 2
- 2a. Anepimeron with 1 to several setulae near anterior margin; wing apex bluntly rounded; apex of vein R_{2+3} slightly sinuate; length of basitarsus larger than combined length of remaining tarsomeres for each leg (Peru)
..... *D. hitchcocki* Mathis and Wirth
- b. Anepimeron bare of setulae; wing apex more narrowly rounded; vein R_{2+3} nearly parallel to vein R_{4+5} ; length of basitarsus equal to or shorter than combined length of remaining tarsomeres for each leg 3
- 3a. Face wider, facial-head ratio averaging 0.50; brownish coloration of mesonotum extended to posterodorsal corner of anepisternum; anterior scutellar bristles subequal to length of apical pair; length 4 to 4.5 mm (Mexico)
..... *D. aenigma* Mathis and Wirth
- b. Face narrower, facial-head ratio averaging 0.40; anepisternum entirely silvery gray, lacking any brownish coloration; anterior scutellar bristles about $\frac{1}{2}$ length of apical pair; length 2.3 to 3.3 mm (Colombia)
..... *D. roldanorum*, new species

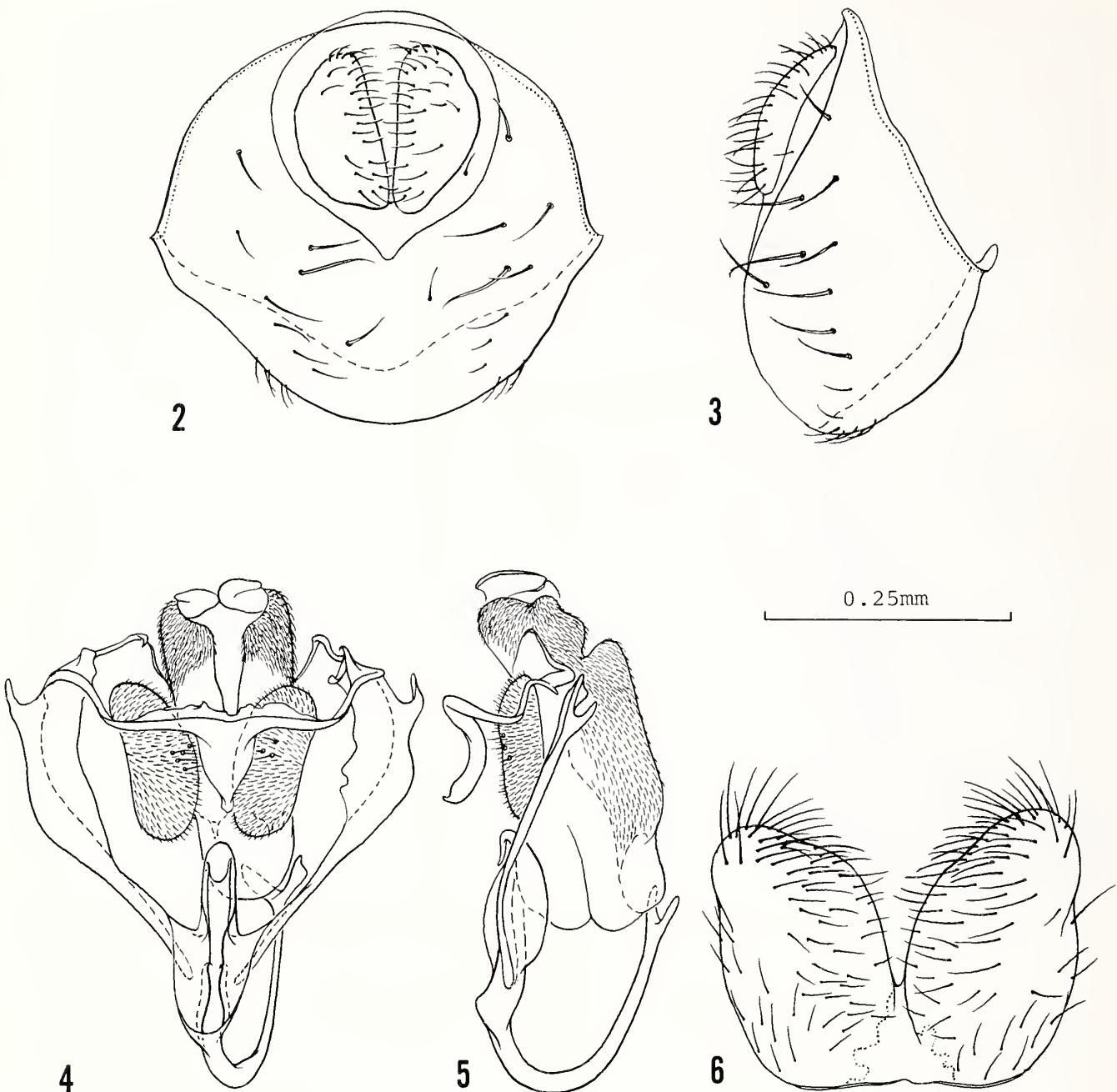
Diedrops roldanorum new species

Figures 1–10

DESCRIPTION. Adult male and female. Moderately small to medium-sized shore flies, length 2.3 to 3.3 mm.

Head. Frons width-to-length ratio 0.30; vestiture of frons uniformly microtomentose, appearing dull, vestiture of mesofrons not distinguished from that of parafrons; face, in lateral view, conspicuously inclined anteroventrally, arched, just below facial prominence, thereafter very shallowly arched, nearly flat; facial setae comparatively longer and more conspicuous immediately below antennae and along oral margin; face unicolorous, grayish silver, lacking a median, vertical, brown stripe; eye width-to-face ratio 0.40; anteroventral margin of eye bluntly rounded; eye-to-cheek ratio 0.60.

Thorax. Setae of dorsocentral and aerostichal series generally weakly developed; only a larger pair of prescutellar acrostichal setae and the posterolateral dorsocentral bristle well developed; anteroventral scutellar bristle more weakly

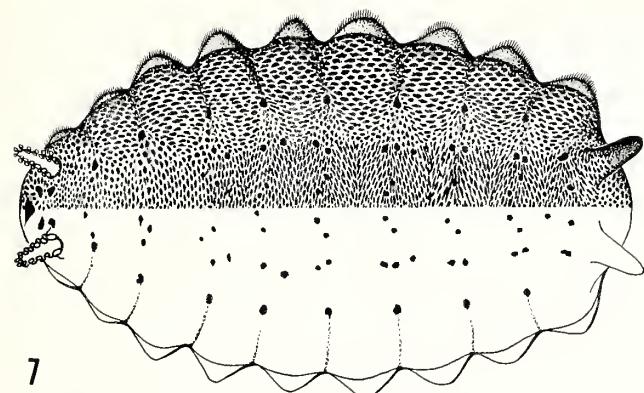


Figures 2–6. *Diedrops roldanorum*: 2, epandrium and cerci, posteroventral view; 3, same, lateral view; 4, internal male genitalia, posterior view; 5, same, lateral view; 6, sternum 5 of male.

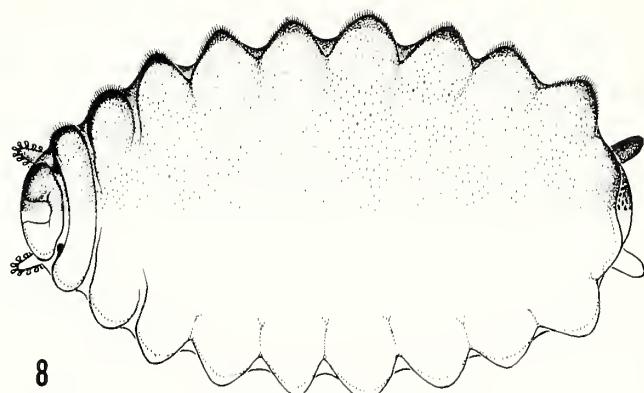
developed, about $\frac{1}{2}$ length of apical scutellar bristle; posterior notopleural bristle inserted at about same level as anterior bristle; anepimeron bare of setulae; anepisternum entirely silvery gray, lacking any brownish coloration. Leg setation of sexes similar, weak, lacking row of robust setae; length of basitarsus slightly longer or subequal to combined length of remaining tarsomeres for each leg; knob of halter mostly pale,

yellowish. Wing with apex more narrowly rounded; vein R_{2+3} evenly and very shallowly arched on basal $\frac{3}{4}$, thereafter very shallowly dipping toward vein R_{4+5} distally; costal vein ratio 15.50; vein M ratio 1.20.

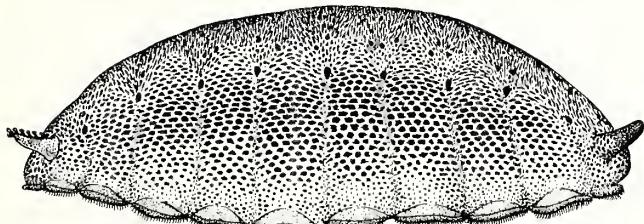
Abdomen (Figs. 2–6). Dorsum slightly lighter in color than mesonotum; tergum 1 and anterior $\frac{1}{2}$ of tergum 2 grayish, other terga blackish brown; length of 3rd tergum of male only



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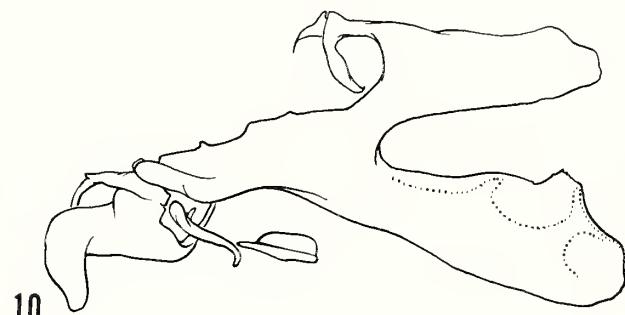


8



9

1.0mm



10

0.25mm

Figures 7–10. *Diedrops roldanorum*: 7, puparium, dorsal view; 8, puparium, ventral view; 9, same, lateral view; 10, cephalopharyngeal skeleton of 3rd instar larva, lateral view.

slightly shorter than combined length of 4th and 5th terga; 5th tergum of male (Fig. 6) with posterior margin deeply emarginate; male terminalia as in Figures 2–5.

Puparium. Shape. Generally oval in dorsal and ventral views (Figs. 7, 8) with 9 ventrolateral, rounded welts forming a crenulate lateral margin, each welt fringed with short setulae (welts probably used for locomotion); retracted margins between welts extended dorsally as shallow, gradually indented furrows that become weaker dorsally to a small black spot, thereafter nonexistent, furrows apparently delimiting segments; in lateral view dome-shaped (Fig. 9), dorsum gently and evenly rounded, venter mostly flat; 2 dorsal, more or less prominent, digitiform projections near anterior (anterior spiracles) and posterior ends (respiratory tubes), anterior spiracles with small funnel-like structures around lateral margin; respiratory tubes larger than anterior spiracle but unadorned, apical $\frac{1}{3}$ to $\frac{1}{2}$ completely dark brown.

Coloration. Dorsum generally dark brown; venter paler, yellowish to whitish laterally, darker medially. Surface pattern: dorsum appearing shagreened, with granulations elliptical; medial longitudinal $\frac{1}{3}$ with granulation pattern oriented from side to side, orientation of lateral pattern from front to back; a regular pattern of small black spots, as in Figures 7 and 9, in addition to granulations.

Dimensions. Length 3–3.5 mm; width 1.9–2.1 mm; height 0.8–1.1 mm.

Cephalopharyngeal skeleton of third instar larva. Mandibles paired, not connected dorsally, length of anteroventral projection variable (Fig. 10 shows it at its longest); dental sclerite and other detached ventral sclerite as in Figure 10; hypopharynx with slender, delicate, dorsal bridge, sclerite broadly fused posteriorly with dorsal and ventral cornua; both dorsal and ventral cornua pigmented dark brown, posterior portions of each cornu with irregularly shaped windows, these paler; parastomal bar bifurcate, with 2 slender connections to dorsal cornu; ventral cornu more robust than dorsal cornu, becoming irregularly thicker posteriorly and posterior margin with a median, shallowly pointed projection (not evident on some specimens). Length 1.9 mm.

TYPE MATERIAL. The holotype male is labeled “COLOMBIA, Tolima [Departamento]: 3 km W Boquerón 22 June 1984/see field notes Chas. L. Hogue No: CLH 343.1.” The holotype is pinned directly, is in good condition (slightly teneral), and is in the Natural History Museum of Los Angeles County. The allotype female and 44 paratypes (11♂, 33♀; LACM, USNM) bear the same locality data as the holotype. All adult specimens of the type series were reared from mature puparia.

ADDITIONAL MATERIAL. In addition to the type series of adults from the type locality, there are several hundred larvae, puparia, and puparial skins preserved in alcohol (LACM, USNM).

DISTRIBUTION. Presently known only from the type locality in Colombia.

BIONOMICS. The type locality is a small stream feeding into the Rio Sumapaz through a deep, steep gorge (Fig. 1a). The area is heavily vegetated near the stream and located generally in Dry Tropical Forest (Holdridge System). A stream of water drops over the face of a large (30–40 m) undercut cliff and continues onto the wide face of strongly tilted (20°), stratified, fine grain, compact, black and gray sandstone (Fig. 1c). Large boulders broken from this bed and the surrounding cliffs clutter the course of the stream below, before it runs under the nearby highway in a concrete culvert. The largest numbers of puparia are located on these beds, especially along the drier, eroded edges, wet only with spray and mist (Fig. 1b). The larvae were found within the direct strike zone of the fall, amidst a fairly thick growth of algae. They apparently migrate to the drier periphery of the inundated area for pupariation. Many puparia, especially those farthest from the fall, were completely dry, and often found to be empty skins from which the adults had already emerged. Hogue netted many hundreds of adult ephydrids of several genera from the immediate vicinity of these microhabitats in June of 1983, but failed to turn up any *Diedrops*; adults were only obtained by rearing puparia. The latter continued issuing from their puparia for a period of 11 days before emergence ceased.

Several hymenopterous parasitoids emerged from larvae and puparia that were being reared. They are as follows: Family Diapriidae: *Trichopria* new species (determination provided by Dr. L. Masner); Family Eucoilidae: new genus (determination provided by Dr. G. Nordlander).

ETYMOLOGY. It is a pleasure to name this species after Dr. and Mrs. Gabriel Roldán P., both of whom figured prominently in the success of fieldwork conducted in Colombia through their gracious hospitality, detailed knowledge of the terrain, and significant contributions to the study of aquatic insects in Latin America.

REMARKS. The narrower face, which is unicolorous, grayish silver; the unicolorous, grayish anepisternum; the bare anepimeron; the short anterior scutellar bristle; the more narrowly rounded wing apex; and characters of the male terminalia distinguish this species from congeners.

The type locality (Fig. 1) is situated immediately upstream from a road culvert passing under the highway connecting Boquerón and Melgar, 3.3 km west of the bridge crossing the Rio Sumapaz at Boquerón (2.4 km west of Nariz del Diablo, a prominent rock jutting over the pavement) (4°16'N, 74°34'W), 500 m elevation. Extremely large numbers of immatures have been observed here by Hogue over a period of

several years, in June–July, the driest months of the first of the region's biphasic dry seasons.

ACKNOWLEDGMENTS

We thank Drs. Norman E. Woodley and Douglas A. Craig for reviewing the manuscript. The illustrations were produced by George Venable and are gratefully acknowledged. For assistance in providing determinations of the parasitoids we thank Dr. Arnold S. Menke (SEL, USDA), Dr. L. Masner (CNC), and Dr. Goran Nordlander (Swedish University of Agricultural Sciences, Uppsala, Sweden). We are indebted particularly to the Servicio de la Erradicación de la Malaria, Bogotá (Drs. Michael J. Nelson and Marco F. Suárez) for providing logistical assistance in obtaining specimens of the new species, and to INDERENA (Instituto Nacional de Recursos Naturales del Ambiente), University of Antioquia (Laboratorio Alexander Humboldt—Dr. Gabriel Roldán P.), and Museo de Historia Natural, Universidad Nacional de Colombia (Dr. Reuben Restrepo), for cooperation in collecting collateral material at various times in Colombia. Hogue wishes to acknowledge the general financial help of the Los Angeles County Museum of Natural History Foundation and, in other countries, specifically the following individuals and agencies for making it possible to obtain *Diedrops*: Organization for Tropical Studies, Eric Fischer and D. Baird (Costa Rica); Dr. Gerardo Lamas M., Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Peru); Mr. George V. Caldwell, Los Angeles and Dirección General de la Fauna Silvestre, Secretaría de Agricultura y Recursos Hidráulicos (Mexico).

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Authors proposing new taxa must indicate that primary types have been deposited in accordance with the recommendations of the appropriate code, citing the collection by name and providing the relevant identifying details. The depository of other study material should also be indicated.

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Number 378
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CONTRIBUTIONS IN SCIENCE

THE TAXONOMY AND NOMENCLATURE OF SOME AUSTRALIAN PARAGHINE WASPS (HYMENOPTERA: MASARIDAE)

Roy R. Snelling



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

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THE TAXONOMY AND NOMENCLATURE OF SOME AUSTRALIAN PARAGIINE WASPS (HYMENOPTERA: MASARIDAE)

Roy R. Snelling¹

ABSTRACT. New taxa are described among the Australian masarid wasps. The genera known to occur in Australia are separated by a key. A new genus, *Ammoparagia* (type-species: *A. hua*, new species), is described. Two new species of *Rolandia*, *R. boreriae* and *R. houstoni*, are described and *Rickia angulata* Richards is transferred to *Rolandia*; the four known species of *Rolandia* are separated in a key.

The genus *Metaparagia* and the subgenera *Cygnaea* and *Paragiella* of *Paragia* are synonymized under *Paragia*. Three new species of *Paragia* are described: *P. oligomera*, *P. confluens*, and *P. monocesta*. Comments on distribution and synonymy are made on *P. magdalena* Turner, *P. nasuta* F. Smith, *P. sobrina* F. Smith, and *P. walkeri* Meade-Waldo. Important taxonomic features of the new taxa are illustrated.

INTRODUCTION

The masarid wasps of the world were reviewed by Richards (1962); three subfamilies were recognized: Gayellinae, Euparagiinae, and Masarinae. The first two are small groups limited to the Western Hemisphere. The worldwide subfamily Masarinae was divided into two tribes, the Paragiini and the Masarini. Only the tribe Paragiini was known to be present in Australia, where there were four genera to accommodate about two dozen species.

Most recently, Carpenter (1982) has demonstrated that the Masaridae, as conceived by Richards, are an unnatural group, since the Euparagiinae are a sister group to the Masarinae + Gayellinae of Richards. In Carpenter's view, the several former families of Vespoidea are united into the single family Vespidae, with the Masarinae + Gayellinae as a subfamily, these groups assuming tribal rank; the erstwhile Paragiini of Richards is merged with the Masarini.

While, on the whole, I am in agreement with Carpenter's proposals, for purposes of discussion of the various taxa here, I am following the scheme of Richards (1962). This is, at present, the only recent monograph of the group. Therefore, it seems expedient for discussions to relate to the hierarchy used there. The higher classification of the masarids is presently being studied by Carpenter.

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The following new taxa are described so that the names might be available to Terry Houston for his studies on their biologies.

SPECIMENS EXAMINED

Most of the material recorded below is from the collections of the Western Australian Museum, Perth (WAM); other specimens are from the collections of the British Museum (Natural History), London (BMNH); Australian National Insect Collections, Canberra (ANIC); National Museum of Victoria, Abbotsford (NMV); University of Queensland, St. Lucia (UQLD).

TERMINOLOGY

All measurements were made by means of a micrometer disc within one eyepiece of a binocular microscope.

Ammochaetae. Ammochaetae are present in a few genera of masarids. These are long bristles or setae, somewhat flattened, that form a definite fringe along the genal margin of the head and the lower margin of the mandibles. Since their tips curl inward, the ammochaetae form a "basket." Although the function of the ammochaetae is presently unknown, presumably they form a psammophore used to transport sand particles excavated from a nest. Note that most masarids have hairs on the underside of the head, but these are irregularly distributed, uneven in length, and do not form a definite, close-set row along the genal margin.

Clypeal length is measured along the midline, from base to apical margin.

Clypeal width is the maximum width across the clypeus at the level of the lateral angles. The distance between the clypeus and the inner eye margin is measured from the lateral angle of the clypeus to the nearest point on the eye margin.

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Head length is measured along the midline of the face and is the maximum measurable distance between the apical margin of the clypeus and the dorsal (preoccipital) margin of the head, when both are in focus in frontal view.

Head width is the maximum measurable width, in frontal view, across the eyes.

Occipital carinae (Figs. 25–27) have been used by Richards as both generic and specific diagnostic characters; the two carinae were designated the “dorsal occipital keel” and the “ventral occipital keel.” The “dorsal occipital keel” is the preoccipital carina (Fig. 27, prc) and begins on the preoccipital margin a little mesad of the summit of the compound eyes and follows the genal margin ventrad, and usually becomes obsolete before attaining the hypostomal carina. Richard’s “ventral occipital keel” extends dorsad from the posterior mandibular articulation along the posterior eye margin. I prefer the term *postocular carina* (Fig. 27, poc) for the latter since it better describes the position of the carina; use of the term “keel” suggests a higher and thinner structure than is the case. When the gena is greatly narrowed, as in most *Rolandia*, the preoccipital and postocular carinae become confluent.

Pretegular groove and *carina* are used to describe features on the dorsal, posterior portion of the pronotum anterior to the tegula. These are best developed in species of *Paragia* and consist of a broad, shallow groove followed by a low, but usually sharp, carina immediately anterior to the posterior margin of the segment. The description used by Richard (e.g. “Spiracular lobe of pronotum well marked off by a furrow”) seems less efficient than “pretegular groove present”; the terms used here are in accord with usage elsewhere among the vespid wasps (e.g. Bohart, 1984; Giordani Soika, 1978).

Punctures are described according to size, as follows: *fine* (0.02–0.035 mm diameter), *moderate* (0.036–0.055 mm diameter), *coarse* (0.056–0.070 mm diameter), or *very coarse* (over 0.070 mm diameter). Distances between punctures are: *contiguous* (punctures so crowded as to often be deformed and interspaces are sharp-edged), *subcontiguous* (interspaces up to 0.30 times a puncture diameter), *dense* (interspaces ranging between 0.30 and 0.70 times a puncture diameter), *close* (interspaces 0.70–1.50 times a puncture diameter), *sparse* (interspaces from 1.50–3.00 times a puncture diameter), *scattered* (interspaces irregular and ranging 3.00–6.00, or more, times a puncture diameter). Variations in puncture size and/or density may be described by combining terms (punctures moderate to coarse; punctures subcontiguous to dense, etc.).

Total length is the sum of head length + thorax length + gaster length. Because gastric segments may be contracted or extended, this measurement is inexact and is made only to the nearest tenth of a millimeter. Note that *head length* is included, not from “front of head” or some such equally imprecise method; consequently, total lengths given here will seem larger than those of other authors. For example, Richards (1962) gives length for *Paragia excellens* (as *P. sobrina*) as 13.0–14.0 mm; my method for this species yields 16.6–17.2 mm.

KEY TO AUSTRALIAN GENERA OF PARAGIINI

- 1a. Parategula absent (Fig. 15); disc of last visible gastral tergum not extended over apical margin (i.e. apical margin is posteriormost portion of segment) (Fig. 12) ... 2
- 1b. Parategula present (Fig. 8); disc of last visible gastral tergum extended so that true apical margin is ventral and anterior to posteriormost portion of segment (Fig. 3) *Ammoparagia*, new genus
- 2a. Glossa always exposed, not retractile into prementum; gastral tergum 2 constricted at base (Fig. 14); ammochaetae present (Figs. 25, 26) or absent (Fig. 27) along posterior genal margin; propleuron with or without lateral groove 3
- 2b. Glossa retractile into prementum, thus often concealed; gastral tergum 2 not constricted at base (Fig. 13); posterior margin of gena without ammochaetae; propleuron with lateral groove *Riekia*
- 3a. Anterior margin of pronotum convex (Fig. 28); gena without ammochaetae (Fig. 27) *Paragia*
- 3b. Anterior margin of pronotum angulate (Fig. 29); gena with ammochaetae along posterior margin (Figs. 25, 26) *Rolandia*

SYSTEMATICS

Ammoparagia, new genus

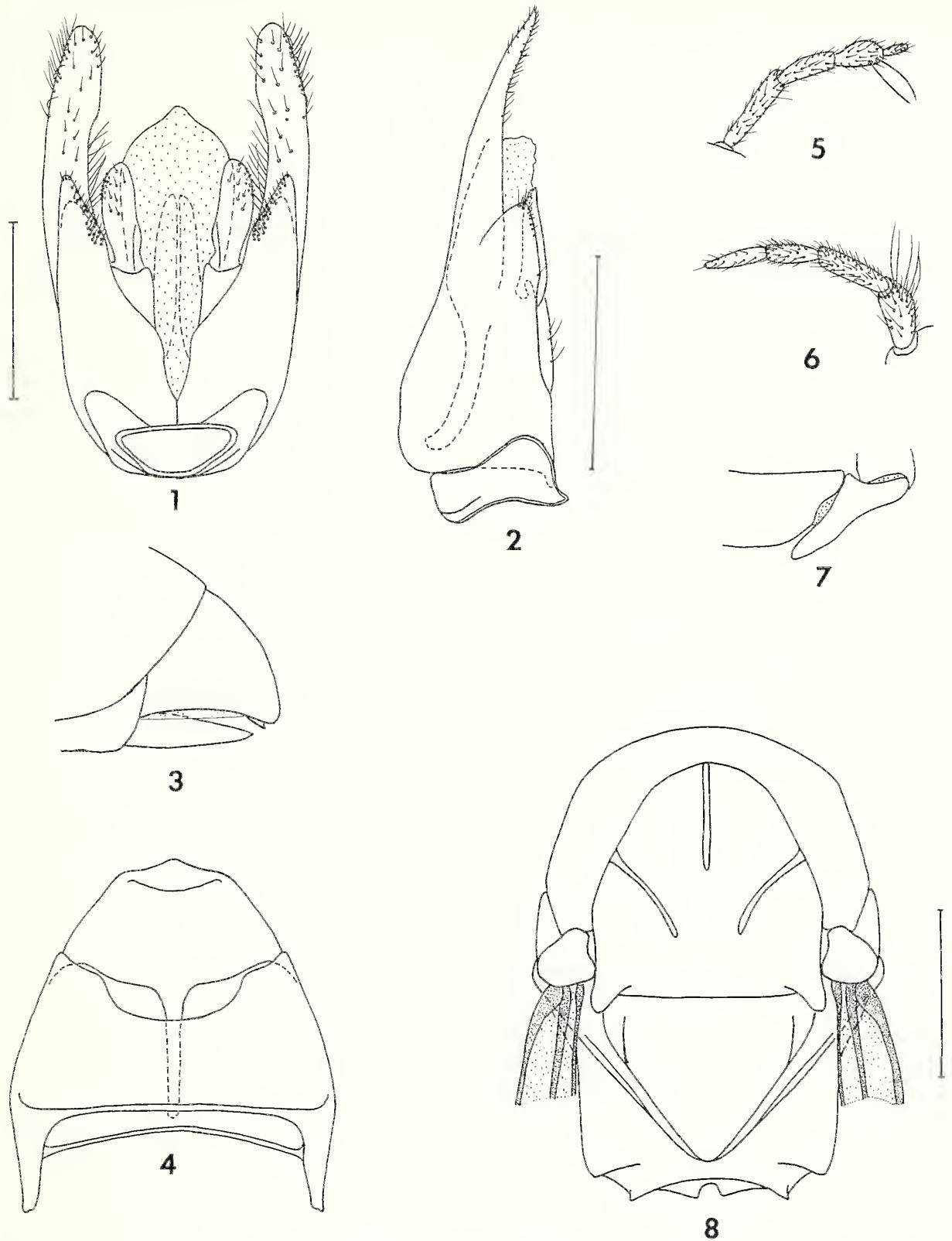
Figures 1–8

DIAGNOSIS

A member of the tribe Paragiini as defined by Richards (1962), recognizable by the following combination of characteristics: glossa retractile into prementum; parategula present; scutellum produced over metanotum and base of propodeum; gastral terga 2–4 (♀) or 2–5 (♂) with transverse basal groove; ocular sinus moderately deep; head hollowed out beneath and distinct genal ammochaetae present.

DESCRIPTION

Mandible with three acute apical teeth, decreasing in size from lower to upper; blade broad, narrowest at base. Maxillary palpus (Fig. 6) four-segmented, first segment short and stout, second segment longer and narrower; next two progressively a little shorter, each with fine bristles, most numerous on second. Prementum triangular in profile, little longer than high, uniformly sclerotized ventrally; labial palpus (Fig. 5) four-segmented, first segment longest, second and third subequal, last segment much narrower than others, third segment (♀) with two stout recurved bristles that extend much beyond tip of last segment; paraglossa and glossa with terminal sclerotized pads; paraglossa little longer than mentum; glossa about three times as long as prementum, bifurcated portion a little longer than basal portion, without dorsal comb-like processes proximally, entire dorsal surface finely imbricate, less strongly so distad. Hypostomal apodeme triangular; hypostomal bridge moderately broad, not depressed. Labrum flat, apieal margin transverse (♂) or rounded (♀).



Figures 1–8. *Ammoparagia hua*. 1, 2, male genital capsule, ventral and lateral views, respectively; scale lines = 0.50 mm. 3, female gastric apex, lateral view. 4, male gastric apex, ventral view. 5, 6, labial and maxillary palpi, respectively. 7, male protrochanter and -femur base. 8, female thorax, dorsal view; scale line = 1.00 mm.

Clypeus about 1.4 times as broad as long, apical margin transverse and wider than distance from its lateral angle to lateral angle of clypeus, disc raised above paraocular area. Malar space absent. Antennal club stout and moderately defined (♀) or flagellum weakly broadened distad (♂).

Ocular sinus moderately deep, obtuse. Interantennal area flat, without median tubercle; antennal sockets separated from inner eye margin by less than a socket diameter; interantennal distance about five times antennal socket diameter. Preocipital carina low, postocular carina weak to absent; subocipital furrow deep. Ammochaetae present along genal margin and lower margin of mandible.

Side of pronotum without oblique impressed line; humeral margin obtuse and ill-defined; pretegular carina absent; pretegular groove shallow (more so in ♂). Outer margin of tegula subcircular. Notauli of mesoscutum well marked anteriorly, but not extending much distad of level of anterior margin of tegula; parapsidal line long, narrow; parategula present (Fig. 8). Anterior margin of scutellum confluent with posterior margin of mesoscutum; disc of scutellum convex along midline and obtusely produced over metanotum and base of propodeum (Fig. 8); disc evenly rounded onto axilla. Median portion of metanotum hidden under scutellum, vertical. Angles of propodeum obtuse.

Pterostigma of forewing about three times longer than broad, lower margin rounded, prestigma about one-third as long as stigma; marginal cell about 2.5 times longer than wide, apex abruptly curved away from wing margin; junction of M and Rs moderately swollen; first submarginal cell, on Rs, about one-third longer than second, second receiving both recurrent veins; cu-v considerably distad of separation of M and Cu; junction of Cu_{1a} and 2 m-cu rounded. Anal lobe of hindwing less than one-third as long as cell Cu; veins 1A and cu-a rounded together; 13 hamuli present. Tegula subcircular.

Protrochanter of male (Fig. 7) with distal process elongate and spine-like in ventral view, its lower margin cariniform; first three segments of protarsus of both sexes strongly asymmetrical, posterior lobe, much the longer, especially on second and third segments; mesotibial spurs short and stout; femora without basal ring; outer metatibial spur much shorter than inner, inner spur trifid at apex; first and second metatarsal segments combined longer than metatibia; tarsal claws with small erect tooth at about midlength.

Gastral tergum 1, in dorsal view, more than twice wider than long; terga 2–5 (♂) or 2–4 (♀), depressed at basal and apical margins, especially in male; distal margin of last tergum (both sexes) hidden under protuberant “hood” of disc (Fig. 3); basal groove of sternum 2 very shallow and poorly defined; sterna flat (both sexes) and male without discal protuberances on any segment; sternum 6 of female broadly rounded at apex; apical margin of last visible sternum of male broadly rounded.

MALE GENITALIA (Figs. 1, 2). Parameral spine dorsoventrally flattened, apex simple, not recurved; digitus of volsella long and with tubercles along outer margin; cuspis of volsella prominent and fused to paramere.

TYPE-SPECIES. *Ammoparagia hua*, new species.

ETYMOLOGY

The generic name is combined from the Greek ammos (sand) plus the generic name *Paragia*.

DISCUSSION

The presence of parategulae and the four-segmented maxillary palpus will immediately separate *Ammoparagia* from all other known Australian paragiine genera. The genus is monotypic at the present time.

In the key to Australian genera of Paragiini by Richards (1962) *Ammoparagia* fails at the first couplet. It agrees with *Riekia* Richards, 1962, in that the glossa is retractile into the prementum, a feature previously believed unique to *Riekia* in the Australian fauna. *Ammoparagia* differs from *Riekia* in that the head is moderately concave beneath and there is a strong fringe of ammochaetae along the genal and lower mandibular margins, there is no lateral pronotal furrow, the scutellar disc extends over the metanotum and base of the propodeum, there is a definite propodeal angle, the gastral terga are depressed at the base, and the apical margin of the last exposed tergum is hidden under the disc of the segment in both sexes.

From *Rolandia* Richards, 1962, *Ammoparagia* is further separable by the lack of a lateral pronotal furrow, the lack of an impressed line on the propleuron, the shape of the scutellum, the shape of the last visible tergum, the lack of a definite basal furrow on sternum 2, and the lack of comb-like processes on the glossa.

Ammoparagia differs, also, from *Metaparagia* Meade-Waldo, 1911, in the presence of ammochaetae, the presence of notalices, the subcircular tegula, asymmetrical protarsus, the presence of an erect tooth on each tarsal claw, the shape of the scutellum, the anteriorly constricted gastric terga, and the shape of the last gastric tergum.

Finally, from *Paragia* Shuckard, 1837, *Ammoparagia* may be further separated by the moderately developed ocular sinus, the presence of ammochaetae, the lack of a groove setting off the spiracular lobe of the pronotum, the lack of an impressed line on the side of the pronotum, the poorly developed furrow at the base of gastric sternum 2, the shape of the last visible tergum, the much longer glossa, the non-recurred parameral spines of the male, and the broadly rounded last exposed male sternum.

Outside of the Australian fauna there are two paragiine genera: *Ceramius* Latreille, 1810, in Eurasia and Africa, and *Ceramiopsis* Zavattari, 1910, in South America. Both of these genera differ from *Ammoparagia* in the absence of parategulae, the shape of the scutellum, the lateral (rather than dorsal) placement of the propodeal spiracle, the shape of the last gastral tergum as well as in many details of the mouthparts, wing venation, and male genital structure.

So far as I have been able to determine, no other masarid wasp possesses parategular processes on the mesoscutum, except in the Euparagiinae which have a minute process. However, in *Euparagia* Cresson, 1879, the mesoscutum has a sharp, raised margin adjacent to the tegula and the parategular process appears to be an extension of this margin. In

Ammoparagia the mesoscutum is not marginate and the parategular process is digitiform and bends down over the anterior portion of the scutellar axilla. This is a common feature in the related family Eumenidae. The shape of the last gastric tergum appears to be unique within the Masaridae.

Aside from these two unusual features, *Ammoparagia* seems to be nearest to *Riekia* and *Rolandia*. The retractile glossa is shared with *Riekia*, as well as the truncate clypeus and the poorly developed oecipital ridges. The more prominent differences have already been noted above. There is a resemblance, too, to *Rolandia*, especially in the presence of genal ammochaetae and the reduced number of segments in the maxillary palpus, though *Rolandia* has lost only one, rather than two segments.

Ammoparagia hua, new species

Figures 1–8

DIAGNOSIS

Same as for the genus.

DESCRIPTION

MALE. Measurements. Holotype head width 2.03; head length 1.95, wing length 6.09; total length 9.4 mm. Paratypes: HW 2.06–2.13; HL 1.77–1.87; WL 5.85, TL 8.8–9.1 mm. Head 1.14–1.16 times as broad as long; mandible short and broad, tridentate, teeth acute and on strongly oblique margin, inner tooth much the shortest, dorsal margin straight, broadly rounded onto apical margin. Clypeal disc moderately shiny between subcontiguous to contiguous coarse, elongate punctures; vertex similar but punctures less elongate, moderate in size. Interocellar distance about twice diameter of anterior ocellus; ocellocular distance about 1.7 times diameter of anterior ocellus; ocellooccipital distance about 2.5 times diameter of anterior ocellus. Antennal scape shorter than interantennal distance; first flagellar segment a little more than twice as long as wide and about two-thirds as long as scape; following flagellar segments a little shorter than first; flagellum gradually broadened distad, apical segments about 1.5 times as broad as apical breadth of first segment.

Anterior margin of side of pronotum straight, not angled below midlevel; pronotal humerus obtuse at side; pronotum moderately shiny, interspaces slightly sculptured between moderate, subcontiguous punctures. Mesoscutum moderately shiny between moderate punctures that tend to be arranged in short rows, punctures more elongate cephalad. Scutellum dull, punctures coarse and elongate, mostly subcontiguous, but with linear impunctate area on center of disc, integument microstriate, appearing somewhat silky. Metanotum visible only at sides, visible portion concave, shiny, coarsely areolate. Mesopleuron shiny between dense to subcontiguous, moderate to coarse punctures, and with sparse, minute setigerous punctures. Propodeal angle obtuse; disc moderately shiny between coarse, dense punctures and with short, irregular rugulae; side shiny, with irregular impunctate areas in

middle, punctures coarse and dense above, finer and more separated below.

Ventral process of protrochanter (Fig. 7) longer than segment, apex narrowly rounded in profile, ventral margin compressed and subcarinate.

Gastral terga moderately shiny between coarse, dense punctures, last tergum subcontiguously to contiguously punctate; sternal punctures coarse, dense to subcontiguous interspaces with minute piliferous punctures, surface appearing dull due to numerous fine hairs.

Erect hairs yellowish and abundant on all body surfaces, especially long and dense on frons, vertex, and dorsum of thorax; hairs conspicuously shorter, but no less abundant, on gastral terga; gastral sterna with hairs shorter and less abundant and with numerous short appressed hairs.

Head black, the following yellowish with a weak orange tint: mandible; clypeus; ocular sinus, narrowly extended along inner orbit nearly to base of mandible; large, irregular frontal band, narrowly separated from clypeus and from ocular sinus mark; linear band along upper outer orbit.

Thorax black, the following yellowish with a weak orange tint: most of pronotum except anterior margin of propleuron, mark along margin of collar adjacent to anterior margin of mesoscutum, and narrow mark in front of tegula; parategula of mesoscutum; tegula, except transparent central spot; most of upper plate of mesopleuron; linear bar in middle of scutellum, not reaching anterior margin; metanotum with minute median spot; dorsolateral spot on propodeum, including angle. Legs principally yellowish, but with irregular black marks ventrally on all coxae. Wings dusky, veins dusky ferruginous basad to brownish distad.

Gaster largely orange-yellow; base and obscure submedian spot on dorsal surface of tergum 1 (absent in one paratype) blackish; tergum 2 with small, irregular dark blotch on either side of middle; terga 3–6 with large, submedian blackish spots that extend nearly to apical depression, their respective inner margins obliquely convergent basad; tergum 7 more ferruginous, with a pair small, submedian dark blotches at base; ventral segments yellowish ferruginous, a little dusky basad.

FEMALE. Measurements. Head width 2.16–2.19; head length 1.94–1.97; wing length 5.97; total length 9.2–9.5 mm.

Head similar to that of male with the following differences: about 1.11–1.12 times as broad as long; frons and vertex duller, contiguously rugosopunctate; preocciput similar, punctures a little coarser. First flagellar segment about twice as long as wide and about one-half as long as scape; remainder of flagellum forming a stout club, antepenultimate segment about twice broader than long. Interocellar and ocellocular distances about 2.5 times diameter of anterior ocellus; ocellooccipital distance about 2.7 times diameter of anterior ocellus.

Thoracic structure similar to that of male, but dorsum duller, interspaces minutely lineolate; angles of propodeum distinctly short-dentiform.

Legs as described for male, but without protrochanteral process.

Gaster as described for male, with usual sexual differences. Pilosity much shorter than in male, that of front of head

about as long as an ocellar diameter; that of pronotal dorsum a little shorter, the hairs of the middle portion more or less spatulate at tips, a few longer hairs along posterior portions of humeral angle; hairs of mesoscutum distinctly shorter; hairs of side of thorax longer than on pronotal dorsum; gastral hairs very short and sparse (longer and more abundant caudad), but with abundant fine, appressed hairs.

Head black, the following yellow-orange: mandible, except reddish margins and apical teeth; clypeus; broad band across lower frons, ending about midway between clypeus and anterior ocellus, and with a narrow stripe along inner orbit nearly to base of mandible; broad upper outer orbital mark.

Thorax similar to that of male, but marks yellow-orange and with the following additional markings: narrow, rectangular posteromedian mark on mesoscutum; most of dorsum of scutellum (but not reaching anterior margin); large spot on lower plate of mesopleuron; propodeal mark extended onto side. Legs yellow-orange. Gastral terga yellow-orange, with irregular, obscure basal areas dusky, last segment mainly dusky; ventral segments ferruginous.

TYPE MATERIAL (All Western Australia)

Holotype male, eight male and four female paratypes: 43 km ENE Landor Homestead ($25^{\circ}08'S$, $116^{\circ}54'E$), 23 Aug. 1984 (T.F. Houston and B.P. Hanich, no. 596-1), on flowers of *Goodenia berardiana* (Goodeniaceae). Additional paratypes: 1 ♂, 2 ♀♀, 16 km WSW Lyons River Homestead ($24^{\circ}38'S$, $115^{\circ}20'E$), 30 Aug.–1 Sept. 1980 (C.A. Howard and T.F. Houston, no. 344-9), on flowers of *G. berardiana*; 5 ♂♂, 9 km SW Gifford Creek Homestead ($20^{\circ}03'S$, $116^{\circ}13'E$), 2 Sept. 1980 (C.A. Howard and T.F. Houston, no. 350-1), on flowers of *G. berardiana*. Holotype and most paratypes in WAM; additional paratypes in BMNH and LACM.

ETYMOLOGY

The specific name is an arbitrary combination.

DISCUSSION

All the males are very similar to one another, except for minor variations in color. One of the Gifford Creek males has a minute preapical yellowish spot on the right antennal scape; presumably, males with more conspicuously maculate scape will eventually be discovered. Two males have the lower plate of the mesopleuron wholly black and two (including the holotype) have a small irregular yellowish spot a short distance in front of the posterior margin.

The six available females are very similar to one another. The distally clavate hairs on the pronotal dorsum are an unusual feature; they are not present in the males, nor in females of other Australian paragiines that I have examined.

Riekia Richards

Riekia Richards, 1962:54–55. Type-species: *Riekia nocatunga* Richards, 1962; monotypic and original designation.

This genus was established by Richards (1962) for a species

known only from females from New South Wales. Additional females of *R. nocatunga* were recorded from New South Wales by Richards (1968). In the latter paper a second species, *R. angulata*, was described from females from Queensland and New South Wales; in my opinion this is not a *Riekia*, but rather a species of *Rolandia* (see below).

In his key to the Australian paragiine genera, Richards stated that the first recurrent vein (1 m-cu) is received by the first submarginal cell. In the description of *Riekia*, however, it is stated that the vein is received in the second submarginal cell. In the two specimens of *R. nocatunga* (including a paratype) that I have seen, the latter statement is correct, and presumably that in the key is a *lapsus*.

A further source of possible confusion lies in the characterization of the occipital carinae or “keels.” In the key Richards states: “Occipital keels not developed.” The detailed description of *Riekia* does not agree: “Dorsal occipital keel not developed, ventral occipital keel long and strong . . .”. In the specimen I have studied the preoccipital carina (= “dorsal keel” of Richards) is present and well developed along the posterior genal margin from the occiput to the base of the mandible. There is no postocular carina (see TERMINOLOGY). The table by Richards (1962) on p. 12 indicates that both are absent in *Riekia*.

In addition to the characters cited by Richards that distinguish between *Riekia* and *Rolandia*, it should be noted that in the latter genus the anterior margin of the pronotum is abruptly angulate opposite the base of the procoxa (Fig. 29). In *Riekia* the margin is evenly and very broadly curved (much as in Fig. 28). The lateral furrow of the pronotum is sharply defined, crenate, and extends to the posterior margin of the segment, above the lower corner, in *Riekia*. There is no lateral furrow in *Rolandia*. Instead there is a blunt ridge that extends dorsomesad from the angulation of the anterior margin, behind which the disc is very broadly and shallowly depressed. The depressed portion is crossed by a few widely spaced, weak rugulae.

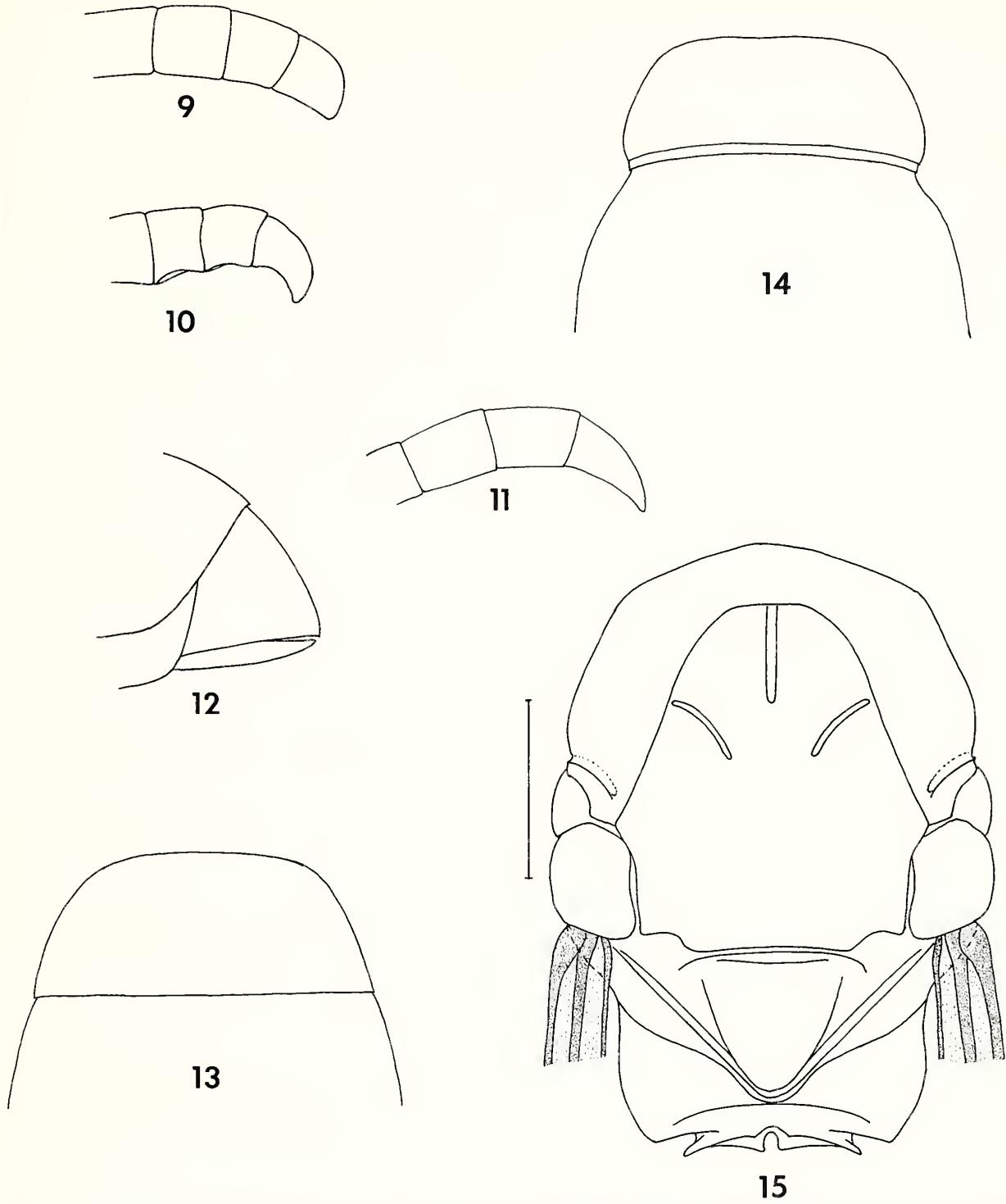
Riekia sp.

Figures 10, 19–21

A male specimen from 43 km ENE Landor Homestead ($25^{\circ}08'S$, $116^{\circ}54'E$), Western Australia, 23 Aug. 1984 (T.F. Houston and B.P. Hanich, TFH #596-1; WAM), on flowers of *Goodenia berardiana*, is obviously a species of *Riekia*. There is, however, no certainty that it is the opposite sex of *R. nocatunga*, and I suspect that it is not. More material must be available before the specific status of this male can be determined.

The male will key to *Riekia* and agrees generally with the original description of *Riekia*, except for the expected sexual differences. Agreement with females of *R. nocatunga*, sexual differences aside, is good, but the shape of the scutellum is different; the posterior margin is broad and abruptly declivitous, rather than gradually descendant to the metanotum. The pretegular carina is distinct. There are differences, too, in surface sculpturing but these might be sexual differences.

The last three flagellar segments are slightly concave be-



Figures 9–15. *Riekia* and *Rolandia* spp. 9–11, apex of male antenna of *Rolandia houstoni*, *Riekia* sp., and *Rolandia boreriae*, respectively. 12, female gastric apex, *Rolandia houstoni*. 13, 14, base of gaster of *Riekia nocatunga* and *Rolandia houstoni*, respectively. 15, female thorax, dorsal view, *Rolandia houstoni*.

neath and the apical segment is long and distinctly curved (Fig. 10). The protrochanter lacks a ventral process and the profemur is narrow at the base. Genitalic and associated structures are shown in Figures 19–21; the parameral spine is broad and thick, not at all hook-like.

Rolandia Richards

Rolandia Richards, 1962:57. Type-species: *Paragia maculata* Meade-Waldo, 1910; monotypic and original designation.

In describing *Rolandia*, Richards stressed the reduced number of segments in the maxillary palpus (five, or rarely six, segments) and the obtusely truncate clypeus, as seen in profile. The following additional species agree generally with the description of *Rolandia*, but have the clypeal profile normal for a paragiine, i.e. low and somewhat convex for most of its length and flattened or a little concave toward the apex.

Other departures from the original characterization of *Rolandia* include the presence of a minute tooth on the tarsal claws; the propodeal angle may be obtuse and not at all spine-like; the hind wing may possess a very small anal lobe (this actually is a correction, for while Richards stated that the anal lobe is absent, it is present though quite small in *R. maculata*).

The four species of *Rolandia* may be separated as follows.

KEY TO SPECIES OF *ROLANDIA*

- 1a. Apical portion of clypeus, in profile, flattened and thin (Figs. 26, 27); longest hairs in center of second gastral tergum about one-half as long as transverse diameter of anterior ocellus; scutellum finely, contiguously punctate and with longest hairs on disc shorter than diameter of anterior ocellus 2
- 1b. Anterior portion of clypeus, in profile, obtuse (Fig. 25); longest hairs in center of second gastral tergum about as long as transverse diameter of anterior ocellus; disc of scutellum coarsely rugosopunctate and with erect hairs very long, some more than twice diameter of anterior ocellus *maculata* (Meade-Waldo)
- 2a. Punctures on discs of second and third gastral terga clearly delimited by slightly shiny interspaces; hairs of female clypeus whitish and distinctly shorter than transverse diameter of anterior ocellus; male profemur broad at base (Fig. 18) and flagellar segments beyond first no longer than broad 3
- 2b. Discs of second and third gastral terga contiguously punctate and without definite interspaces; hairs of female clypeus yellow to reddish, mostly distinctly longer than transverse diameter of anterior ocellus; male profemur narrow at base (Fig. 17) and flagellar segments beyond first distinctly longer than broad *borreriae*, new species
- 3a. Frons weakly shiny, contiguously finely punctate and without shiny, linear, raised interspaces, midline raised and shiny, ending short of anterior ocellus by about its own length; scutellum, in profile, evenly sloping to meta-

- notum, without definite posterior face; maxillary palpus six-segmented *angulata* (Richards)
- b. Frons with numerous irregular, elongate, shiny interspaces between otherwise contiguous punctures; midline present as a short interanntenal tubercle separated from anterior ocellus by several times its own length; scutellum, in profile, with a short, abruptly descending posterior face; maxillary palpus five-segmented *houstoni*, new species

Rolandia angulata (Richards), new combination

Riekia angulata Richards, 1968:101–102. ♀.

I have been able to examine a paratype of this species and cannot agree with its placement in *Riekia*; it is possible that its description in *Riekia* is a *lapsus*. The paratype differs from a paratype of *Riekia nocatunga* Richards, 1962 (the type-species of *Riekia*), in the following characteristics, all shared with *Rolandia*: the glossa is not retractile; ammochaetae are present along the genal margin; the anterior margin of the propleuron is angulate; the propodeal angle is obtuse and ends in an obtusely tooth-like projection; gastral tergum 2 is constricted at the base.

This species was described from females only from Queensland and New South Wales. I have examined one paratype female; it differs from *R. houstoni* in the features discussed under that species. Although males of *R. angulata* are unknown, they will presumably differ from those of *R. houstoni* by the same features that separate the female in the key.

In addition to a paratype of *R. angulata*, I have examined eight females from Cunnamulla, Queensland, 7 Oct. 1949 (N. Geary; NMV).

Rolandia houstoni, new species

Figures 9, 12, 14, 15, 18, 22, 23, 26, 29

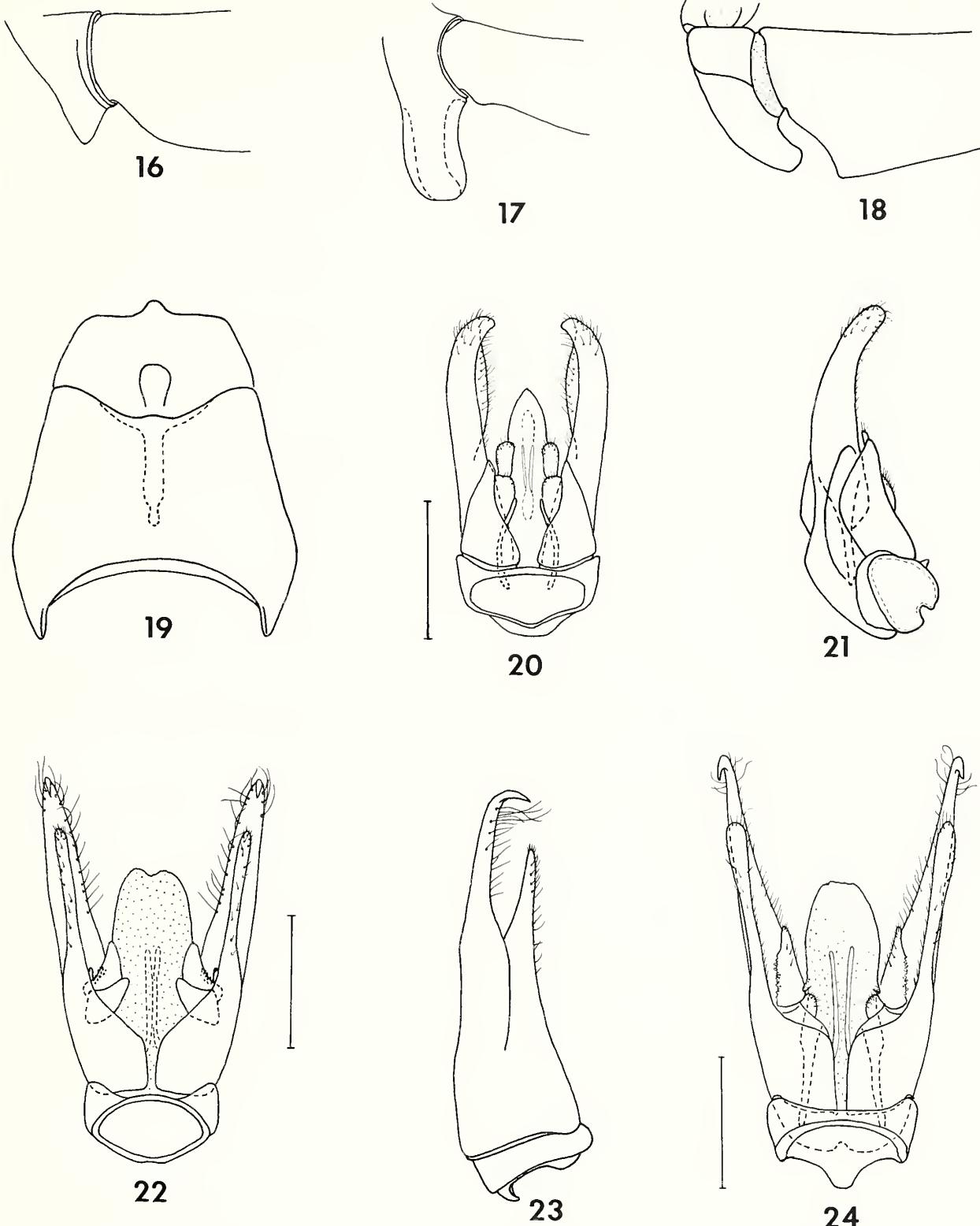
DIAGNOSIS

Mandibular teeth of female subacute and upper margin not conspicuously concave basad of inner tooth; clypeus not obtuse in profile and apical margin broadly truncate; scutellum with short, abruptly descendant posterior face; midline of face reduced to short interantennal tubercle.

DESCRIPTION

MALE. Measurements. Holotype head width 2.61; head length 2.58; wing length 6.77; total length 11.2 mm. Paratypes: head width 2.48–2.63; head length 2.42–2.58; wing length 6.56–6.82; total length 10.7–11.4 mm.

Head 1.01–1.03 times as broad as long; mandible short and broad, tridentate, teeth subacute, inner tooth smallest, upper margin basad of inner tooth weakly convex. Clypeus about 1.2 times as broad as long, gently convex in profile, merging into weakly concave apical one-third; apical margin, in frontal view, truncate, truncate portion subequal to dis-



Figures 16–24. *Rolandia* and *Riekia* sp. 16–18, protrochanter and femur base of *Rolandia maculata*, *R. boreriae*, and *R. houstoni*. 19–21, male gastric apex (ventral) and genital capsule (ventral and lateral) of *Riekia* sp. 22–24, male genital capsules of *Rolandia houstoni* (ventral and lateral) and *R. boreriae*; scale line for 19–24 = 0.50 mm.

tance from end to truncation to lateral angle of clypeus; disc moderately shiny between dense fine to moderate punctures. Interantennal tubercle low, obtuse, its lower facet moderately shiny and impunctate. Frons dull, finely rugosopunctate, with occasional flat interspaces that are dull and finely lineolate; vertex and preoccipital areas finely, contiguously to subcontiguously punctate, interspaces shinier than on frons. Interoocular distance about two times diameter of anterior ocellus; ocellocular distance subequal to interocellar distance; ocellocipital distance about three times diameter of anterior ocellus. Antennal scape shorter than interantennal distance; first flagellar segment a little less than four times as long as thick, about four-fifths as long as scape, and about twice as long as following segment; segments gradually broader distad, antepenultimate segment about twice as thick as first and about as long as broad; apical segment short and stout (Fig. 9).

Dorsum of pronotum dull, moderately rugosopunctate; pretegular groove well defined; side of pronotum with broad, shallow impressed area behind anterior margin that does not reach anterior angle, depressed area with a few very short longitudinal ridges that originate at anterior margin (Fig. 29). Mesoscutum slightly shiny, finely to moderately rugosopunctate. Scutellum dull and roughened between dense to subcontiguous, obscure, fine punctures; axilla with a few, fine, longitudinal rugulae. Mesopleuron slightly shiny and roughened between close to dense fine punctures. Side of propodeal angulation, in dorsal view, straight, its terminus bluntly rounded; dorsal area moderately shiny and roughened and moderately shiny between sparse obscure punctures that are a little coarser than those of dorsal area; side shiny and weakly roughened between scattered fine punctures.

Process of protrochanter large, broadly digitiform in posterior view (Fig. 18) and slightly curled forward; profemur compressed over basal one-half, ventral margin acute, angulate near base.

Gastral tergum 1 with dorsal face moderately shiny between dense, fine punctures; punctures of remaining terga subcontiguous, progressively finer on succeeding segments; sterna moderately shiny, with mixed minute and fine punctures that become very obscure toward margins; middle of juncture of sterna 7 and 8 deeply and narrowly impressed; genitalia as in Figures 22 and 23.

Pilosity abundant, hairs fine and mostly shorter than diameter of anterior ocellus, but a few longer hairs on side of frons, on mesopleuron, and on gastral sterna; mesoscutum with some very short, erect, brownish hairs.

Head black, the following yellowish white: mandible; clypeus; side of face from above ocular sinus nearly to base of mandible; large frontal mark, very narrowly separated from lateral face mark. Underside of scape and large spot on upper outer orbit yellow-orange.

Thorax black, with yellow-orange marks: pronotum (dusky ferruginous near tegula and on propleuron); tegula; obscure posterolateral spot on mesoscutum and adjacent axilla; most of disc of scutellum, not attaining anterior margin; middle one-third of metanotum; large spot on mesopleuron below wing base; lateral angle of propodeum. Legs mostly dusky

ferruginous, but coxae largely blackish and profemur yellowish apicad and along lower margin. Wings dusky, veins reddish basad, becoming brownish apicad.

Gastral segments dusky ferruginous, becoming darker caudad; terga 1–5 with lateral yellow blotches, largest on second, progressively smaller on segments 3–5; terga 1–6 with more or less quadrate yellow blotch or spot on apical middle; sterna without defined yellowish marks, all segments more or less ferruginous to dusky.

FEMALE. Measurements. Head width 2.48–2.65; head length 2.45–2.58; wing length 6.56–7.13; total length 10.9–12.5 mm.

Head 1.00–1.04 times as broad as long. Otherwise similar to male, with following differences: frons and vertex duller, a little more coarsely rugulose; ocellocular distance distinctly greater than interocellar distance; first flagellar segment about twice as long as thick; flagellar club weakly defined.

Thorax about as described for male, but mesoscutum more sharply rugosopunctate; protrochanter and profemur simple.

Gaster about as described for male, except usual sexual differences.

Pilosity about as in male, but everywhere shorter, especially on head and thorax; profemur with ventral fringe of long hairs, some longer than apical thickness of femur.

Markings about as in male, and uniformly orange-ferruginous, but: frontal and lateral face marks confluent; entire pronotum colored; mesoscutum with irregular lateral marks along posterior three-fourths; scutellum largely colored; dorsal area and disc of propodeum colored; yellow marks of gastral dorsum weakly defined.

TYPE MATERIAL (All Western Australia)

Holotype male, four male and four female paratypes: 10 km ESE Meedo Homestead (25°40'S, 114°37'W), 23–26 Aug. 1980 (C.A. Howard and T.F. Houston, no. 336-8), on flowers of *Goodenia berardiana* (Goodeniaceae). Additional paratypes: 1 ♂, 1 ♀, 7 km N Boologooro Homestead (24°29'S, 113°42'W), 27–29 Aug. 1980 (C.A. Howard and T.F. Houston, no. 338-13), on *G. berardiana*; 1 ♂, same data except no. 338-115, on *Pileanthus peduncularis* (Myrtaceae); 1 ♀, 16 km WSW Lyons River Homestead (24°38'S, 115°20'W), 30 Aug.–1 Sept. 1980 (C.A. Howard and T.F. Houston, no. 344-9) on *G. berardiana*; 1 ♀, same data except no. 344-24, ex burrow in sand. Holotype and most paratypes in WAM; three paratypes in LACM.

ETYMOLOGY

This species is dedicated to Terry F. Houston who collected many of the type series and who has made available much of the material on which this paper is based.

DISCUSSION

Both sexes of *R. houstoni* and *R. angulata* may be separated from *R. maculata* by the shape of the clypeal profile; in *R. maculata* the clypeus is obtusely truncated at the apex (Fig. 25) while that of *R. angulata* and *R. houstoni* (Fig. 26) is not

much different from that of other paragiines. The sculpture, especially of the dorsum of the thorax, is much less coarse in *R. angulata* and *R. houstoni*.

In *R. maculata* the mandibular teeth are broad, with rounded apices and the upper margin, basad of the inner tooth is concave for a short distance. The mandibular teeth are narrower and more acute, and the upper margin does not have the characteristic profile in *R. angulata* and *R. houstoni*.

I have seen males of *R. maculata*, and the genital structures suggest further differences between the two species. The digitus (Fig. 23) is shorter and less digitiform in *R. houstoni*. The ventral process of the paramere is sharply narrowed to an acute apex in *R. maculata*; in *R. houstoni* the process is approximately parallel-sided for most of its length and the apex is narrowly rounded (Fig. 23).

This species is very similar to *R. angulata*. Although males of *R. angulata* are not presently known, they will presumably differ from those of *R. houstoni* in the same characters as do the females.

In addition to the characters cited in the key, females of *C. houstoni* differ from the paratype of *R. angulata* in the following: clypeal interspaces shiny (dull in *R. angulata*); in dorsal view, anterior margin of pronotal collar slightly convex and humeral margin broadly rounded (in *R. angulata*, straight, humeral margin subangulate); long hairs on pronotal dorsum about 0.1 mm long (about 0.2 mm long in *R. angulata*).

Rolandia boreriae, new species

Figures 11, 17, 24

DIAGNOSIS

Clypeus of both sexes low-convex; male flagellar segments all longer than broad, last segment slightly curved and acute at apex (Fig. 11); male profemur narrow at base (Fig. 17); hairs of female clypeus stout and bristle-like, distinctly longer than transverse diameter of anterior ocellus.

DESCRIPTION

MALE. Measurements. Holotype head width 2.65; head length 2.48; wing length 6.23; total length 11.1 mm. Paratypes: HW 2.45–2.68; HL 2.33–2.50; WL 5.91–6.33; TL 10.2–10.9.

Head 1.05–1.07 times as broad as long; mandible short and broad, tridentate, teeth acute on strongly oblique margin, inner tooth much the shortest, dorsal margin weakly convex. Clypeal disc moderately shiny and microscopically lineolate between contiguous to subcontiguous, round to oblong punctures. Interocellar distance 2.00–2.30 times anterior ocellus diameter; ocellocular distance 3.12–3.40 times anterior ocellus diameter. Antennal scape a little shorter than interantennal distance; first flagellar segment about 0.8 times scape length and about 1.7–1.8 times length of second segment; all flagellar segments longer than broad, last segment about 2.4 times as long as broad, slightly curved in profile, apex acute (Fig. 11).

Pronotal humerus broadly rounded, transverse carina extended nearly to posterior margin; propleural ridge short, weak, curved; pretegular groove distinct and narrow, pretegular carina weak; disc slightly shiny, punctures moderate to coarse, mostly contiguous. Mesoscutum slightly shiny, finely to coarsely vermiculate-punctate. Disc of scutellum dull and roughened between subcontiguous to close moderate punctures; lateral portions slightly shiny between coarse, longitudinal rugae; disc, in profile, evenly and strongly curved from anterior declivity to posterior margin. Metanotum dull and densely tessellate across middle, laterally a little shinier between coarse, longitudinal rugae. Disc of mesopleuron dull and densely tessellate between subcontiguous to close, fine punctures, becoming moderate and contiguous above. Propodeal angle obtuse; disc and laterobasal surfaces slightly shiny between fine punctures that are mostly contiguous on disc, becoming close to sparse on laterobasal area; side shiny between scattered minute punctures.

Process of protrochanter much longer than segment (Fig. 17); profemur narrow at base.

Dorsal face of gastral tergum 1 slightly shiny between contiguous to subcontiguous minute punctures; following terga dull, punctures in middle of tergum 2 so dense as to be indistinguishable, becoming slightly more separated laterad and on following segments; all segments with scattered, barely discernable, fine, setigerous punctures. Gastral sterna shinier, but otherwise similar, fine setigerous punctures more distinct. Genital capsule shown in Figure 24.

Very short, fine hairs abundant on thorax and gaster, mostly appressed, but erect on mesoscutum; brownish on mesoscutum, lighter elsewhere and white on mesopleuron. Front of head with numerous long, slender hairs, longest on clypeus equal to about diameter of anterior ocellus and longest on vertex equal to about twice diameter of anterior ocellus; hairs on pronotal dorsum a little longer than on clypeus; longest hairs on gastral dorsum equal to about one-half diameter of anterior ocellus.

Head black, the following whitish: mandible, except reddish teeth; clypeus; large supraclypeal mark; narrow stripe along inner orbit almost to top of eye; large postocular spot; underside of scape. Upperside of scape and flagellum blackish, flagellar segments irregularly dull reddish beneath.

Thorax black, the following yellowish white: broad band on pronotal collar, short stripe anterior to tegula, joined to stripe across posterior lobe; tegula, except small ferruginous spot; large subtegular mark; small mesoscutal spot adjacent to tegula; disc of scutellum; large mark along lateral ridge of propodeum. Legs mostly yellowish, but upper side of femora yellowish ferruginous. Wings slightly brownish, veins brown, becoming reddish toward base.

Gaster blackish brown, the following yellowish white: apical bands on terga 1–5, narrowed sublaterally and broadened at extreme side; similar on tergum 6, but only weakly, or not at all, narrowed sublaterally; tergum 7 brownish ferruginous; sterna dusky ferruginous, with irregular blackish bands basad and transverse, preapical whitish mark on middle of segments 2–5.

FEMALE. Measurements. Head width 2.60–2.83; head

length 2.50–2.65; wing length 6.70–6.93; total length 10.6–11.7 mm.

Head 1.04–1.07 times as broad as long. Otherwise similar to male, with following differences: interocellar distance 2.08–2.27 times anterior ocellus diameter; ocellocular distance 2.75–3.00 times anterior ocellus diameter; interantennal distance 1.31–1.35 times scape length; first flagellar segment 0.51–0.56 times scape length and 2.09–2.30 times length of second flagellar segment; flagellar segments, except first, broader than long.

Thorax about as in male but mesoscutum more rugoso-punctate; protrochanter and profemur simple.

Gaster about as described for male except usual sexual differences.

Pilosity about as in male, but everywhere shorter; clypeus with abundant suberect, bristle-like, slightly brownish hairs with attenuate apices. Profemur abundantly hairy on ventral and posterior faces, but without definite fringe.

Markings about as in male, but some black partially replaced by ferruginous, especially on pronotum and gaster; lateral mark on mesoscutum over half of segment length; axilla yellowish; tergum 6 ferruginous. Legs yellowish ferruginous, becoming yellowish externally on tibiae and basitarsi.

TYPE MATERIAL

Holotype, 3 male and 4 female paratypes: Cooper Creek (12°06'S, 133°04'E), 19 km E by S Mt. Borradaile, Northern Territory, 5–6 June 1973 (J.C. Cardale), on flowers of *Borreria exserta* (Rubiaceae). Holotype and most paratypes in ANIC; one paratype pair in LACM.

ETYMOLOGY

Of, or pertaining to, the plant genus *Borreria* on which the type series was collected.

DISCUSSION

Males are easily separable from those of other *Rolandia* species by the elongate flagellum, with the apical segment curved and pointed, and by the narrow profemur base and comparatively large protrochanteral process. Similarly, the female, although superficially similar to *R. angulata* and *R. houstoni*, is characterized by the peculiar, bristle-like hairs of the clypeus. In both of the other species the hairs are slender and flexuous and not notably different from those of the frons except by being shorter. They are whitish in color, rather than brownish yellow, as in *R. borrieriae*.

Paragia Shuckard

Paragia Shuckard, 1837:81. Type-species: *Paragia decipiens* Shuckard, 1837; monotypic.

Metaparagia Meade-Waldo, 1911:748. Type-species: *Paragia pictifrons* F. Smith, 1857; original designation. NEW SYNONYMY.

Paragia subg. *Cygnaea* Richards, 1962:53, 60. Type-species:

Paragia vespiformis F. Smith, 1865; monotypic and original designation. NEW SYNONYMY.

Paragia subg. *Paragiella* Richards, 1962:53, 67. Type-species: *Paragia odyneroides* F. Smith, 1850; original designation. NEW SYNONYMY.

Metaparagia was established for two species, both apparently rare and known from unique female type specimens. These types are in the BMNH and I have examined both. While I agree with Richards that they are distinct species, I do not agree that there is any justification for the separation of *Metaparagia* from *Paragia*.

Several of the features used by Richards to distinguish between *Metaparagia* and *Paragia* are based on the relative expression of a given character. Thus, the development of the ocular sinus, amount of ventral "excavation" of the head, the shape of the pterostigma, the development of the furrow at the base of gastral sternum 2, development of the occipital carinae, the relative size of the hindwing anal lobe, and the development of the tooth of the tarsal claw, all are characters of this type. Their expression is matched by one or more of the more typical species of *Paragia*, and, in any case, none of these characteristics can be readily quantified, and I attach no significance to them.

The structure of the pronotum is not quite like that of other *Paragia*: the pretegular groove and carina are absent, as in the groove of the propleuron. All other *Paragia* do possess a pretegular groove, but it is weak in some species that also lack the pretegular carina. Similarly, the groove across the disc of the propleuron seems always to be present, though it is weak in some species. Again, I believe the character states seen in the two *Metaparagia* are the end point of a continuum and attach to them no significance beyond species level value. Much the same may be said of the lamelliform humeral carina, a conspicuous feature not stressed by Richards.

The only truly distinctive characteristic is the pyriform tegula of *Metaparagia*, contrasted with the subcircular tegula of *Paragia*. In the two species assigned to *Metaparagia*, the inner, posterior angle of the tegula is distinctly produced. The surface of the tegula bears a few irregular rugulae, but is otherwise smooth and shiny. Since variations in tegular shape are not unusual in other vespid genera, I do not believe this character state to be of value above species-group level.

Metaparagia is therefore to be considered a junior synonym of *Paragia* and its two species, *M. doddi* Meade-Waldo, 1911, and *M. pictifrons* (F. Smith), transferred to that genus as NEW COMBINATIONS.

Richards (1962), in his study, recognized a total of 19 species of *Paragia* in Australia, and added two more in 1968. These he assigned to three subgenera: *Paragia* Shuckard, 1837, and two new subgenera, *Cygnaea* and *Paragiella*.

The most distinctive of these is the subgenus *Cygnaea*, largely because of unusual modifications of the abdominal segments. However, I am philosophically opposed to monotypic subgenera, especially within genera as small as *Paragia*. For this reason I treat *Cygnaea* as a synonym of *Paragia*.

The only included species in *Cygnaea* is *P. vespiformis* F. Smith, 1865.

The distinctions that Richards attempted to enumerate between the subgenera *Paragia* and *Paragiella* are weak and unconvincing. Even Richards noted these difficulties when he cited species in each of his subgenera that were exceptional to the characterization in one or more features. The several new species described below further weaken the differences between these two groups. No distinctive features were cited by which these two subgenera were to be separated. Most characteristics were cited as "usually" or as "more or less." Others, described in less ambiguous terms, were noted to have exceptions. The two subgenera are thus perceived to be coextensive through continuous series of character state variation.

Richards' key to the species of *Paragiella* is not satisfactory since many of the features are cited in subjective terms and a user without access to a good representative collection will experience difficulty and uncertainty in interpreting the key statements. Since I have not been able to examine all the species, I cannot offer a better key at this time. Similarly, the treatment of previously described species is unsatisfactory since Richards usually commented largely on the color patterns of these species, rather than important morphological characteristics. Color patterns in these masarids are very unreliable since there is a considerable amount of variation in most species. There are also several complexes of mimetic color patterns.

Paragia oligomera, new species

DIAGNOSIS

Separable from all other *Paragia* by the reduced palpal segmentation: three labial and five maxillary palpal segments; in addition: propodeal process obtuse; distance between clypeus and eye equal to diameter of anterior ocellus; mesopleuron rugosopunctate and propodeal disc irregularly rugose between close, coarse punctures; metanotum protuberant and with horizontal basal face.

DESCRIPTION

FEMALE. Measurements. Holotype head width 5.03; head length 4.36; wing length 12.21; total length 22.8 mm. Paratype: head width 4.51; head length 3.85; wing length 11.13; total length 18.4 mm.

Head 1.15–1.17 times as broad as long. Mandibular teeth broad and blunt. Clypeus separated from inner eye margin by about diameter of anterior ocellus; about 1.1 times as wide as long; apical truncation broadly rounded, truncation narrower than distance from its end to lateral angle of clypeus; disc dull, anterior portion subcontiguously, finely punctate, grading to coarsely rugosopunctate over most of disc. A short carina-like ridge present supramesad of each antennal socket. Frons and vertex moderately to coarsely rugosopunctate; preocciput similar but punctures coarser and subcontiguous in some areas, especially laterad. Preoccipital and

postocular carinae both present and well developed. Interocular distance two times diameter of anterior ocellus; ocellocular distance about three times diameter of anterior ocellus; ocellooccipital distance a little greater than ocellocular distance. Antennocular distance about twice diameter of antennal socket; interantennal distance more than three times diameter of antennal socket; scape a little longer than interantennal distance and about 1.7 times longer than first flagellar segment; flagellum not clavate, antepenultimate segment a little broader than long.

Humeral angles of pronotum present, obtuse; dorsal face and propleuron above lateral furrow dull to slightly shiny, coarsely rugosopunctate; area anterior to lateral furrow moderately shiny between dense, moderate punctures. Mesoscutum moderately rugosopunctate, with numerous linear interspaces. Scutellum dull, coarsely rugosopunctate to anterior margin; lateral scutellar furrow distinct. Metanotum with both horizontal and vertical faces, their juncture subcarinate, fully visible in dorsal view. Mesopleuron moderately shiny between moderate to coarse, subcontiguous to contiguous punctures. Propodeal angles obtuse; dorsal face slightly shiny between subcontiguous moderate punctures; disc moderately shiny between short irregular rugae and close moderate punctures; side moderately shiny between dense, moderate punctures.

Probasitarsus a little more than twice longer than wide, margins nearly parallel; tibiae each with apical row of short, flattened ferruginous setae, those of metatibia difficult to see under long, dense, reclinate hairs that cover most of outer face; metabasitarsus without paired row of stout ferruginous setae along anterior margin; tarsal claws each with a long tooth.

Anal lobe of hindwing small but distinct; r-m perpendicular to Rs and M.

Gastral terga slightly shiny between moderate, dense punctures that become fine on tergum 5; sterna moderately shiny between close to dense moderate punctures, interspaces densely minutely punctate.

Pilosity abundant on frons and vertex, longest hairs on frons shorter than diameter of anterior ocellus and longest on occiput distinctly longer than diameter of anterior ocellus; long hairs of genal fringe more than twice diameter of anterior ocellus. Pronotal dorsum with a few long hairs across middle one-third, longest about equal to ocellar diameter, hairs otherwise very short and sparse; mesoscutum with a few scattered moderately long hairs, about as long as on frons, but mostly with sparse, very short stiff hairs; sides of thorax with numerous erect, slender hairs, some equal to ocellar diameter, or a little greater. First gastral tergum with sparse, moderately long, erect, slender hairs at sides and across base, hairs short, stiff, scattered on dorsal face; second tergum with scattered very short, stiff hairs; following terga similar, but hairs progressively longer on succeeding segments. Femora and tibiae with dense, stout, bristle-like hairs on all except dorsal faces of femora, some of which are more or less distinctly curled at tips; tarsi with dense, shorter, straight hairs.

Black, the following yellowish: clypeus, except margins and large, bifurcate mark on median lobe; stripe mesad to antennal socket; large irregular blotch on inner orbit at ocular sinus; large outer orbital spot; broad band across pronotal collar, extended posteriorly at each end, and on posterior corner in front of tegula; most of tegula; small posterolateral spot on mesoscutum; band across posterior scutellar disc, sharply narrowed in middle; large mesopleural spot; propodeal angles; broad posterior bands on gastric terga 1–4, slightly broadened on each side; large median spot on tergum 6; broad marginal bands on sterna 2–4, that on sternum 3 broadest. Legs black, apices of femora and tibial stripe yellow. Wings brownish, with dark brown veins; most of marginal cell and parts of first submarginal, radial, and first discoidal cells clouded.

The paratype is similar in color to the holotype, but the mandibles are ferruginous, the clypeus does not have a black preapical spot, a dull reddish interantennal spot is present; the pronotal dorsum is almost wholly yellow with an obscure, reddish area anterior to tegula, mesoscutum has a large posteromedian yellow spot, disc of scutellum largely yellow, and legs are largely yellow.

TYPE MATERIAL (All Western Australia)

Holotype female: 10 km NE Wanneroo, 4 Jan. 1982 (T.F. Houston, no. 418-3), on flowers of *Regelia ciliata* (Bromeliaceae). Paratype: ♀, Mogumber, no date (A. Douglas, no. 53-3310). Both in WAM.

ETYMOLOGY

Combines the Greek *oligos* (few) with *meros* (part), in reference to the reduced palpal segmentation.

DISCUSSION

This species differs from all other *Paragia* in the reduced number of palpal segments: all others have four labial and six maxillary palpal segments. This is a member of the subgenus *Paragiella* as defined by Richards (1962) and in his key to the species will fail at the third couplet because it does not accord with either alternative. The three species in that section of the key (*P. venusta* F. Smith, 1865, *P. generosa* Richards, 1962, and *P. australis* Saussure, 1853) are all smaller, less than 15 mm long, and are more finely and less closely punctate; in none are the head and thorax rugosopunctate.

Paragia magdalena Turner

Paragia magdalena Turner, 1908:89. ♀. Richards, 1962:67, 68–69.

This species is still known only from the type in the BMNH, from Mackay, Queensland. It is separable from all species of *Paragiella*, except *P. confluens*, by the lack of a propodeal process; for differences between these two species, see the description of *P. confluens*. Richards noted that the whole body is covered with pubescence; in particular, the discs of the gastric terga bear abundant suberect hairs, the longest

hairs on the third segment longer than the diameter of the anterior ocellus. Conspicuously longer hairs are present on the first tergum and on the propodeum. Surface sculpture tends to be coarsely and contiguously punctate to rugosopunctate, but the clypeus is shiny between contiguous to subcontiguous punctures and the frons is roughened between moderate to coarse, mostly subeontiguous punctures. The second tergum is likewise dull, the punctures fine to moderate and subcontiguous to dense. Total length is 16.7 mm. The wings are too badly frayed to be accurately measured, but Richards gives wing length as 10.5 mm. The color pattern has been described by Richards.

Paragia confluens, new species

Figure 28

DIAGNOSIS

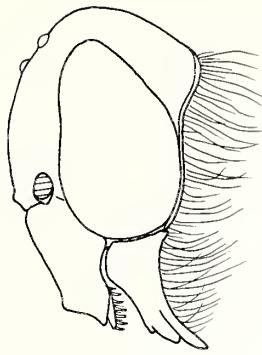
Belongs to *Paragiella* as defined by Richards (1962); differs from other species (except *P. magdalena*) in lacking lateral processes on propodeum; differs from *P. magdalena* in possessing anal lobe on hindwing and entire posterior face of propodeum without obvious punctures. This species is further characterized by the short, broad clypeus, asymmetrical protarsal segments 2–4, possessing only a single ferruginous seta at apex of meso- and metatibiae, and there are few or no erect, apically hooked, hairs on the ventral femoral surfaces.

DESCRIPTION

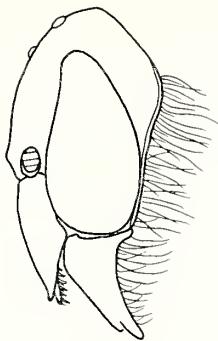
FEMALE. Measurements. Holotype head width 2.65; head length 2.35; wing length 7.28; total length 10.8 mm. Paratype: head width 2.42; head width 2.19; wing length 6.77; total length 9.9 mm.

Head 1.10–1.12 times as broad as long; mandibular teeth broad and blunt. Clypeus nearly touching inner eye margin; about 1.6 times as broad as long; apical truncation straight, wider than distance from its end to lateral angle of clypeus; disc slightly shiny, finely lineolate between dense, fine, elongate punctures, becoming subrugose in apical area. Frons slightly shiny, interspaces distinctly roughened between subcontiguous, fine punctures; vertex and preocciput similar, but with some larger punctures. Preoccipital and postocular carinae congruent. Interocellar distance about two times diameter of anterior ocellus; ocellocular distance about three times diameter of anterior ocellus; ocellooccipital distance subequal to ocellocular distance. Antennocular distance less than diameter of antennal socket; interantennal distance more than six times diameter of antennal socket; scape about two-thirds as long as interantennal distance and a little more than twice as long as first flagellar segment; flagellum stout and clavate, antepenultimate segment about twice as wide as long.

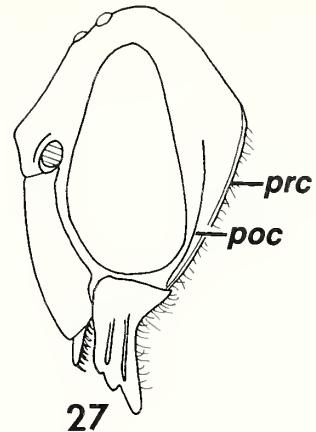
Pronotum without humeral angles, broadly rounded onto side; pretegular groove absent, but with a distinct pretegular carina; propleural furrow distinct; pronotal dorsum and propleuron above furrow dull, finely, contiguously punctate; propleuron below furrow moderately shiny, roughened between dense to close, fine punctures. Mesoscutum slightly shiny,



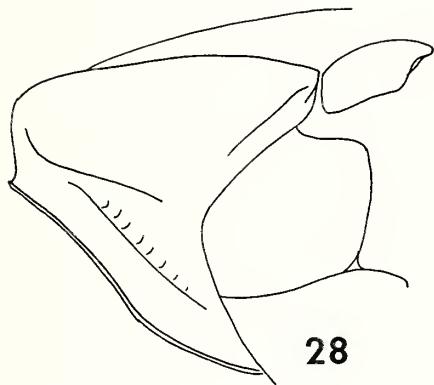
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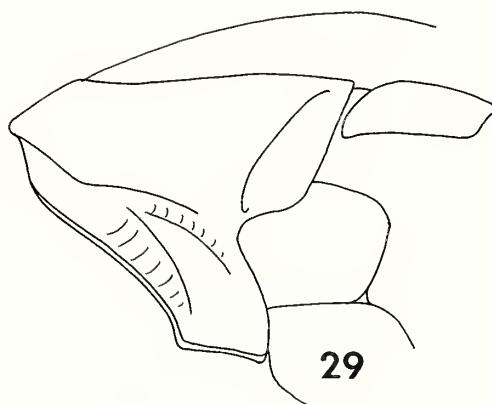
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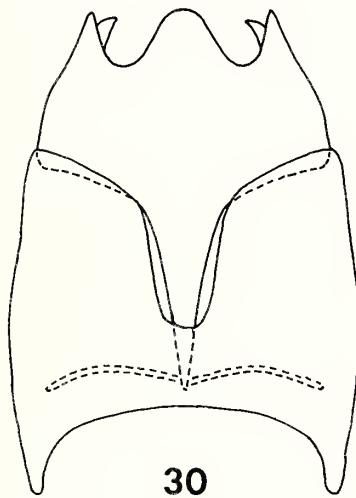
27



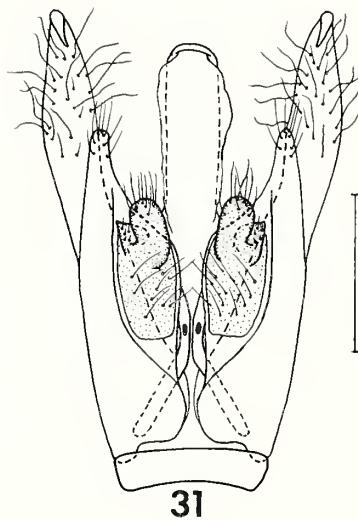
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29



30



31

Figures 25–31. *Rolandia* and *Paragia* spp. 25–27, lateral view of head of female, *R. maculata*, *R. houstoni*, and *P. monocesta*. 28, 29, lateral view of pronotum, *P. confluens*, and *R. houstoni*. 30, 31, *P. monocesta*, male gastric apex and genitalia, ventral view; scale line = 0.50. Abbreviations: poc = postocular carina, prc = preoccipital carina.

finely rugosopunctate anteriorly, becoming finely, contiguously punctate; a pair of raised, impunctate submedian welts at level of anterior margins of tegulae. Scutellum dull, disc contiguously minutely punctate; no furrow between disc and side of scutellum. Metanotum dull, middle portion vertical, roughened but without distinct punctures. Upper plate of mesopleuron dull, moderately rugosopunctate; lower plate slightly shiny and sharply roughened between close, fine punctures. Metapleuron slightly shiny, contiguously micro-punctate. Propodeal angles absent; posterior face slightly shiny, subcontiguously micropunctate and with a few fine oblique rugules in center of disc; side similar, but punctures tending to be aligned so surface appears to be finely obliquely striate near juncture of lateral and posterior surfaces.

Protibia with two or three stout, ferruginous spine-like setae at apex; probasitarsus slightly more than twice wider than long; protarsal segments 2–4 with anterior distal corner produced so that segments are asymmetrical; meso- and metatibiae each with a single stout, ferruginous, spine-like seta on outer side of apex; metabasitarsus about four-fifths as long as metatibia; tarsal claws each with minute erect tooth.

Hindwing with distinct anal lobe.

Gastral terga slightly shiny and roughened between sub-contiguous to contiguous minute punctures; sterna similar but punctures a little coarser.

Pilosity abundant on head and thorax, especially on frons, mostly about as long as, or slightly longer than, diameter of anterior ocellus; hairs mostly slender and slightly curled at tips; side posterior face of propodeum and side of first gastric tergum with numerous longer hairs of variable length; remainder of gaster with hairs mostly short, stiff, and reclinate and with abundant fine, appressed pubescence, especially distad and on sterna. Femora and tibiae with abundant fine, appressed pubescence and scattered short erect hairs, specifically lacking dense cover of fully erect, fine, hairs with curled apices.

Black, the following orange-yellow: mandible, except margins and teeth; clypeus, except margins; supraclypeal area + frons, extending nearly to top of eye on each side, but in middle only a little over midpoint between clypeus and anterior ocellus, and not extended ventrad along inner eye margin; large blotch on upper gena; dorsum and side, down to furrow, of pronotum; tegula; axillar spot; disc of scutellum; median portion of metanotum; upper plate of mesopleuron; large spot on each side of propodeal disc; dorsal face of first gastral tergum; second tergum, except narrow basal band and small, obscure, sublateral, preapical spots; small transverse, preapical median blotch and lateral band on third tergum; fourth and fifth terga except very narrow basal band; legs, except coxae. Second to fourth gastral sterna wholly yellowish-orange. Wings transparent, light brown and with dark brown veins and stigma.

Markings of the paratype are similar to those of the holotype but the apical one-third of the clypeus is black, the propleuron is wholly black, the median spot on tergum 3 is larger and triangular in shape and sterna 2–4 are yellowish-orange in the middle one-half only.

TYPE MATERIAL (All Western Australia)

Holotype female: 36 km ESE Minnie Creek Homestead, 24°38'S, 115°42'E, 2 Sept. 1980 (C.A. Howard and T.F. Houston, no. 349-2), at pool in creek. Paratype: 1 ♀, 16 km WSW Lyons River Homestead, 24°38'S, 115°20'E, 30 Aug.–1 Sept. 1980 (C.A. Howard and T.F. Houston, no. 344-9), on *Goodenia berardiana* (Goodeniaceae). Both in the collection of the Western Australian Museum.

ETYMOLOGY

The specific name is Latin and refers to the confluence of the preoccipital and postocular carinae.

DISCUSSION

This is an unusually distinctive species. Especially noteworthy is the confluence of the postocular and preoccipital carinae. In other species of *Paragia*, when they do possess occipital carinae, the postocular carina remains close to the outer eye margin, while the preoccipital carina passes behind it along the margin of the gena. In *P. confluens* the postocular carina follows the genal margin also, so that the two carinae merge. Another interpretation may be that the postocular carina is, in fact, wholly absent and that its position along the lower genal margin is taken over by the greatly extended preoccipital carina. The effect is the same.

Females of other species of *Paragia* have densely hairy legs. Typically, many or most of the hairs are fully erect, somewhat stiff and bristle-like, and are distinctly curved at their tips. Hairs of this type are present on the meso- and metalegs as well, especially on the femora and tibiae. Such hairs are not present on the legs of *P. confluens*.

Other unusual features of *P. confluens* include the short, broad clypeus, the presence of only a single spine-like seta at the apex of the outer face of the meso- and metatibiae, and the lack of propodeal angles. The latter characteristic is shared with *P. magadalena* Turner, in which the anal lobe is lacking, the posterior face of the propodeum is punctured throughout, the entire body is densely hairy, the legs possess the usual curled hairs, and the color pattern is very different; this species is apparently known only from the type from Queensland (Mackay).

Paragia monocesta, new species

Figures 27, 30, 31

DIAGNOSIS

Runs to *P. nasuta* in key by Richards (1962) but differs in color pattern, especially much more extensive orange marks, particularly of face and abdomen, the latter with tergum 2 mostly black, with a basal orange band.

DESCRIPTION

FEMALE. Measurements. Holotype head width 3.23; head length 2.87; wing length 8.77; total length 12.8 mm. Para-

types: head width 3.03–3.49; head length 2.62–3.03; wing length 8.10–9.18; total length 12.0–13.8 mm.

Head 1.12–1.20 times as broad as long. Mandibular teeth broad and blunt, inner tooth subacute. Clypeus separated from eye margin by more than one-half diameter of anterior ocellus; about 1.2 times as wide as long; broadly convex truncation wider than distance from end of truncation to lateral angle of clypeus; disc slightly shiny between subcontiguous fine to moderate punctures, becoming subrugose toward apical margin. Supraclypeal area broadly elevated between antennal sockets, shiny and with punctures separated by up to a puncture diameter in middle; a raised carina-like ridge adjacent to each antennal socket and extending well above socket; frons slightly shiny, moderately to coarsely rugosopunctate, becoming contiguously, moderately punctate on vertex and preocciput. Preoccipital and postocular carinae present. Interocellar distance about two times diameter of anterior ocellus; ocellocular distance about three times diameter of anterior ocellus; ocellooccipital distance subequal to ocellocular distance. Antennocular distance distinctly greater than antennal socket diameter; interantennal distance about 4.5 times antennal socket diameter; scape about as long as interantennal distance and about twice as long as first flagellar segment; flagellum gradually thickened distad, antepenultimate segment about 1.3 times as broad as long.

Humeral angles of pronotum weak, rounded; pre tegular groove distinct; dorsal face dull, contiguously moderately punctate; propleuron above furrow dull between subcontiguous moderate punctures, surface below furrow slightly shiny, punctures fine to moderate, irregularly spaced up to two diameters apart; furrow distinct, but anterior edge blunt. Mesoscutum slightly shiny, subrugose to contiguously, moderately punctate, with a pair of submedian, mostly impunctate, welts anteriorly; notauli distinct to posterior margin. Disc of scutellum slightly shiny between very coarse, subcontiguous punctures, narrow anterior margin of disc nearly impunctate, but distinctly sculptured; side separated from disc sharply defined crenate furrow and without longitudinal ridges. Middle portion of metanotum slightly convex and visible in dorsal view. Upper plate of mesopleuron slightly shiny between moderate to coarse, subcontiguous, elongate punctures; lower plate with punctures dense to subcontiguous, mostly moderate, some interspaces with minute to fine punctures. Metapleuron a little shinier, punctures very irregularly spaced, many minute punctures in interspaces between fine punctures. Propodeal angles prominent but broadly obtuse; posterior face slightly shiny and distinctly roughened between dense, fine punctures; lateral face similar, but spacing variable, sparse along anterior margin, becoming close to dense distad. Probasitarsus about three times longer than wide, segments 2–4 symmetrical; metabasitarsus about 0.8 times length of metatibia; tarsal claws each with a large, oblique tooth.

Anal lobe of hindwing small but distinct; r-s perpendicular to Rs and M.

Second gastral tergum distinctly constricted at base; dorsum of tergum 1 dull, appearing velvety, and roughened be-

tween dense, moderate punctures; remaining terga similar but punctures a little smaller, but still moderate, spacing variably close to dense; sterna distinctly shinier, punctures similar, a little smaller, but still moderate, spacing variably close to dense; sterna distinctly shinier, punctures similar but variably sparse to close.

Erect hairs short and sparse on clypeus, hairs longer and denser on frons, longest hairs of vertex distinctly longer than diameter of anterior ocellus; hairs on thoracic dorsum sparse, longest on mesoscutum about as long as diameter of anterior ocellus; hairs more abundant on sides of posterior face of propodeum; first tergum with numerous erect hairs, longest slightly longer than diameter of anterior ocellus; second tergum with a few short, erect hairs basad at side, otherwise second and third with scattered very short, stiff, reclinate hairs; following segments with sparse, short erect hairs, longer distad.

Prolegs with normal complement of short, stiff, erect, apically curled hairs; mesofemur with similar hairs (except on upper face), mesotibia with similar hairs on inner face and some along anterior margin of outer face.

Black, the following orange: clypeus, except dark margins; frons from clypeus to over one-half of distance to anterior ocellus, but extending nearly to top of eye at side; narrow stripe along inner eye margin to lateral angle of clypeus; most of gena, including narrow stripe almost to base of mandible; antennal scape; pronotum; short lateral stripe and postero-median spot on mesoscutum; scutellar disc and side, except along lateral furrow; most of upper mesopleural plate; propodeum except anterolaterad and large quadrate blotch on posteromedian portion of disc; legs; entire first, third, fourth (except small basomedian spot), narrow apical band on fifth, and all of sixth terga; second tergum with broad basal band, narrowed in middle; second (except large triangular patch on each side), third, and sixth sterna.

Forewings transparent, yellowish brown at base, becoming brown distad; apical portion of costal cell, most of first submarginal cell, marginal cell, all dark brown; veins yellow-orange to about level of prestigma, brown beyond.

MALE. Measurements. Head width 2.72–2.97; head length 2.44–2.56; wing length 7.54–8.41; total length 10.1–11.4 mm.

Head 1.12–1.18 times as broad as long. Mandibular teeth acute. Clypeus separated from eye margin by about 0.5 times diameter of anterior ocellus; about 1.1 times as wide as long, apical truncation gently convex and slightly longer than distance from end of truncation to lateral angle of clypeus; disc shiny between dense to subcontiguous fine to moderate punctures. Interantennal tubercle obtuse, shiny, nearly impunctate on lower facet. Frons, vertex, and preocciput slightly shiny between contiguous to subcontiguous, fine to moderate punctures. Interocellar distance about two times diameter of anterior ocellus; ocellocular distance about 2.5 times diameter of anterior ocellus; ocellooccipital distance about two times diameter of anterior ocellus. Antennocular distance less than antennal socket diameter; interantennal distance about 2.0 times antennal socket diameter; scape about 1.6 times longer than either interantennal distance or first flagellar segment, latter about three times as long as wide at apex; flagellum

moderately thickened distad, antepenultimate segment slightly broader than long.

Thorax about as in female, but posterior face of propodeum with distinct short rugulae extending laterad from median groove.

Process of protrochanter somewhat quadrate in anterior view, not extending over base of femur; in profile, thin and with anterior face slightly concave, lower edge subcarinate.

Gaster as described for female; sterna without tubercles.

Apical sterna and genitalia as in Figures 30 and 31.

Pilosity similar to that of female but hairs longer, longest on vertex and dorsum of pronotum about twice as long as diameter of anterior ocellus, those of mesoscutum not quite so long; propodeum, pleura, and first tergum also with numerous long hairs. Legs with numerous, but not dense, short, erect hairs, none curled at tips.

Black, the following yellowish: mandibular spot; clypeus; vertical bar on frons extending more than halfway between base of clypeus and anterior ocellus; narrow stripe along inner orbit from lateral angle of clypeus to level of upper end of frontal bar; antennal scape; large postocular spot (somewhat orange). The following orange: pronotum, except spiracular lobe; minute posterolateral spot on mesoscutum; posterior two-thirds of scutellar disc; large spot below wing base; angles of propodeum; legs, except coxae in large part; gastral terga as in female, but segments 5–7 black. Second sternum wholly yellowish, and following segments dark.

TYPE MATERIAL (All Western Australia)

Holotype female, 10 female and four male paratypes: 10 km ESE Meedo Homestead, 25°40'S, 114°37'E, 23–26 Aug. 1980 (C.A. Howard and T.F. Houston, no. 336-19), on *Calythrix oldfieldii* (Myrtaceae). Additional paratypes: 1 ♀, 7 km N Boologoro Homestead, 24°39'S, 113°42'E, 27–29 Aug. 1980 (C.A. Howard and T.F. Houston, no. 338-5), on *Verticordia forrestii* (Myrtaceae); 1 ♀, Gascoyne Junction, 2 Sept. 1968 (F.H.U. Baker) (this locality is about 150 km E Carnarvon at 25°03'S, 115°13'E; T. Houston, pers. comm.). Holotype and most paratypes in WAM; 2 ♀♀, 1 ♂ in LACM.

ETYMOLOGY

The specific name is Greek (one band or girdle) and refers to the single black band on metasomal tergum 2.

DISCUSSION

Although this will run to *P. nasuta* in the key by Richards (1962) it does not resemble that species; *P. nasuta* is a primarily black wasp with limited orange marks, while *P. monocesta* is largely orange. In addition to being larger (total length 13.4–16.5 mm), females of *P. nasuta* have a largely rugosopunctate clypeus, the humeral carina reaches the posterior margin of the pronotum, and the fine to moderate punctures on the disc of the second gastral tergum are mostly separated by three or more times a puncture diameter.

Males of the two species, except in the clypeal sculpturing, differ from one another in the same characteristics as do their

females. Additionally, males of *P. nasuta* have the median lobe of the eighth gastric sternite a little longer than broad and narrower than the emargination between it and the lateral lobes. In males of *P. monocesta* the median lobe is much broader than long and much broader than the emargination between it and the lateral lobes.

Paragia nasuta F. Smith

Paragia nasuta F. Smith, 1868:252. ♂, ♀. Richards, 1962:68, 76–77. ♂, ♀.

Richards has described the color pattern of both sexes and recorded specimens from Queensland and Western Australia.

New records of this species in Western Australia are as follows: 5 ♀♀, 4 ♂♂, 70–75 km ENE Norseman, 10–16 Nov. 1978 (T.F. Houston et al., no. 220-18), on flowers of *Melealeuca fulgens* (Myrtaceae); 1 ♂, 3.5–5.5 km S Yellowdine, 31°18'S, 119°39'E, 27 Oct. 1978 (T.F. Houston, no. 216-15), on flowers of *Grevillea paradox* (Proteaceae) (all in WAM).

Paragia sobrina F. Smith

Paragia excellens F. Smith, 1869:309. ♂, ♀.

Paragia sobrina F. Smith, 1869:309. ♀. Richards, 1962:75–76. ♂, ♀.

Paragia excellens and *P. sobrina* were described on the same page, with *P. excellens* appearing first and the more completely described of the two. The description of *P. sobrina* is based on those characteristics by which it differs from *P. excellens*. Richards (1962) correctly recognized that the two forms were conspecific, but for unknown reasons chose to use *P. sobrina* as the name for this species.

Smith (1869) cited the type locality for both names as "Champion Bay," in Western Australia. According to Bequaert (1928) the female types of both are labelled "Swan River." Richards (1962), however, cited Champion Bay as the type locality for *P. sobrina*. I have examined both types and confirm Bequaert's statement: the types of both *P. excellens* and *P. sobrina* are clearly labelled "Swan River."

Two additional specimens of *P. sobrina* from Western Australia were examined; 2 ♀♀, near Emu Rock, 53 km E Hyden, 32°27'S, 119°25'E, 8–10 Nov. 1979 (T.F. Houston, no. 280-1), on flowers of *Beaufortia bracteosa* (Myrtaceae) (WAM).

These have been compared with the types of both *P. excellens* and *P. sobrina*. In both types, the propodeum is mostly orange; the propodeum is black in the Emu Rock females, with the lateral processes orange and, in one specimen, there is a narrow orange mark in the middle of the posterior face. The pronotum is entirely orange in the types, but in the Emu Rock specimens it is largely black below the humeral carina and with an extension of black in front of the posterior lobe. The second tergum of the *P. sobrina* type is wholly black. Broad orange bands are present across the second tergum in the type of *P. excellens* and the two Emu Rock specimens, though narrower in the latter two. These two specimens also bear small orange marks on the third tergum, which is black in the two types.

The most characteristic morphological feature of *P. sobrina* is the shape of the propodeal process. Specialized, hooked hairs are abundant on the prolegs and mesofemur and the protarsal segments are robust and are weakly asymmetrical; the last protarsal segment is especially stout, about two-thirds as broad as long.

Paragia walkeri Meade-Waldo

Paragia walkeri Meade-Waldo, 1910:32. ♂. Richards, 1962: 68, 72–73. ♂, ♀.

A single female, although not associated with males, probably belongs to this species. It shares with the described males the peculiarly colored wings ("yellow with dark tips"), the velvety appearance of the black areas of the body, the bluntly spine-like propodeal process, the sparsely punctate gastral terga, and the large size. The specimen is 25.6 mm long; the forewing is 18.0 mm long.

This is a very attractively marked specimen. The head (except around the ocelli), pronotum, scutellum, metanotum, most of the propodeum, prepectus, all of gastral tergum 1 and sternum 1, a narrow basal band on tergum 2, and two small basolateral spots on sternum 2, are dull yellowish. The mandible, antenna legs, and fourth to sixth abdominal segments are reddish yellow, except that tergum 4 is blackish across the base.

The specimen was collected 9 km N by E Mudginberry Homestead, 12°31'S, 132°54'E, Northern Territory, 10–11 June 1973 (J.C. Cardale; ANIC).

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PROPODIAL ELABORATION IN SOUTHERN AFRICAN AND INDIAN
OCEAN FISSURELLIDAE (MOLLUSCA: PROSOBRANCHIA)
WITH DESCRIPTIONS OF TWO NEW GENERA
AND ONE NEW SPECIES

James H. McLean and R. N. Kilburn



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**PROPODIAL ELABORATION IN SOUTHERN AFRICAN AND INDIAN
OCEAN FISSURELLIDAE (MOLLUSCA: PROSOBRANCHIA)
WITH DESCRIPTIONS OF TWO NEW GENERA
AND ONE NEW SPECIES**

James H. McLean¹ and R. N. Kilburn²

ABSTRACT. Species previously assigned to *Amblychilepas* Pilsbry, 1890, in southwestern, southern, and eastern Africa and the western Indian Ocean are reviewed. *Amblychilepas* has an unmodified propodium and is represented in southern Africa by *A. platyactis*, new species. Two kinds of elaborate propodial processes form the basis for new genera. *Dendrofissurella*, type species *Patella scutellum* Gmelin, 1791, from southern Africa, has a large body and a trunklike propodium with side branches. The genus is monotypic, although two subspecies are recognized. *Medusafissurella*, type species *Fissurella salebrosa* Reeve, 1850, has a smaller body and a propodium of radiating tentacles. Three species are known: *M. salebrosa* (Reeve), in the Arabian Sea and east Africa, *M. dubia* (Reeve, 1849), in southern and eastern Africa, and *M. chemnitzii* (Sowerby, 1835) in southwestern Africa. The function of the propodium remains to be investigated.

INTRODUCTION

The propodium (anterior end of the foot) in fissurellids has not heretofore been reported to have unusual features. Here we describe elaborate propodial tentacles in four fissurellid species occurring in the Arabian Sea, and along the eastern, southern, and southwestern coasts of Africa. These species were previously assigned to *Amblychilepas* Pilsbry, 1890, the type species of which lacks these processes. Two genera are proposed, each strikingly different in shell and body proportions, as well as propodial elaboration. Three of the species are poorly known and have rarely been discussed subsequent to their original descriptions.

The genera treated here (*Amblychilepas*, *Medusafissurella*, new genus, and *Dendrofissurella*, new genus) are closely related in radular and shell characters and are assigned to the subfamily Fissurellinae. We follow Thiele (1929) and McLean (1984a, 1984b) in recognizing two subfamilies in the Fissurellidae: Emarginulinae and Fissurellinae. The Emarginulinae are the oldest, originating in the Mesozoic. Despite major

differences among genera in shell characters, the radula in the Emarginulinae has unifying features; further subdivisions are therefore recognized only at the tribal level. The relatively few genera in the Fissurellinae are relatively young, appearing in the Cenozoic.

Fissurelline genera differ from emarginuline genera in the following features: 1) the rachidian plate of the radula has a broad base and a narrow tip, rather than the broad or moderately broad tip of the emarginuline rachidian; 2) the large outer lateral tooth is so long that it is aligned with the inner lateral teeth of the row above, rather than the same row as in emarginuline genera (Hickman, 1984); 3) the shell muscle lacks the inwardly directed hook-shaped process of emarginuline genera (Odhner, 1932); 4) the selenizone that is present at least in the early juvenile of emarginuline genera is lacking (McLean, 1984a, 1984b).

This paper treats those fissurelline genera in which the body tends to be larger than the shell. Shells in this group have been confused with emarginuline genera in the tribe Fissurellidini; the latter—*Lucapinella* Pilsbry, 1890; *Leurolepas* McLean, 1970; *Fissurellidea* Orbigny, 1841; *Pupillaea* Sowerby, 1835; and *Buchanania* Lesson, 1830—were treated by McLean (1984a).

Material upon which this paper is based is housed in the following museums or collections: AMS, Australian Museum, Sydney; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; JC, J. Christiaens collection, Hasselt, Belgium; LACM, Los Angeles County Museum of Natural History, Los Angeles; MNHN, Muséum National d'Histoire Naturelle, Paris;

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2. Natal Museum, Pietermaritzburg 3201, Natal, South Africa.



Figures 1–4. SEM views of radulae, showing a narrow rachidian with expanded base, four narrow laterals, a large quadricuspid outer lateral, an uncusped lateromarginal plate, and slender marginals; all $\times 200$. 1. *Medusafissurella dubia* (Reeve, 1849). Salt Rock, Umlahli District, Natal, South Africa, NM B9928. 2. *Dendrofissurella scutellum hiantula* (Lamarck, 1822). Algoa Bay, Eastern Cape Province, South Africa, NM B9919. 3. *Amblychilepas platyactis*, new species. Paratype, Kwelera, Eastern Cape Province, South Africa, NM B9929/T3058. 4. *Fissurella nimbosa* (Linnaeus, 1758). Puerto La Cruz, Venezuela, LACM 76-30.

NM, Natal Museum, Pietermaritzburg; USNM, United States National Museum, Washington, D.C.

Family Fissurellidae

Subfamily Fissurellinae

Three genera having no reported modification of the pro-
podium are currently recognized in the subfamily Fissurel-
liniae: 1) *Fissurella* Bruguière, 1798 (with several subgenera), in which the size of the body does not greatly exceed that of the shell and the large outer lateral radular plate has four cusps; 2) *Amblychilepas* Pilsbry, 1890, with an oval shell, central foramen, and large body; the large outer lateral has

four cusps as in *Fissurella*; 3) *Macrochisma* Sowerby, 1839 (with several subgenera), in which the shell is narrow, the foramen is elongate and posterior, the body much longer than the shell and the large outer lateral has three cusps (one very small); Kilburn has noted (unpublished observation) that *Macrochisma africana* Tomlin, 1932, has a deeply bifid pro-
podium. McLean (1970) included the monotypic genus *Leu-
rolepas* McLean, 1970, in the Fissurellinae, but later (1984a) transferred it to the Emarginulinae, tribe Fissurellidini.

Radulae within the Fissurellinae show few generic and specific differences. Radulae of members of four genera (*Fissurella*, *Amblychilepas*, *Medusafissurella*, and *Dendrofissurella*) are illustrated here (Figs. 1–4). Each has a narrow rachidian with expanded base, four narrow laterals, a large

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quadricuspid outer lateral, an uncusped lateromarginal plate, and slender marginals. The marked asymmetry of the fissurellid radula, which places the laterals of the left side of the ribbon higher than those of the right, has been discussed by Hickman (1981).

The five genera (two new) here recognized in the subfamily Fissurellinae may be keyed as follows:

- | | | |
|-----|---|-------------------------|
| 1a. | Propodium without tentacles | 2 |
| b. | Propodium with elaborate tentacles | 4 |
| 2a. | Body not or not greatly exceeding size of shell | |
| | | <i>Fissurella</i> |
| b. | Body at least twice shell length | 3 |
| 3a. | Foramen oval, central | <i>Amblychilepas</i> |
| b. | Foramen elongate, posterior | <i>Macrochisma</i> |
| 4a. | Propodium with numerous subequal tentacles | |
| | | <i>Medusafissurella</i> |
| b. | Propodial outgrowth with main trunk and side branches | <i>Dendrofissurella</i> |

Medusafissurella new genus

Type species: *Fissurella salebrosa* Reeve, 1850. Recent, Arabian Sea, Indian Ocean.

DESCRIPTION. Shell markedly narrowed anteriorly; anterior end raised; anterior shell edge thinner and sharper than elsewhere; posterior end only slightly or not at all raised; anterior slope concave. Foramen oval, interior callus not truncated posteriorly. Sculpture of strong, scabrous ribs. Posterior portion of foot covered by shell; shell edge only slightly enveloped by mantle folds; propodium with radiating tentacles, sometimes branched, subequal in length. Large outer lateral tooth of radula quadricuspid.

REMARKS. On the basis of shell characters alone, the species grouped here have been variously assigned to other fissurellid genera. The shell of *Medusafissurella* differs from that of most *Fissurella* species in having a prominently raised anterior end with thin edge, and from *Amblychilepas* and *Dendrofissurella* in having strong, scabrous primary ribs, and a less raised posterior end. Body differing in being nearly covered by the shell and in having numerous propodial tentacles, not the single main, branching structure of *Dendrofissurella*.

The quadricuspid outer lateral tooth of *Medusafissurella* is similar to that in *Dendrofissurella*, *Amblychilepas*, and *Fissurella*.

Medusafissurella comprises three allopatric species: *M. salebrosa* (Reeve, 1850), *M. dubia* (Reeve, 1849), and *M. chemnitzi* (Sowerby, 1835).

ETYMOLOGY. The prefix is suggested by the propodial tentacles, which recall the serpentine locks of Medusa in Roman mythology; gender feminine.

Medusafissurella salebrosa (Reeve, 1850)

Figures 5–7, 14, 26

Fissurella salebrosa Reeve, 1850:pl. 11, sp. 78; Bosch and Bosch, 1982:29, 3 figs. Type locality: Karachi, Pakistan.

Glyphis salebrosa; Pilsbry, 1890:208, pl. 39, fig. 7 [copy Reeve, 1850:fig. 78].

Diodora salebrosa; Christiaens, 1974:91.

Lucapinella salebrosa; Biggs, 1969:202 [checklist only].

“*Fissurella subrostrata* Guilding”; of Sowerby II, 1862:192, fig. 215, not *F. subrostrata* “Gray”; Sowerby, 1835b:6, fig. 35.

DESCRIPTION. Shell markedly narrowed anteriorly; anterior end raised; anterior slope concave; sculpture of strong, scabrous ribs; rib interspaces broad, foramen nearly circular, broader posteriorly. Posterior portion of foot covered by shell, shell edge only slightly enveloped by mantle folds; exterior color gray-brown, interior white. Propodium with about 15 radiating tentacles, subequal in size, anteriomost the largest. Maximum shell length 35 mm (JC colln.).

The description of the propodium is based on the only preserved specimen available (CAS 031984, Figs. 14, 26).

TYPE MATERIAL. Lectotype here designated, BMNH 1975078 (Fig. 5), one of two original syntypes so catalogued.

DISTRIBUTION. Indian Ocean, northernmost Arabian Sea, Pakistan to Somalia.

MATERIAL EXAMINED. PAKISTAN: Buleji Point, Sind Province (LACM 79-34) (Fig. 6); Goth Jafar, west of Karachi (CAS 031984) (Figs. 14, 26); Karachi (NM H5382). OMAN: Muscat (JC colln.); Masirah Island (NM J3845). SOMALIA: Alula (JC colln.); Socotra Island (JC colln.) (Fig. 7).

COMPARISONS. The anterior end of *M. salebrosa* is more tapering and the primary ribs are more strongly defined and broadly separated than those of *M. dubia* and *M. chemnitzi*.

REMARKS. This enigmatic species is poorly known, partly because of its localized distribution. The first illustration with a properly documented locality subsequent to that of Reeve's original figure is that of Bosch and Bosch (1982), who indicated it as common, “distributed generally on rocks or in crevices.”

Sowerby II (1862) incorrectly placed *F. salebrosa* in the synonymy of *F. subrostrata* “Guilding,” Sowerby, 1835, a yet unrecognized taxon (see synonymy above), said to be from St. Vincents, West Indies. The original illustration shows more numerous, less pronounced radial ribs than those of *F. salebrosa*. Christiaens (1973:91) tentatively placed *F. salebrosa* in the synonymy of *F. subrostrata*. He now considers (pers. comm.) the specimen figured by Perez-Farfante (1943: 20, pl. 6, figs. 9–11) as “*F. subrostrata*” to be a mislocalized specimen of *Medusafissurella salebrosa*.

Medusafissurella dubia (Reeve, 1849)

Figures 1, 8–10, 15

Fissurella dubia Reeve, 1849:pl. 6, fig. 35. Type locality: Port Natal [= Durban], South Africa.

Lucapina dubia; Sowerby II, 1862:193, pl. 9, fig. 208.

Glyphis dubia; Pilsbry, 1890:217, pl. 39, fig. 6 [copy Reeve, 1849:fig. 35].

Amblychilepas dubia; Kilburn and Rippey, 1982:35, pl. 6, fig. 2.

Fissurellidea genevieveae Dautzenberg, 1929:546, pl. 1, figs. 3–7. Type locality: Madagascar (several localities cited).

DESCRIPTION. Shell outline oval, slightly narrowed anteriorly; anterior end raised, concave at early stage, all slopes convex at later stage. Sculpture of strong scabrous ribs, rib interspaces relatively narrow; foramen oval. Posterior portion of foot covered by shell, shell edge slightly enveloped by mantle folds. Propodial tentacles approximately 12 on ventral side, some branching up to 4 times so that 2 or 3 layers of tentacles project in anterior view. Maximum shell length 36 mm (Kilburn and Rippey, 1982).

The description of the animal is based on preserved specimens from Salt Rock, Umhlali District, Natal (NM B9915) (Fig. 15), collected by R.N. Kilburn, November, 1970.

TYPE MATERIAL. Holotype, BMNH 198495 (Fig. 9). Type material of *Fissurellidea genevieveae* has not been located. It is not in the Dautzenberg collection at the Brussels Museum.

DISTRIBUTION. East Africa to South Africa: Mogadiscio, Somalia, to Kelso, Natal, South Africa; Madagascar. Living in submerged rock crevices, intertidal fringe to a depth of several meters.

MATERIAL EXAMINED. SOMALIA: Mogadiscio (USNM 673793; LACM 25051); Socotra Island (JC colln.). MOZAMBIQUE: Bazaruto Island, near lighthouse (NM G4599) (Fig. 8); Cabo de Santa Maria, Bay of Maputo (NM 6238); Mozambique (LACM 25206). SOUTH AFRICA, NATAL: Kosi Bay, Zululand (NM B2092); Mvoti River mouth (NM 9350); 3 mi. off Umhlanga Rocks, 12–13 fm. (NM A269); Salt Rock, Umhlali district (NM B9928) (Fig. 15); Tongaat (NM 7132); Durban (NM 9489, NM B2093, NM 8989, NM 267, NM 7139, NM 9004) (Fig. 10); Isipingo (NM 5883); Umkomas (NM 9132); Park Rynie (NM 5870); Kelso (NM B2095).

COMPARISONS. Shell differing from that of *M. salebrosa* in having a less tapered anterior end, a greater number of radial ribs, a more elongate foramen; propodium differing in having the tentacles branched.

REMARKS. Kilburn and Rippey (1982) were the first to recognize the occurrence of this species subsequent to the original description of Reeve. They noted that it differed anatomically from “*Amblychilepas*” *scutellum* but did not provide details. *Fissurellidea genevieveae* Dautzenberg has not been noticed in subsequent literature, but the original figures are adequate to allocate it to *Medusafissurella dubia*, with which it was not originally compared.

Medusafissurella chemnitzii (Sowerby, 1835)

Figures 11–13, 16

Fissurella chemnitzii Sowerby, 1835a:126; Sowerby, 1835b: 5, fig. 55; Reeve, 1849:pl. 1, fig. 1 (part). Original locality unknown [“Benguela, West Africa,” cited by Reeve, 1849].

Fissurellidea chemnitzii; Sowerby II, 1862:202, pl. 2, fig. 29, pl. 8, fig. 192 (part).

Megatebennus (section *Amblychilepas*) *chemnitzii*; Pilsbry, 1890:185, pl. 39, fig. 90 [copy Reeve, 1849:fig. 1].

DESCRIPTION. Shell outline oval, slightly narrowed anteriorly; anterior end markedly raised; posterior end slightly raised. All slopes straight to slightly concave. Sculpture of strong irregular, finely scabrous ribs; rib interspaces narrow. Foramen elongate oval. Posterior portion of foot projecting $\frac{1}{4}$ shell length beyond shell, shell edge slightly enveloped by mantle folds. Propodial tentacles numerous, irregular. Maximum shell length 52 mm (East London Museum 11001).

The description of the animal is based on four poorly preserved specimens from Baia de Santa Maria, Benguela Prov., Angola (MNHN uncat.), collected by S. Gofas, December, 1982 (Figs. 12, 16).

TYPE MATERIAL. Neotype (here designated), MNHN uncat., Baia de Santa Maria, Angola (Fig. 12). Dimensions: 24.8 × 15.2 × 7.2 mm. Sowerby’s original material is unknown; it has not been recognized in the British Museum.

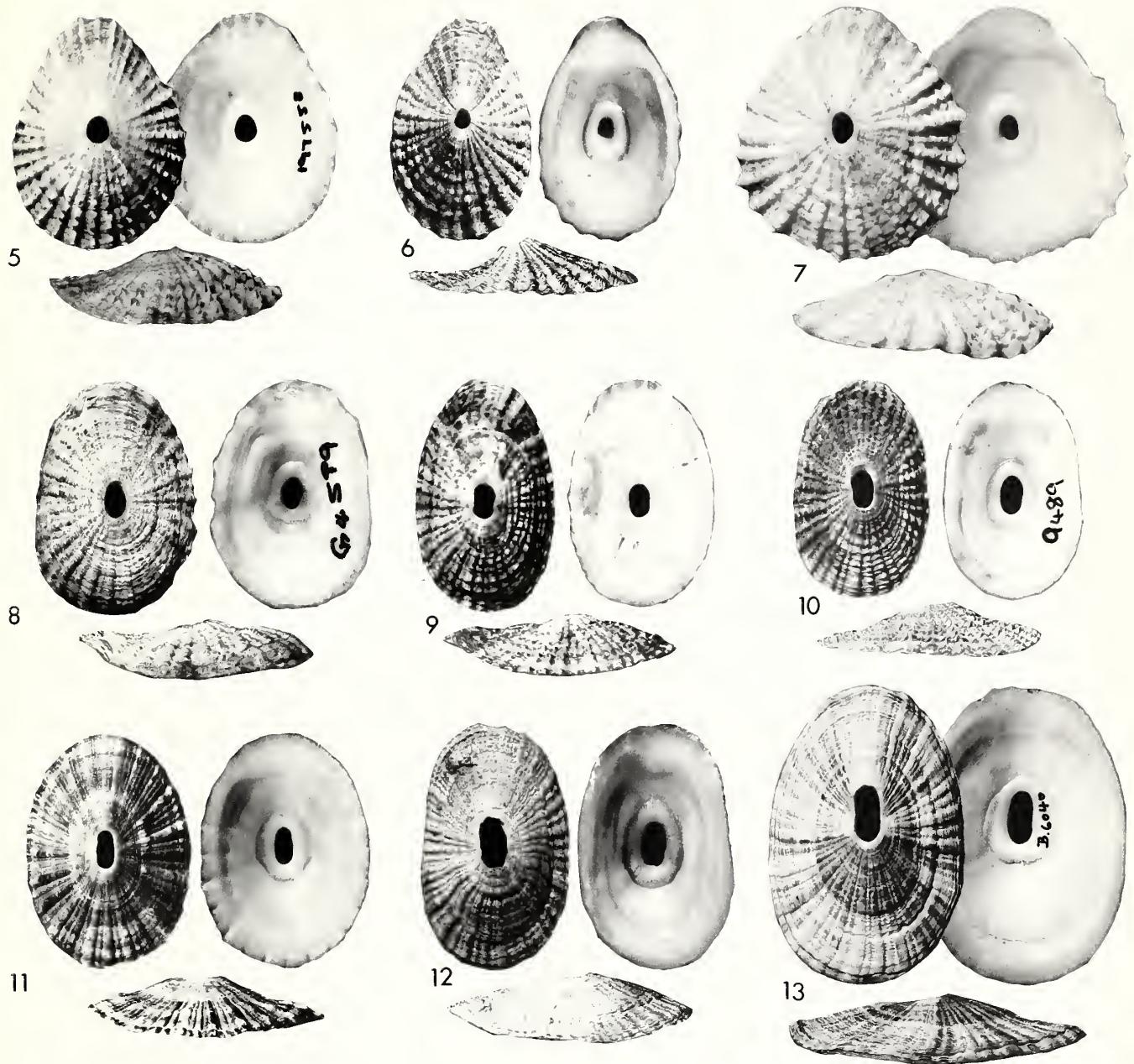
DISTRIBUTION. Southwestern Africa: Pointe Noire, Congo, to Kunene River Mouth, Angola/Namibia border. Rocky intertidal to 2 m.

MATERIAL EXAMINED. CONGO: Pointe Noire, Côte Sauvage (JC colln.) (Fig. 11). ANGOLA (all MNHN uncat., collected by S. Gofas): Ambrizete, Zaire Prov.; Baia de Santa Maria, Benguela Prov. (Figs. 12, 16); Sao Nicolau, Mocamedes Prov.; Chapeu Armado, Mocamedes Prov.; Lunda, Luanda Prov. (JC colln.). NAMIBIA: Kunene River mouth (NM B6040; East London Museum 11001) (Fig. 13).

COMPARISONS. *Medusafissurella chemnitzii* differs from *M. salebrosa* and *M. dubia* in its larger size, more elongate foramen, less scabrous ribs, and in having red rather than brown or gray coloration.

REMARKS. This is the most enigmatic of the three *Medusafissurella* species. A neotype is here designated because original material cannot be located and none of the illustrations purported to represent this species are completely accurate. The history of the name *Fissurella chemnitzii* is detailed below.

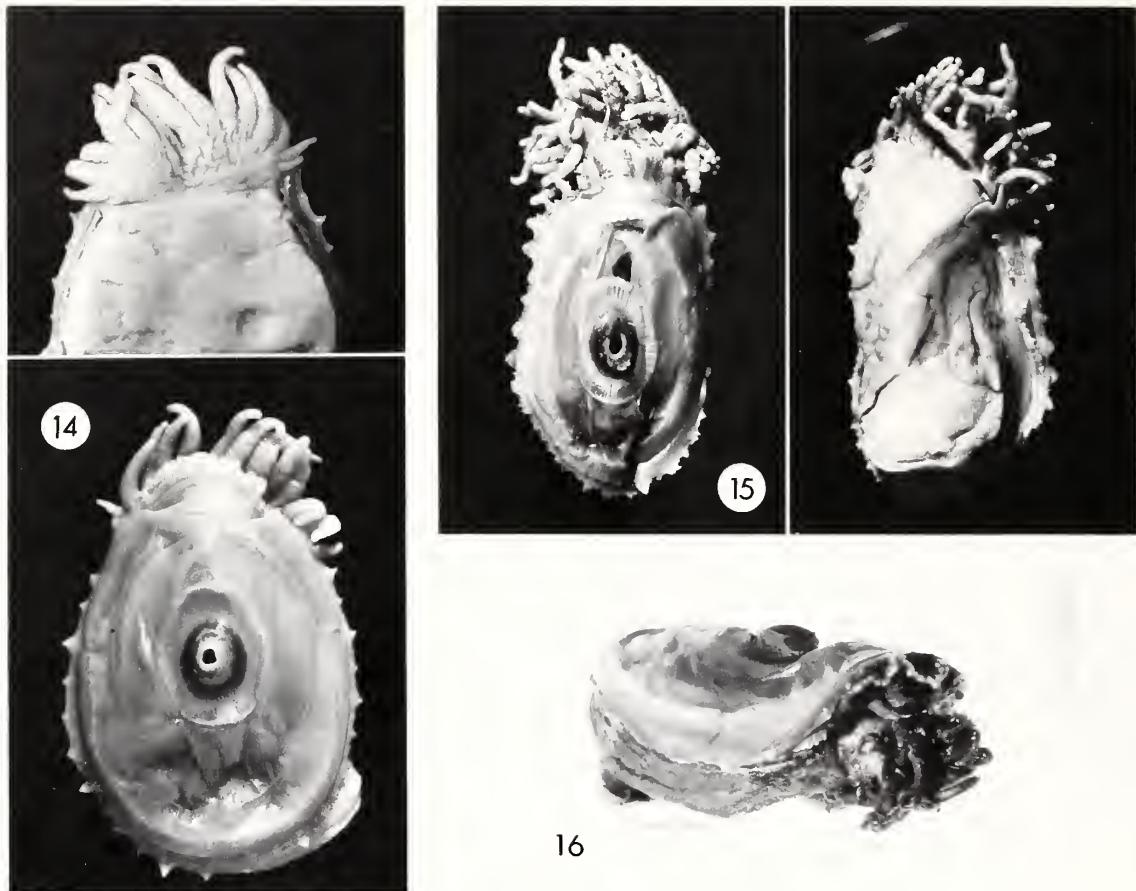
The descriptions of Sowerby (1835a) and Reeve (1849) agree with the species as here interpreted. Sowerby (1835a) remarked that “the only specimen I have ever seen of this species was in the Tankerville Collection, from which after several vicissitudes, it has at length found its way to Mr. Cuming’s.” Although he also noted: “This remarkable shell is represented by Martini (I, t. xi, fig. 100),” the shell illustrated by Sowerby (1835b) is not copied from Martini’s figure 100 (Martini and Chemnitz, 1769–1795) (which we consider to represent the Mediterranean *Diodora italicica* (Defrance, 1820)), but could only be the Tankerville shell. The original figure of Sowerby (1835b) does not show the primary ribs as sufficiently prominent and the foramen is somewhat too large; however, the proportions are correct and it conceivably could



Figures 5–13. Shells of *Medusafissurella* species; exterior and interior views with anterior at top; lateral views of left side. **Figs. 5–7.** *M. salebrosa* (Reeve, 1850). 5. Lectotype, Karachi, Pakistan, BMNH 1975078, 27.0 × 20.7 × 8.9 mm. 6. 7 km WNW Buleiji Point, Sind Province, Pakistan, LACM 79-34, 20.0 × 12.5 × 5.4 mm. 7. Socotra Island, Somalia, JC colln., 29.2 × 26.7 × 10.2 mm. **Figs. 8–10.** *M. dubia* (Reeve, 1849). 8. Bazaruto Island, Mozambique, NM G4599, 22.4 × 15.5 × 4.0 mm. 9. Holotype, Durban, Natal, South Africa, BMNH 1984195, 22.1 × 13.7 × 5.3 mm. 10. Durban, NM 9489, 19.4 × 12.1 × 4.6 mm. **Figs. 11–13.** *M. chemnitzii* (Sowerby, 1835). 11. Pointe Noire, Côte Sauvage, Congo, JC colln., 23.1 × 16.4 × 5.9 mm. 12. Neotype, Baia de Santa Maria, Angola, MNHN uncat., 24.8 × 15.2 × 7.2 mm. 13. Kunene River Mouth, Namibia, NM B6040, 42.9 × 28.9 × 10.7 mm.

have been based on the species treated here. The specimen figured by Reeve from “Benguela, West Africa, collected by Dr. Tams” has not been located in the British Museum; this illustration is inaccurate because it depicts primary ribs that

are too prominent, too few, and with interspaces too broad, and a foramen that is broader posteriorly. A later illustration (Sowerby II, 1862), which has no documentation, is based on a still different specimen; in fact, it is a better rendition



Figures 14–16. Preserved bodies of *Medusafissurella* species. **14.** *M. salebrosa*, dorsal and ventral views of preserved body out of shell, Goth Jafar, 10 mi. west of Karachi, Pakistan, CAS 031984, shell dimensions $26.5 \times 20.0 \times 9.6$ mm. **15.** *M. dubia*, dorsal and ventral views of preserved body out of shell, Salt Rock, Umhlali Dist., Natal, South Africa, NM B9928, shell dimensions $29.0 \times 16.9 \times 7.2$ mm. **16.** *M. chemnitzii*, Baia de Santa Maria, Angola, MNHN uncat., lateral view of preserved specimen, shell dimensions $27.7 \times 16.5 \times 7.5$ mm.

of *M. dubia* than anything else. Despite these discrepancies, we retain the name of Sowerby (1835), basing it on his description (1835a) and his figure (1835b), to which we relate the neotype specimen designated here.

Dendrofissurella new genus

Type species: *Patella scutellum* Gmelin, 1791. Recent, southern Africa.

DESCRIPTION. Shell oval, anterior end narrower than posterior, ends raised; foramen nearly central, elongate-oval. Sculpture of fine radial ribs. Foot projecting posterior to shell for distance greater than length of shell; shell edge slightly enveloped by mantle fold; propodium with single tapering, trunklike elongation, with approximately 9 irregularly placed lateral branches. Large outer lateral tooth of radula quadricuspid.

REMARKS. Differing from *Amblychilepas* in having an elaborate propodium, minimal envelopment of the shell by the mantle, and minor development of the papillae of the

upper lobe of the mantle. Differing from *Medusafissurella* in having a trunklike propodium rather than a broad propodium with subequal tentacles. The foot projects posteriorly to a greater extent than in *Medusafissurella*.

The quadricuspid outer lateral tooth of *Dendrofissurella scutellum* is similar to that of species of *Fissurella*, *Amblychilepas*, and *Medusafissurella*.

The genus contains a single species, for which we recognize two geographic subspecies.

ETYMOLOGY. The prefix is suggested by the trunklike propodium, a Greek word for tree; gender feminine.

Dendrofissurella scutellum (Gmelin, 1791)

(a) *D. scutellum scutellum*

Figures 17, 18

Patella scutellum Gmelin, 1791:3731. Original locality unknown [Table Bay, designated by Kilburn and Rippey, 1982:211].

Fissurella scutellum; Krauss, 1848:63.

Megatebennus (section *Amblychilepas*) *scutellum*; Pilsbry, 1890:184, pl. 39, fig. 89, pl. 44, figs. 99, 100, 1, 2.

Fissurellidaea scutella [sic]; Turton, 1932:207.

Amblychilepas scutella [sic]; Barnard, 1963:286, figs. 21b, 22d-f.

Amblychilepas scutellum; Kensley, 1973:29, fig. 30 [drawing of animal]; Tietz and Robinson, 1974:48, pl. 26 [photograph of animal].

Amblychilepas scutellum scutellum; Kilburn and Rippey, 1982:35, 212, pl. 6, fig. 1 (part).

Not *Fissurella scutella* of Reeve, 1849:pl. 6, fig. 33 [= *A. javanicensis* (Lamarck)].

Not *Fissurellidea scutella* of Sowerby II, 1862:203, pl. 9, fig. 207 [= *A. javanicensis* (Lamarck)].

Fissurellidea sella Sowerby, II, 1862:203, pl. 8, fig. 197; Turton, 1932:207. Type locality: "South Africa."

Megatebennus (section *Amblychilepas*) *sella*; Pilsbry, 1890: 185, pl. 62, fig. 3 [copy Sowerby II].

(b) *D. scutellum hiantula* (Lamarck, 1822)

Figures 2, 19–22

Fissurella hiantula Lamarck; 1822:14; Mermod, 1950:708, figs. 18.1, 18.2, 18.3 [syntypes, Lamarck Collection]. Type locality: "Mer des Indes" [Algoa Bay, here designated].

Fissurellidea hiantula; Sowerby II, 1862:202, pl. 8, figs. 193–195.

Not *Fissurellidea hiantula* of Pilsbry, 1890:179, or other authors treating species from Argentina [= *Fissurellidea megalotrema* Orbigny, 1841].

Amblychilepas scutellum hiantula; Kilburn and Rippey, 1982: 35, 211, pl. 6, fig. 1 (part).

Fissurella incarnata Krauss, 1848:65, pl. 4, fig. 7; Janus, 1961:3, pl. 1, figs. 4–6. Type locality: "In sinu tabulari et falso, in litore natalensi."

Fissurellidea incarnata; Sowerby II, 1862:203, pl. 8, fig. 109.

Megatebennus (section *Amblychilepas*) *incarnata*; Pilsbry, 1890:186, pl. 35, figs. 4, 5 [copy Krauss].

Fissurellidea incarnata maculata Turton, 1932:206, pl. 53, fig. 1431. Type locality: Port Alfred.

Fissurellidea multilineata Turton, 1932:206, pl. 53, fig. 1432. Type locality: Port Alfred.

Fissurellidea albanyana Turton, 1932:207, pl. 54, fig. 1433. Type locality: Port Alfred.

Fissurellidea nigrostrigata Turton, 1932:207, pl. 54, fig. 1435.

Type locality: Port Alfred.

DESCRIPTION. Shell saddle-shaped, anterior and posterior ends raised; sculpture of fine raised ribs of nearly equal size, but with some ribs twice the width of adjacent ribs.

Following Kilburn and Rippey (1982), we recognize two geographic subspecies, with distributions overlapping in False Bay, where they intergrade. To the west (on the cold temperate Atlantic coast) occurs the typical *D. scutellum scutellum*, which has a large thick shell (attaining 40 to 50 mm in length) with moderately to extremely raised ends, and a drab pattern of dark gray to olive-brown. To the east (on the warm temperate south coast) it is replaced by *D. scutellum hiantula*,

which is smaller (length 30 mm or less), thinner-shelled, with ends less raised, and a more vividly and delicately colored pattern, generally pink or brown with white rays or spots.

TYPE MATERIAL. As noted by Pilsbry (1890) and Kilburn and Rippey (1982:211), Gmelin (1791) cited a clearly recognizable figure of Meuschen (1782:pl. 2, fig. 3) to represent *Patella scutellum*. Meuschen's illustration is a type figure; a type specimen is not available.

There are three specimens labeled *Fissurella hiantula* in the Lamarck collection, as discussed by Mermod (1950). These specimens clearly relate the name to the eastern subspecies of *D. scutellum*. Of three syntypes figured by Mermod, specimen number 1, at 31 mm in length, is close to Lamarck's cited dimensions. Lamarck's (1822) reference to an illustration of Born (which we now identify as *Pupillaea aperta* (Sowerby, 1825)) is discounted because type material of *F. hiantula* is available.

Type material for *F. incarnata* Krauss, was not located by Janus (1961), who designated a neotype in the Stuttgart Museum. Janus selected a specimen that agrees with our concept of *F. scutellum scutellum*, but Krauss's figures agree with *F. scutellum hiantula*. We therefore retain the name in the synonymy of *F. scutellum hiantula*.

The holotype of *Fissurellidea sella*, from "South Africa" is in the BMNH.

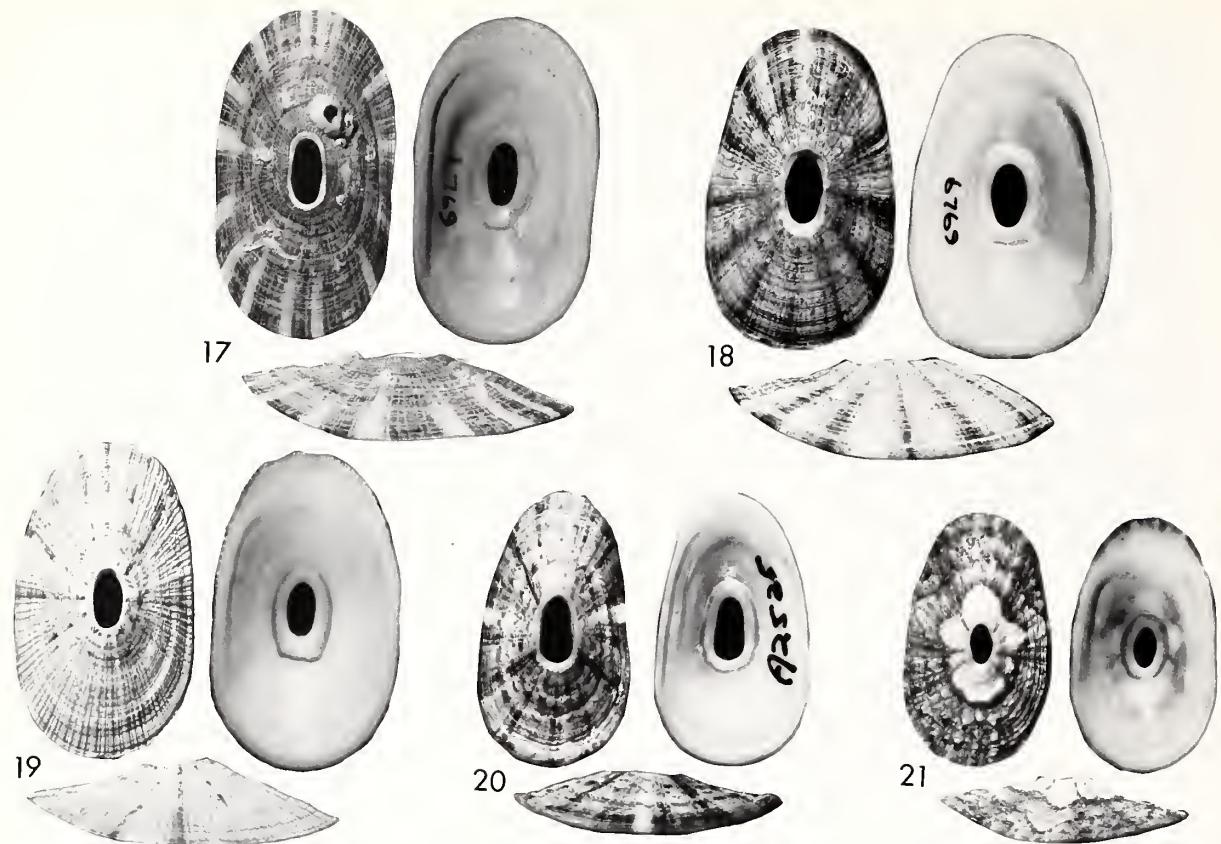
Turton's types, all from Port Alfred, are in the Oxford University Museum.

DISTRIBUTION. South Africa: Natal North Coast to Saldanha Bay, Cape Province.

Shells of both subspecies are well represented in museum collections from numerous localities. The following preserved specimens of the typical subspecies have been examined: Saldanha Bay (NM B9918); Table Bay (NM B9917); Cape Town (LACM 25203). These specimens tend to have the propodium contracted, some to the point of nearly concealing the feature. Preserved specimens of *D. scutellum hiantula* are scarce in museum collections. Our evidence that the eastern subspecies has a propodium similar to that of *D. scutellum* is based on: 1) the specimen illustrated by Tietz and Robinson (1974:pl. 46), presumably from the Tsitsikama coast, which shows a pink, rather than drab shell, as expected in the eastern subspecies; 2) a single specimen from Still Bay (NM A2536), which has an intact, dried animal with well-developed propodium; and 3) three preserved specimens from Algoa Bay (NM B9919).

Some specimens provisionally identified as *D. scutellum hiantula* have fewer ribs overall and have ribbing of alternating strength (Figs. 20, 21). Color variation is similar to that of *D. scutellum hiantula*. Until preserved specimens become available, the identity of this form is not certain. It could be a variant of this species, or it could prove to be yet another species of *Amblychilepas*.

MATERIAL EXAMINED. (a) *D. scutellum scutellum*: SOUTH AFRICA: Saldanha Bay (NM 5584); Shell Bay (NM 8725); various localities in Table Bay (NM 6381, NM 1271, NM 6641, NM A2975); Kommetjie, west coast Cape Peninsula (NM 5586, NM A4189). Simonstown, shallow dredgings (NM 8976, NM 6769) (Figs. 17, 18); Strandfontein, False



Figures 17–21. Shells of *Dendrofissurella* species; exterior and interior views with anterior at top; lateral views of left side. **Figs. 17, 18.** *Dendrofissurella scutellum scutellum* (Gmelin, 1791). **17.** Simonstown, False Bay, Western Cape Province, South Africa, NM 6769, 33.7 × 18.8 × 8.4 mm. **18.** Same lot, 32.5 × 19.8 × 9.8 mm. **Figs. 19–21.** *D. scutellum hiantula* (Lamarck, 1822). **19.** East London, Eastern Cape Province, South Africa, NM A4186, 30.0 × 17.6 × 8.0 mm. **20.** Cape Agulhas, Western Cape Province, South Africa, NM A2535, 20.0 × 11.6 × 4.8 mm. **21.** Port Elizabeth, Eastern Cape Province, South Africa, LACM 3765, 15.0 × 8.8 × 3.9 mm.

Bay (NM A3961); off Macassar Beach, False Bay, 10 fm. (NM A3123).

(b) *D. scutellum hiantula*: SOUTH AFRICA, CAPE PROVINCE: Cape Agulhas (NM A2535); Still Bay (NM A2536, NM A2531); Mossel Bay (NM A5307); Jeffreys Bay (NM 5886, NM B6143); Algoa Bay (NM B2868, NM B1795, B439); Port Alfred (NM B440-2, NM B6142, NM B6355); East London (NM A4186, NM 8363) (Fig. 19). TRANSKEI: Kei River mouth (NM C3476); Nxaxo River mouth (NM C3773); Qolora River mouth (NM C3406); Sandy Point (NM C3665); Dwesa (NM C5961); Lwandile/Mdumbi (NM C75); Hluleka (NM C1500); Coffee Bay (NM A801, NM B6139); Nthlonyanane (NM B1430); Mkambati (NM C5608); Mbotsy (NM A2534); Mzamba (NM B4550, NM 7142). NATAL: Port Shepstone (NM 8986, NM 9128); Kelso (NM 5885); Mtwalume (NM B8605); Umkomaas (NM 1273, NM 7151); Durban (NM B4884); Tongaat (NM 7141); 3 mi. off Umhlanga Rocks, 12–13 fm. (NM A272); Umhlali beach (NM A4575); Mvoti River mouth (NM 7144).

COMPARISONS. On shell characters both subspecies of *D. scutellum* differ from the three species of *Medusafissurella* in having less prominent, nonscabrous ribs and in having the posterior end more raised.

REMARKS. Reeve (1849) and Sowerby II (1862) incorrectly considered *F. scutellum* an earlier name for the Australian *A. javanicensis*; their figures show the latter. Krauss (1848) and Barnard (1963) used *A. scutellum* for the South African species, but incorrectly placed *A. javanicensis* in its synonymy. Pilsbry (1890) erroneously used the name *Fissurellidea hiantula* for an Argentinean species, which McLean (1984a) relegated to the synonymy of *Fissurellidea megatrema* Orbigny, 1841.

The prominent dendritic propodium of *D. scutellum* has previously been figured by Kensley (1973) and by Tietz and Robinson (1974); the latter figure is reproduced here (Fig. 22). Kensley (1973) illustrated a bifurcation in the propodium, although all specimens that we have examined have a single central trunk.

Genus *Amblychilepas* Pilsbry, 1890

Amblychilepas Pilsbry, 1890:184. Type species: *Fissurella trapezina* Sowerby, 1835 (= *F. javanicensis* Lamarck, 1822). Recent, Australia.



22



23

Figures 22, 23. Living animals of *Dendrofissurella* and *Amblychilepas*. 22. *Dendrofissurella scutum hiantula*, dorsal view of living animal, Tsitsikama Coastal National Park, Eastern Cape Province, South Africa; overall length about 80 mm; after Tietz and Robinson (1974). 23. *Amblychilepas nigrita* (Sowerby, 1835), dorsal view of living animal, New South Wales, Australia, overall length about 80 mm; photograph by John Fields, courtesy AMS.

Sophismalepis Iredale, 1924:219. Type species: *Fissurella nigrita* Sowerby, 1835. Recent, Australia.

DESCRIPTION. Shell oval, anterior end narrower than posterior, ends raised; sculpture of radial striae; foramen nearly central, elongate oval. Foot projecting posterior to shell for distance greater than length of shell; shell edge enveloped by upper fold of mantle, from which long papillae extend toward foramen; propodium unmodified. Massive outer tooth of radula quadricuspid.

REMARKS. Except for *A. platyactis* new species, species of *Amblychilepas* are restricted to Australia. Figured here for comparison (Fig. 23) is a living animal of the Australian *A. nigrita* (Sowerby, 1835). As in the new species here described, the papillae of the upper fold of the mantle of *A. nigrita* are well developed and project toward the foramen. The propodium of the Australian type species (*A. javanicensis*) is unmodified (based on AMS C.117375).

The following species has been confused with the common south African species here reassigned to *Dendrofissurella scutellum hiantula*.

Amblychilepas platyactis new species

Figures 3, 24, 25

Amblychilepas scutellum [non Gmelin, 1791]; Odhner, 1932: 298, fig. 31 [drawing of animal].

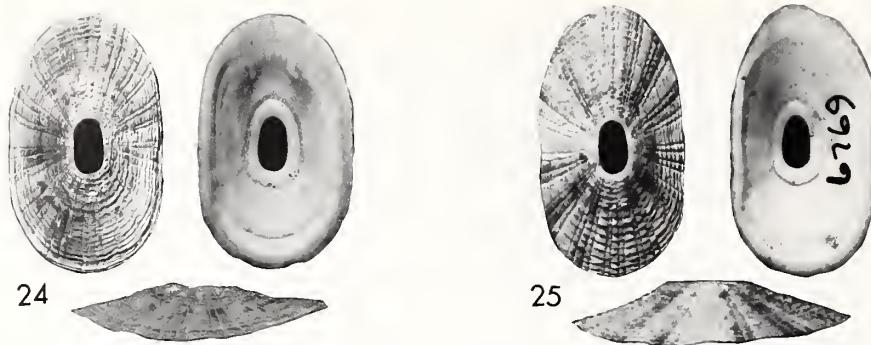
DIAGNOSIS. Shell to 30 mm in length, saddle-shaped, narrowed anteriorly; anterior markedly raised; posterior slightly raised; radial ribs alternating in strength, separated by deeply incised grooves. Primary ribs broad, low, and flat-

topped, up to twice as broad as secondary ribs and 3 times broader than tertiary ribs; primary ribs broader on sides of shell than on ends; concentric growth lamellae thin and raised, especially prominent on broad primary ribs. Color dark red with white rays.

Propodium unmodified; body extending posteriorly for one shell length; upper lobe of mantle enveloping edge of shell and having long, elaborate papillae corresponding to broad primary ribs.

DESCRIPTION. Shell outline elongate-oval in dorsal view, slightly narrowed anteriorly; anterior and posterior ends raised, lateral profile of base evenly curved. Radial sculpture of flat-topped ribs separated by narrow incised grooves rather than interspaces. Primary ribs 14, twice as broad as secondary ribs, which in turn are twice as broad as tertiary ribs. Primary ribs at anterior and posterior ends more elevated than those of sides, particularly in early growth stages. Concentric sculpture of thin, raised incremental growth lines, arched upon crossing primary ribs, to a lesser extent on crossing secondary and tertiary ribs. Foramen elongate-oval, slightly broader posteriorly, $\frac{1}{5}$ shell length. Color brick red, with white rays that tend to emerge at later growth stages and correspond to primary ribs. Margin faintly crenulate to correspond with exterior sculpture, shell edge angulate at sides, thinner anteriorly and posteriorly. Callus surrounding foramen faintly outlined in pink, more bluntly terminating posteriorly than anteriorly.

Propodium unmodified, outline of foot elongate-oval, body extending posteriorly for one shell length. Sides of foot with pustulose tubercles; epipodial tentacles of neck weakly developed; mantle lobe with tubercles like those on foot sides but smaller; lower edge of mantle lobe with projecting pa-



Figures 24, 25. *Amblychilepas platyactis*, new species, exterior and interior views with anterior at top; lateral views of left side. 24. Holotype, Port Alfred, Eastern Cape Province, South Africa, NM B6397/T2744, 17.2 × 10.3 × 3.9 mm. 25. Paratype, False Bay, Eastern Cape Province, South Africa, NM 6769/T3009, 20.5 × 11.0 × 4.5 mm.

pillae having numerous projecting points; upper edge of mantle with fewer papillae that are about three times the size of the lower edge papillae, about 14 major papillae altogether, corresponding to broad primary ribs. Major papillae separated by less prominent papillae. Tips of cephalic tentacles reddish in preservative.

DIMENSIONS. Holotype, shell length 17.2, width 10.3, height 3.9 mm. Maximum length 30.8 mm (NM 6769/T3009).

TYPE MATERIAL. Holotype, NM B6397/T2744, Port Alfred, Eastern Cape Province, South Africa, collected by R. Kilburn, 1966 (Fig. 24). Paratype 1, LACM 2108, Port Alfred, collected by E. Warren, July 1912. Paratype 2, NM B9916/T3008, Kommetjie, collected by C.M. Connolly. Paratypes 3–5, NM B9929/T3055, Kwelera, E of East London, collected by C.M. Connolly. Paratypes 6–11, NM 6769/T3009 (Fig. 25) Simonstown, False Bay, collected by C.M. Connolly. Holotype and paratypes wet-preserved, except for paratypes 6–11, shells only.

DISTRIBUTION. South Africa: East London to Kommetjie, Atlantic coast of Cape Peninsula.

COMPARISONS. On anatomical characters, there is no difficulty in distinguishing intact specimens of *A. platyactis* from both subspecies of *Dendrofissurella scutellum*, the former having elaborate papillae on the upper lobe of the mantle and lacking the propodial elaboration; the latter having small, simple papillae on the upper lobe and having the trunklike propodium. Shells, however, closely approach those of *D. scutellum hiantula*, of which there are specimens with broad primary ribs (Figs. 20, 21) up to twice the breadth of the lesser ribs. However, no specimens of *D. scutellum hiantula* are known with the extremely broad ribs of *A. platyactis*, which may be three times the breadth of the lesser ribs. The development of the scaly sculpture on the primary ribs is much more extreme in the young stages of *A. platyactis*. Shells of all specimens are red and white rayed, which indicates that the range of color variation is minimal in *A. platyactis*. The posterior end of the shell of *A. platyactis* is less raised than that of *D. scutellum*.

REMARKS. We name this species with reluctance, considering the large number of synonyms pertaining to *D. scu-*

tellum hiantula. However, original descriptions of all these taxa make no reference to broad ribbing and it is clear that none of them has sculpture to match the type specimens of *A. platyactis*. The specimen figured by Odhner (1932) is presumed to be this species on the basis of lack of propodial development and the papillae of the upper lobe of the mantle.

ETYMOLOGY. The name is Greek, meaning with wide or flat spokes or rays, suggested by the extremely broad ribs of this species.

DISCUSSION. *Dendrofissurella scutellum* (both subspecies) and the three species of *Medusafissurella* have very different expressions of the propodium, here considered diagnostic at the generic level. However, the vexing question of function remains. One might speculate that the propodial tentacles serve to trap or hold food, such as drifting algae. Yet, in these species the snout, which is no larger than in other fissurellid genera, is *dorsal* to the proportionally longer propodium (Fig. 26). A role in feeding would be more readily understood if these tentacles were attached to the snout instead of the propodium, access to the mouth thereby being closer. In the fissurellids described here, the snout would presumably have to be extended through the tentacles to reach the food, but the propodium is not bifid, as would be expected if this were the case. Yet, the mouth and the snout are more laterally compressed than in fissurellid genera lacking the propodium.

Stomach contents of a preserved specimen of *Medusafissurella dubia* included branched coralline algae, suggesting that the diet of this species is comprised of encrusting algae, not unlike the diet of *Fissurella barbadensis* Gmelin, examined by Ward (1966). Thus, there is no indication that propodial development corresponds to an unusual diet in these species.

The two fissurelline genera having these propodial modifications occur in southern Africa and the western Indian Ocean, a region central to the distribution of genera in the subfamily. All five of the genera keyed above are known from South Africa. *Fissurella*, with its unmodified propodium, has more numerous species in the western hemisphere, on both sides of the Atlantic and in the eastern Pacific. *Amblychilepas*

and *Macrochisma* are better represented to the east, *Amblychilepas* in Australia and *Macrochisma* in Japan and Australia.

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We thank J. Christiaens of Hasselt, Belgium for reading the manuscript and loaning specimens of several species from his collection. Barry Roth, California Academy of Sciences, first brought the preserved specimen of *Medusafissurella salebrosa* to our attention. Preserved specimens of *M. chemnitzii* were furnished on loan by Philippe Bouchet of the Paris Museum. Winston Ponder of the Australian Museum arranged the loan of comparative material and the photograph of *Amblychilepas nigrita*. We thank B. Hayes and F. Graeve of Port Elizabeth for preserved *Dendrofissurella scutellum hiantula* and Mrs. S. Muller of the East London Museum for shells of *M. chemnitzii*. The drawing of *M. salebrosa* reconstructed as living was made by LACM volunteer artist Yvonne Albi. SEM photographs were made at the Center for Electron Microscopy and Microanalysis of the University of Southern California with the assistance of Alicia Thompson. LACM museum photographers Dick Meier and John DeLeon assisted in the preparation of the illustrations. We thank our anonymous reviewers for helpful suggestions.

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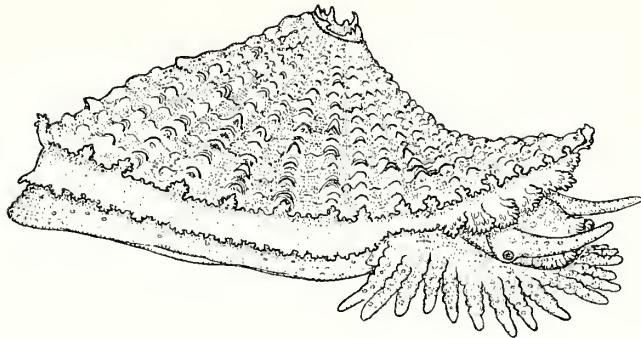


Figure 26. Right lateral view of *Medusafissurella salebrosa*, based on specimen in Fig. 14, reconstructed to show the mantle folds in contact with shell, tentacular propodium, snout, and cephalic tentacles with eyes at base, drawn by Yvonne Albi.

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EVOLUTION AND CLASSIFICATION OF THE
LATE CRETACEOUS-EARLY TERTIARY
GASTROPOD *PERISSITYS*

W.P. Popenoe and L.R. Saul



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**EVOLUTION AND CLASSIFICATION OF THE
LATE CRETACEOUS-EARLY TERTIARY
GASTROPOD *PERISSITYS***

W.P. Popenoe and L.R. Saul

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EVOLUTION AND CLASSIFICATION OF THE LATE CRETACEOUS-EARLY TERTIARY GASTROPOD PERISSITYS

W.P. Popenoe and L.R. Saul¹

ABSTRACT. A new neogastropod family Perissityidae is proposed for several lineages of American Pacific Coast gastropods having species of early Senonian age that are very similar but late Senonian species that are disparate. Four genera of Perissityidae are discussed: the type genus *Perissitys* Stewart, 1927, *Pseudocymia* new genus, *Murphyts* new genus, and *Christitys* new genus. Seven species are assigned to *Perissitys*: *P. cretacea* (Cooper), *P. elaphia* new species, *P. brevirostris* (Gabb) (type species), *P. pacifica* new species, *P. colocara* new species, *P. stantoni* (Stewart), and *P. stewarti* (Zinsmeister). The genus ranges in age from Coniacian through early Paleocene; and its evolutionary changes include reduction and disappearance of tubercles on the inner apertural margins, comparative increase in length of the siphonal canal, and extension of the inner lip callus to finally encompass nearly the entire shell in the later Maastrichtian, followed subsequently by reduction of this callus in the Paleocene.

Pseudocymia new genus, with type species *P. aurora* new species includes *P.(?) aitha* new species, *P.(?) cahalli* new species, and *P.(?) kilmeri* new species and ranges from Turonian into the Maastrichtian. Evolutionary changes in *Pseudocymia* include reduction of denticles on the inner apertural margins and elongation of the entire shell.

Murphyts new genus comprises *M. michaeli* new species (type species), *M. corona* new species, and *M. madonna* new species, and ranges from Coniacian to Maastrichtian. Its evolutionary changes include increasing angularity of whorl profile, development of columellar folds, and expansion of the outer lip to form a rimmed aperture.

Christitys new genus, comprising *C. delta* new species, *C. medica* new species (type species), and *C. martini* new species ranges from Coniacian to Campanian. Its evolutionary changes include development of a more pyriform shape and reduction of the denticulations of the outer lip.

Sequence and rate of morphologic change in these molluscan groups have significance in principles of gastropod taxonomy and utility for correlation.

INTRODUCTION

Erection of a family, Perissityidae, to encompass the enigmatic neogastropod lineages of *Perissitys*, *Cophocara*, and "*Hindsia nodulosa* (Whiteaves)" was first suggested by W.P.

Popenoe at the 1971 Cordilleran section meeting of the Geological Society of America (Popenoe, 1971, p. 179; Saul, 1971, p. 189). Popenoe intended to propose the family and describe half of the perissityid genera; Saul was to (and will) describe the remainder. This paper treats those genera and species of Perissityidae that Popenoe intended to describe. Some problems of biostratigraphic correlation, which we believe are now resolved, delayed the writing of this paper beyond the time allotted to Popenoe; the paper has, therefore, been completed by Saul.

The genera *Perissitys* and *Cophocara* were described by Stewart (1927), but neither was assigned to a family, both being consigned to "doubtful systematic position." Earlier, Cossmann (1901) and later, Wenz (1943), Erickson (1974), and Zinsmeister (1983) placed these genera near *Tudicla*, an association that may be more of form than of phylogeny. As traced in this paper the evolutionary sequence of which *Perissitys brevirostris* (Gabb, 1864) and *Cophocara stantoni* Stewart, 1927, form a part, extends from Coniacian into early Selindian (middle Paleocene). End members of this lineage would scarcely be included in the same family by most systematists were intermediate stages unknown.

Three new genera, *Pseudocymia*, *Murphyts*, and *Christitys*, are represented in the Coniacian by species resembling *Perissitys cretacea* (Cooper). These genera diverged from *Perissitys* and from each other in the Santonian, and by Campanian time all were represented by species of decidedly different aspect.

Six previously described West Coast species are unhesitatingly allotted to the family Perissityidae: *Perissitys brevirostris* (Gabb, 1864), *Fusus kingii* Gabb, 1864, *Cophocara stantoni* Stewart, 1927, *C. stewarti* Zinsmeister, 1983, *Fas-*

1. At the time that the research described in this paper was conducted, both authors were with the Department of Earth & Space Sciences, University of California, Los Angeles. Popenoe died in 1981. Saul is currently with the Invertebrate Paleontology Section of the Natural History Museum of Los Angeles County.

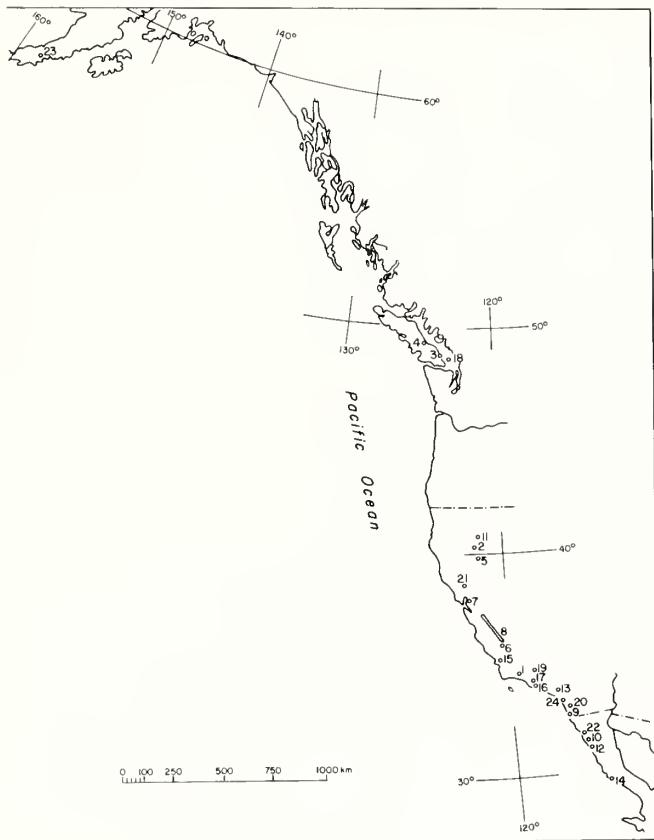


Figure 1. Index map to geographic occurrence of perissityids described in this paper. **1.** Agua Caliente Canyon, San Rafael Mts., Santa Barbara Co., California. **2.** Antelope Creek, Mill Creek, and Tuscan Springs, Tehama Co., California. **3.** Benson (= Brannan Creek), Blundon Point, and Elkhorn Creek, Nanaimo Basin, Vancouver Island, British Columbia. **4.** Browns River, Comax Basin, Vancouver Island, British Columbia. **5.** Butte Creek, Chico Creek, and Pentz, Butte Co., California. **6.** Cottonwood Creek in Cholame Valley Quadrangle, Monterey Co., California. **7.** Deer Valley and vicinity of Martinez, Contra Costa Co., California. **8.** East side of the Diablo Range from Stanislaus Co. south to Fresno Co., California. **9.** Point Loma, San Diego Co., California. **10.** Punta San Jose, Baja California Norte, Mexico. **11.** East of Redding, Shasta Co., California. **12.** San Antonio del Mar and Johnson's Ranch, Baja California, Mexico. **13.** Santa Ana Mountains, Orange Co., California. **14.** Santa Catarina Landing area, Baja California, Mexico. **15.** Lake Nacimiento, southern Santa Lucia Range and Santa Margarita Lake, La Panza Range, San Luis Obispo Co., California. **16.** Santa Monica Mountains, Los Angeles Co., California. **17.** Simi Hills, Los Angeles and Ventura cos., California. **18.** Sucia Island, San Juan Co., Washington. **19.** Warm Springs Mountain, northwestern San Gabriel Mts., Los Angeles Co., California. **20.** Vicinity of Carlsbad, San Diego Co., California. **21.** Rumsey Hills, Yolo Co., California. **22.** Punta Banda, Baja California, Mexico. **23.** Chignik Lagoon, Alaska Peninsula, Alaska. **24.** East of San Juan Capistrano, Orange Co., California. Place names mentioned in text listed alphabetically: **1.** Agua Caliente Canyon; **2.** Antelope Creek; **3.** Bear Creek; **13.** Bee Canyon; **17.** Bell Canyon; **3.** Benson (= Brannan) Creek; **3.** Blundon Point; **4.** Browns River; **21.** Buckeye Creek; **5.** Butte Creek; **15.** Cantinas Creek; **20.** Carlsbad; **5.** Chico Creek; **23.** Chignik Lagoon; **8.** Coalinga; **11.** Clover Creek; **6.** Cottonwood Creek in Cholame

ciolaria nodulosa Whiteaves, 1874, = *Hindsia nodulosa* Whiteaves, 1879, and *Sistrum (Ricinula?) cretaceum* Cooper, 1896. Probably *Nekewis simiensis* Zinsmeister, 1983, and possibly *N. io* (Gabb, 1864), *N. washingtoniana* (Weaver, 1912), and *N. neahaleensis* (Anderson & Martin, 1914) are also perissityids. T. Kase has provided plaster casts of specimens of some Japanese perissityids, including *Surculites?* cf. *S. fusoides* Nagao, 1939, and *Pseudoperissitys bicarinata* Nagao & Otatume, 1938. Additionally, descriptions and figures suggest that *Trachytriton sachalinensis* Schmidt, 1873 [= *Serrifusus? sachalinensis* (Schmidt) in Hayami & Kase (1977, p. 63) non *Serrifusus sachalinensis* (Nagao, 1932)], *T. duiensis* Schmidt, 1873, *Pyropsis* sp. indet. of Nagao (1939), *Pyrifusus (Neptunella) kawakamiensis* Nagao, 1939, and *Fusus* (s.l.) *volutodermoides* Nagao, 1939, from the northwest Pacific are Perissityidae, as is *Perissolax brevirostris* Gabb of Martin (1926) from Alaska. *Fusus dusenianus* Wilckens, 1907, *Struthiolariopsis? tumida* Wilckens, 1907, and *Heteroterma praecursor* (Wilckens, 1907) from the upper Cretaceous of southern Patagonia resemble perissityids, but the aperture of none has been described. *Perissitys?* sp. A and B of Erickson (1974), however, from the Fox Hills Formation of North Dakota do not show any characteristics of this family. We have not seen specimens of the undescribed *Cophocara* sp. of Sohl (1967, p. 34) from the upper Campanian of Wyoming. In previous classifications species assignable to the Perissityidae have been distributed among Cassididae, Thaididae, Buccinidae, Fascioliidae, Xancidae or Vasidae, Tudiclididae, and Turridae.

Much of this diverse family assignment results from the divergent evolutionary paths followed by the several lineages. The lineage with changes best documented by specimens is that of *Perissitys*. Adequate specimens, sufficiently well distributed through the stratigraphic sections, indicate style, pattern, pace, and rate of evolution within this group.

Abbreviations used with catalog and locality numbers are:

ANSP = Academy of Natural Sciences of Philadelphia
CAS = California Academy of Sciences, San Francisco
CGS = Canada Geological Survey
CIT = California Institute of Technology (collections now at LACMIP)
LACMIP = Los Angeles County Museum of Natural History, Invertebrate Paleontology

↑

Valley Quadrangle **17.** Dayton Canyon; **7.** Deer Valley; **3.** Departure Bay; **8.** Diablo Range; **3.** Elkhorn Creek; **12.** Johnson's Ranch; **8.** Laguna Seca Hills; **17.** Lang Ranch; **7.** Martinez; **2.** Mill Creek; **11.** Morley; **11.** Oak Run; **8.** Oil Canyon; **11.** Old Cow Creek; **8.** Ortigalita Creek; **7.** Pacheco; **8.** Pacheco Pass; **8.** Panoche Hills; **5.** Pentz; **11.** Pine Timber Gulch; **9.** Point Loma; **11.** Price Hollow; **22.** Punta Banda; **14.** Punta Canoas; **10.** Punta San Jose; **11.** Redding area; **7.** Riggs Canyon; **21.** Rumsey Hills; **11.** Salt Creek; **12.** San Antonio del Mar; **24.** San Juan Capistrano; **21.** Sand Creek; **13.** Santa Ana Mts.; **14.** Santa Catarina Landing area; **15.** Santa Margarita Lake; **16.** Santa Monica Mts.; **17.** Simi Hills; **18.** Sucia Island; **11.** Swede Basin; **2.** Tuscan Springs; **19.** Warm Springs Mt.; **23.** Whaler's Creek.

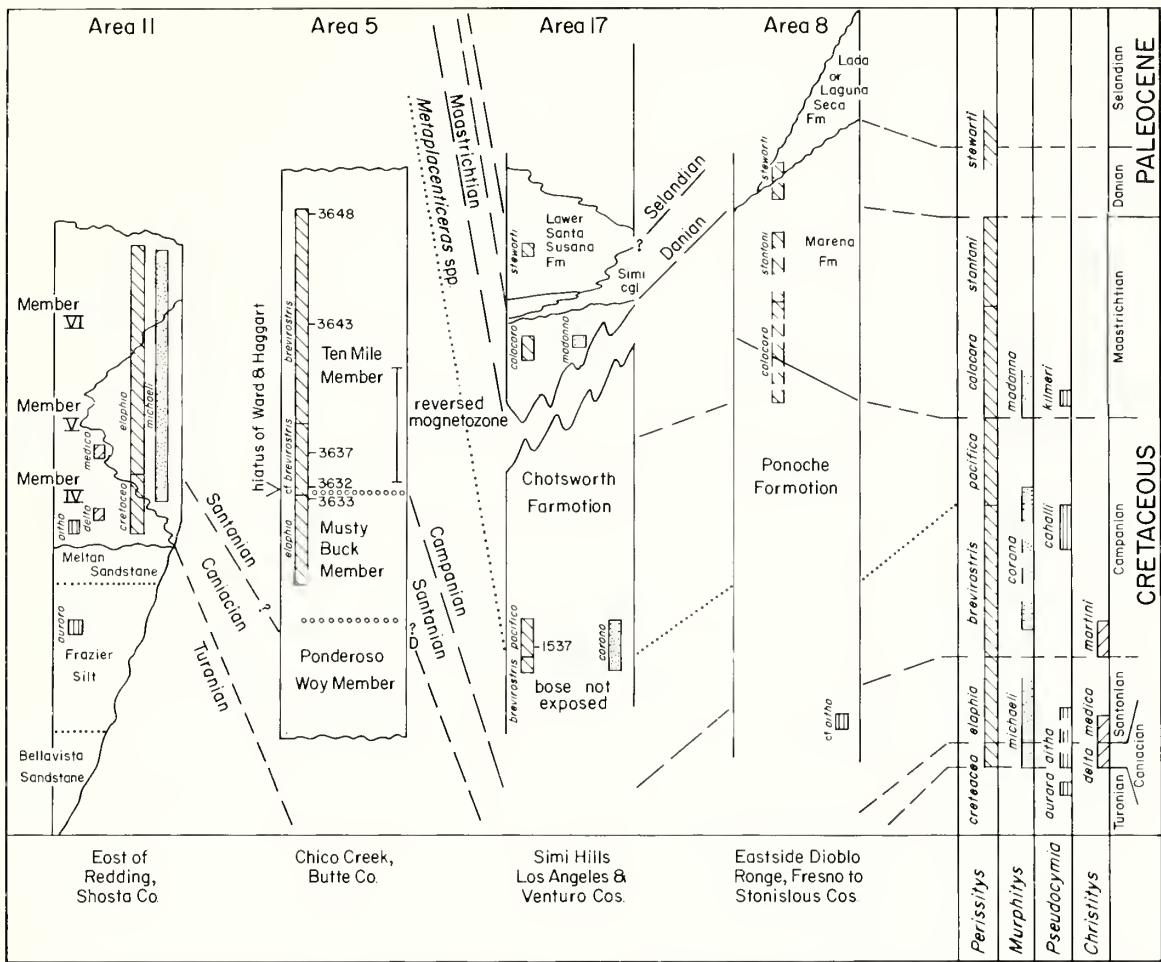


Figure 2. Stratigraphic occurrence of *Perissitys*, *Murphitys*, *Christitys*, and *Pseudocymia* in four California sections: Redding area (area 11), based on Popenoe, 1943, and Matsumoto, 1960; Chico Creek (area 5), after Saul, 1983; Simi Hills (area 17), after Saul, 1983; and east side Diablo Range (area 8), simplified from Saul, 1983. The columns are not all to the same scale. The Redding area, Simi Hills, and east side Diablo Range columns are composites and each represents a considerable area; the Chico Creek column is based on outcrops along Chico Creek. Campanian reversed magnetozone (Chron 33r) is from Ward et al. (1983). The position of some fossil localities is indicated by locality number.

LSJU = Stanford University (collections now at CAS)

SDSNH = San Diego Society of Natural History

UCB = University of California, Berkeley

UCBMP = University of California, Berkeley, Museum of Paleontology

UCLA = University of California, Los Angeles (collections now at LACMIP)

UCR = University California, Riverside

USGS = United States Geological Survey

USNM = United States National Museum of Natural History

OCCURRENCE

Specimens of *Perissitys*, *Pseudocymia*, *Murphitys*, and *Christitys* have been collected from more than 200 localities from Alaska to Baja California, Mexico. Only seven areas

have provided stratigraphic successions of species: in British Columbia on Vancouver Island (Figure 1, area 3), and in California east of Redding (area 11), along Chico Creek (area 5), on the east side of the Diablo Range (area 8), near Warm Springs Mountain (area 19), in the Simi Hills (area 17), and in the Santa Ana Mountains (area 13). Stratigraphic position of the perissityid occurrences at Redding, Chico Creek, Simi Hills, and in the Diablo Range is diagrammed in Figure 2. The probable chronologic ranges of species, derived from their stratigraphic occurrences are plotted on Figure 3 with the position of some Pacific West Coast zonal indicators.

Stratigraphic nomenclature of the Cretaceous east of Redding (area 11) has been revised by Haggart (1986). Popenoe (1943), in a progress report, placed the strata in six Members I–VI. Type sections were left undesignedated, but disposition of the members has been shown on maps (e.g., Popenoe, 1943; Matsumoto, 1960; Trujillo, 1960). M.V. Kirk (*fide*

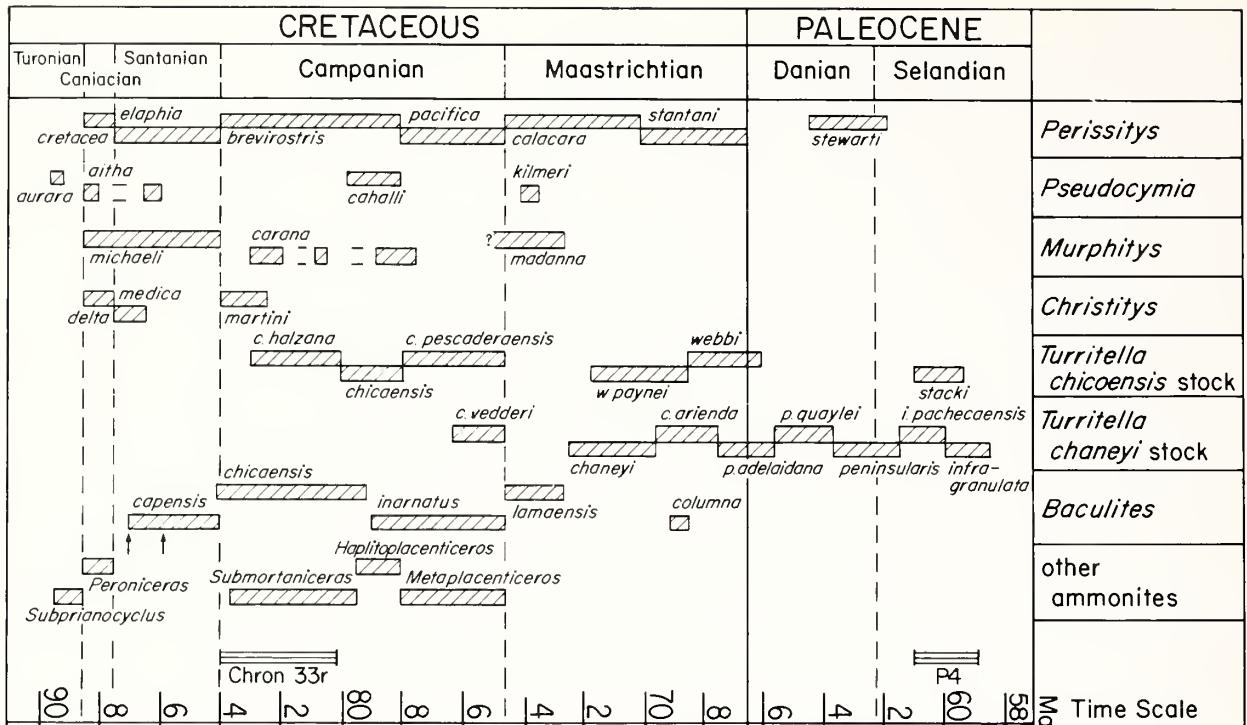


Figure 3. Geologic range of species of perissityids described in this paper, *Turritella chaneyi* and *T. chicoensis* stocks and some ammonites fitted to the time scale of Palmer (1983) and Berggren et al. (1985a). Arrows indicate approximately the range allotted to *B. capensis* by Haggart and Ward (1984) and Haggart (1984). *Turritella* zonation from Saul (1983), and Campanian reversed magnetozone, Chron 33r, from Ward et al. (1983). In Harland et al. (1982, p. 74) Chron 33r is dated as 78.53–82.93 Ma.

Matsumoto, 1960, p. 4) suggested the name Redding Formation for these members. Popenoe (in Jones, et al., 1978) named Members I–III, in ascending order Bellavista Sandstone, Frazier Siltstone, and Melton Sandstone. J.M. Haggart (1986) delimited the outcrop area of the Redding Formation and named Members IV–VI. In his Bear Creek Sandstone he includes Member III and part of Member V of Popenoe (1943) and the Melton Sandstone of Popenoe (in Jones et al., 1978); in the Hooten Gulch Mudstone the mudstones of Members IV and VI of Popenoe (1943), and in the Oak Run Conglomerate part of Member V of Popenoe (1943). Virtually all of the Redding area specimens used in this study were collected by Popenoe, and the recorded locality descriptions reflect his view of the stratigraphy. Conversion to Haggart's stratigraphy would require a more detailed map than that available in Haggart (1986, fig. 4) and would result in a complete revision of recorded names. As Popenoe is senior author of this paper and his view of Haggart's revision unknown, the Redding area column (Figure 2, area 11) is a modification of Popenoe (1943) compatible with his last expressed opinions. Despite the differences regarding stratigraphic nomenclature between Popenoe and Haggart, age assignments are mainly in accord, and stratigraphic position of the specimens within sections exposed in the several creeks is not disputed. The differences arise in recognizing lithologic units present from section to section in the several creeks.

Perissityid gastropods are found in coarse- to very fine-grained sandstone. *Perissitys* is most abundant in medium-

to fine-grained sandstone, and is associated with very shallow-water molluscan assemblages characterized by species of *Yaadia*, *Meekia*, and *Cymbophora*; slightly deeper water assemblages characterized by *Calva*, *Pterotrionia*, and *Tenea*; and softer bottom assemblages characterized by *Crasatella*, *Clisoculus*, *Cucullaea*, *Turritella*, and *Anchura*. *Perissitys* regularly occurs with naticids and may, like them, have been confined to soft substrates (Taylor et al., 1980, p. 380). Its occurrence in several assemblages suggests a fairly wide water-depth range. Perissityids are usually a minor component of these faunas and are inferred to have been predators. Although morphologic changes in the *Perissitys* lineage are apparent, there are neither correlative substrate nor marked faunal association changes suggestive of adaptation to a new habitat. The modifications of form in *Perissitys* may be further adaptations to an infaunal, predatory life style, but not to change in habitat.

The largest specimens of *Perissitys* are from near the top of the Chico Formation on Chico Creek (area 5)—diameter over 45 mm; Pleasants Sandstone Member of the Williams Formation, Bee Canyon, Santa Ana Mountains (area 13)—diameter 51.5 mm; Moreno Formation near Ortigalita Creek (UCB loc. A-6618) (area 8)—diameter about 35 mm; and the top of the Great Valley Series near Martinez (area 7)—diameter 36 mm. Large specimens of *Perissitys* spp. have thus been found in beds of mid Campanian through mid Maastrichtian age.

The geologically oldest species are the most geographically

restricted; whereas those of Campanian age are most widely distributed. However, Campanian sandstones crop out more widely than those of Coniacian-Santonian age, and the absence or abundance of perissityids may be an artifact of the geological record rather than an indication of their place of origin and a record of dispersal. The geologically oldest (Turonian-Coniacian) perissityids from western North America are all from east of Redding (Figure 1, area 11). Ages of Japanese perissityids are roughly contemporaneous with those of the West Coast. Japanese perissityids from the Upper Yezo Group, *Pyropsis* sp. indet. of Nagao, 1939, = *Tudicla* (*Perissitys*) sp. in Hayami & Kase (1977); *Pyrifusus* (*Neptunella*) *kawakamiensis* Nagao, 1939, = *Rhombopsis?* *kawakamiensis* (Nagao) in Hayami & Kase (1977); *Surculites fusoides* Nagao, 1939; and *Fusus* (s.l.) *volutodermoides* Nagao, 1939, are considered by Hayami and Kase (1977) to be of Coniacian or Santonian age. *Trachytriton sachalinensis* Schmidt, 1873, = *Serrifusus?* *sachalinensis* (Schmidt) in Hayami & Kase (1977) and *T. duiensis* Schmidt, 1873, = *S. duiensis* (Schmidt) in Hayami & Kase (1977) from Sachalin are "Campanian or thereabouts" (Hayami and Kase, 1977). *Pseudoperissitys bicarinata* Nagao & Otatume, 1938, is Campanian or Maastrichtian (Hayami and Kase, 1977).

The earliest and most characteristic perissityids are from the North Pacific and this family may be of North Pacific origin as well as of predominantly North Pacific occurrence. Zinsmeister (1983) indicates confamiliality for *Cophocara*, *Heterotermia*, *Nekewis*, and *Tudiclana*; and, as *Heterotermia* spp. have been recognized in the New Zealand Paleocene and Patagonian Cretaceous (Finlay and Marwick, 1937), perissityid distribution apparently extended to South America and New Zealand in the latest Cretaceous and Early Tertiary.

MORPHOLOGIC CHANGE

The earliest perissityids are similar in shape and in aperture and differ mainly in sculpture (Figures 5-9, 104). The latest perissityids are, however, dissimilar, each lineage having evolved a distinctly different aspect. And in most lineages the geologically youngest form differs markedly from the oldest. With the exception of columellar folds (commonly ranked as a generic or familial feature) the characters that change in a lineage are those usually considered to be of no more than specific importance. Sequential ordering of species in the lineages is based upon stratigraphic superposition of specimens in perissityid-bearing sections and biostratigraphic correlation of these and other deposits in which perissityids occur. Although perissityid occurrences in these deposits are spotty, sufficient specimens at close enough intervals have been obtained to make patterns of change within the group apparent. Surprisingly, between the five similar Coniacian species and their disparate Campanian descendants, there are no more than three species in any lineage. In each lineage the species arise by phyletic transitions; lineage splitting, because of the trends in the development of some characteristics within each lineage, results in recognizable genera. Formation of new morphologic species through phyletic transitions is more than four times as common as is lineage splitting; divergence between lineages is more prevalent than para-

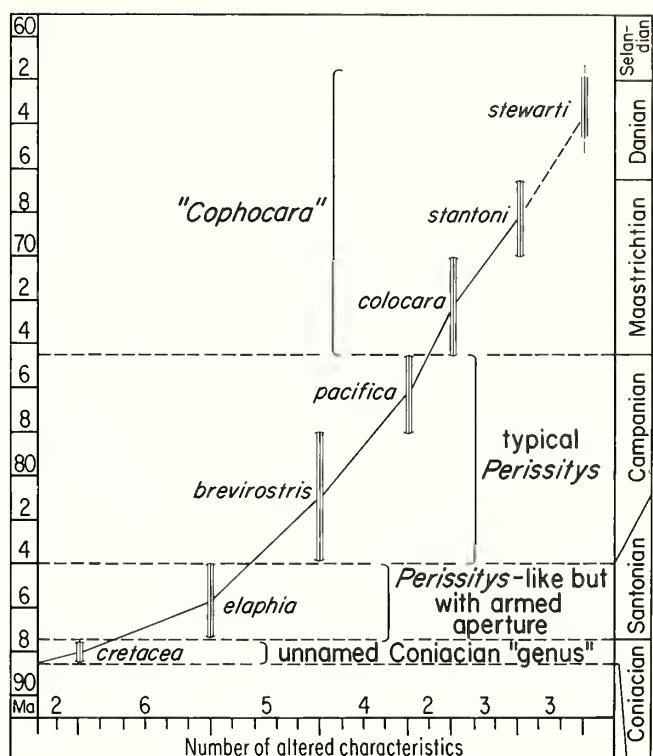
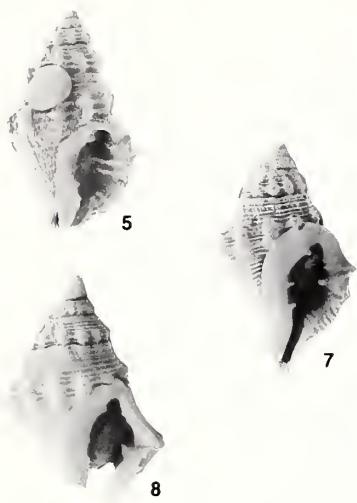


Figure 4. Plot of time versus changed characteristics in the *Perissitys* lineage. Bars indicate recognized range of each specific taxon. Brackets show range of possible genera if the genera were defined according to characteristics commonly considered to be of generic importance. Because there are specimens of intergrading form between the recognized species a sloping line is drawn connecting the mid-point of each range bar. The more horizontal the line the faster the species is changing; the more nearly vertical the slope, the more the species approaches stasis. Two changes are diagrammed within *cretacea* during the Coniacian; six accumulate during the earlier part of the Santonian between *cretacea* and *elaphia*; five during the later Santonian and earliest Campanian between *elaphia* and *brevirostris*; four through the early and mid Campanian between *brevirostris* and *pacifica*; two during latest Campanian and earliest Maastrichtian between *pacifica* and *colocara*; and three from early Maastrichtian into late Maastrichtian between *colocara* and *stantoni*. Three changes are diagrammed between *stantoni* and *stewarti* although the fossil record between these two is incomplete.

lism, and convergence is rare. To determine whether the style of evolution is punctuated or gradual, the rate fast or slow, and its pace steady or varied requires a specimen-rich lineage such as *Perissitys*. Plotting morphologic change against biostratigraphic zonations combined with a time scale, provides apparent rate and pace of change in the *Perissitys* lineage (Figure 4).

PATTERNS OF CHANGE

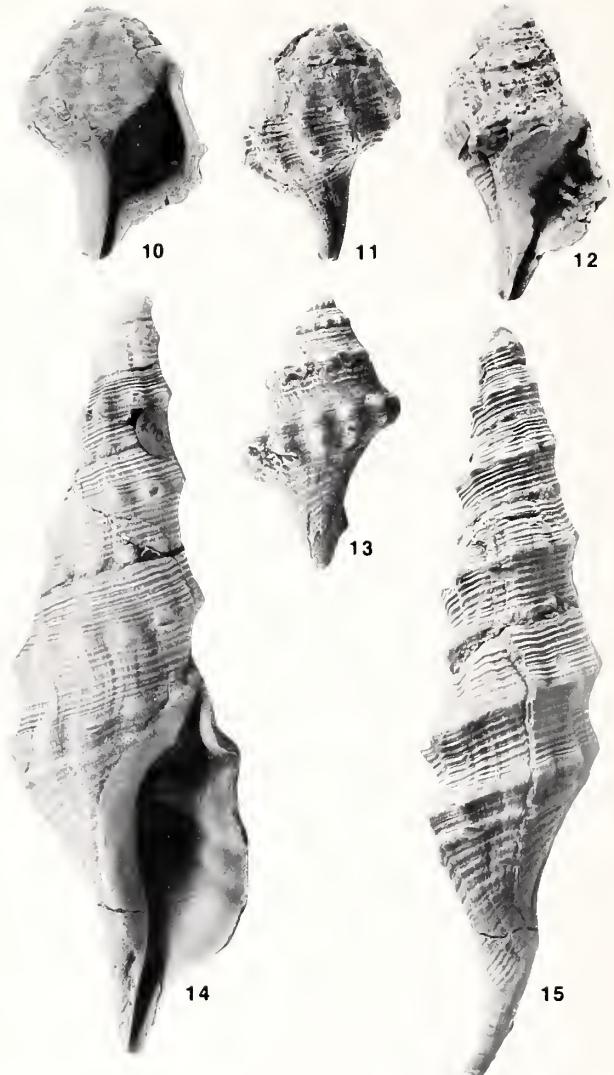
Divergence in the four lineages *Perissitys*, *Pseudocymia*, *Murphytyls*, and *Christityls* (compare Figures 7, 104, 9, and 8 to 93, 100, 127, 160, and 182) is accomplished through mod-



Figures 5–9. Coniacian perissityid species. **5.** *Pseudocymia*(?) *aitha* new species, holotype, $\times 1$, UCLA 39440 from CIT loc. 1007. **6.** “*Fusus*” aff. “*F.*” *kingii* Gabb, hypotype, $\times 1$, LACMIP 7245 from CIT loc. 1007. **7.** *Perissitys cretacea* (Cooper), neotype, $\times 1$, UCLA 59588 from UCLA loc. 4104. **8.** *Christitys delta* new species, holotype, $\times 1.5$, UCLA 59455 from UCLA loc. 4209. **9.** *Murphytys michaeli* new species, paratype, $\times 1.5$, LACMIP 7271 from CIT loc. 1230.

est modifications to different sets of characteristics in each lineage. The degree of differentiation achieved by incremental changes within three perissityid lineages across 10 million years can be seen by comparing Figures 5–9 of Coniacian species with Figures 10–15 of mid Campanian forms. Amount of alteration within each lineage is suggested by comparing Figure 7 to 93 and 100, 104 to 127, 9 to 160, and 8 to 182. Although the morphologic differences between *Perissitys cretacea* (Figure 7), *P. brevirostris* (Figure 10), and *P. stantoni* (Figure 93) have been considered to warrant recognition of distinct genera, these forms result from phyletic transition within a lineage. The differences between species resulting from a lineage split (Figures 5 and 7) are not greater than those between adjacent species in a lineage (Figures 7 and 27).

The genus *Pseudocymia* changes from shortly fusiform in shape to moderately elongate fusiform. The pseudofolds on the columella are reduced as is the posterior sinus in the outer lip. Unifying features include the several nearly equal, distinct spiral ribs that override short, strong axial ribs, a siphonal fasciole, and the thickened outer lip with several subequal, liriform denticulations. The genus *Christitys* develops a more pyriform shape with a broader, more expanded periphery upon which the number of strong spiral ribs is reduced, and weaker outer lip denticulations. Unifying features include the posterior sinus of the growth line, a relatively abapical position for the strong outer lip denticulations, and the columellar fold at the base of the previous whorl. The genus *Murphytys* develops a roundly expanded inner lip, a growth line straightened across the ramp with the



Figures 10–15. Three species of mid Campanian age from the three most complete perissityid lineages. **10, 11.** *Perissitys brevirostris* (Gabb), hypotype, $\times 1.5$, UCLA 59661 from CIT loc. 1400. **12, 13.** “*Hindsia nodulosa* (Whiteaves),” hypotypes, $\times 1$; **12,** UCLA 39464 from CIT loc. 1158; **13,** UCLA 39466 from CIT loc. 1402. **14, 15.** “*Fusus*” cf. “*F.*” *kingii* Gabb, hypotype, $\times 1$, LACMIP 7246 from UCLA loc. 7003.

sinus displaced posteriorly and becoming adjacent to the suture, and more nodulose axial sculpture combined with finer spiral sculpture. Unifying features include the two columellar folds, the rimmed outer lip, and the plumply bucciniform shape. The genus *Perissitys* changes from bucciniform to pyriform, develops an expanded inner lip that eventually envelops most of the spire and last whorl in callus, and reduces and then eliminates columellar pseudofolds and outer lip denticulations.

The sums of these changes are impressive, especially so because the differences between species are not large. Absence of specimens, regarded as constituting a species, from the geological record would produce a punctuational style to the

evolution of these lineages; absence of two such adjacent species would prevent recognition of the lineage.

A gap between the early late Turonian *Pseudocymia aurora* and the five Coniacian perissityid species (Figures 5–9) leaves unrepresented a short period of time during which, if these five species are derived from *P. aurora*, there is an increase in species diversity. The Coniacian–Santonian *Perissitys* record following this gap is of relatively rapid evolution (Figure 4). Similar rates of evolution could produce the five Coniacian perissityid species—*P. cretacea*, *M. michaeli*, *P.(?) aitha*, *C. delta*, and “*F.*” aff. “*F.*” *kingii*—from *P. aurora*. Near the Coniacian–Santonian boundary, another lineage split and increase in species diversity is suggested by the similarity of Coniacian *Christitys delta* (Figures 8, 165–168) and Santonian *C. medica* (Figures 169–170, 172–177) to the early Santonian member of the “*Hindsia nodulosa*” lineage (Saul, in prep.). These possible increases in species and generic diversity involve no greater morphological modifications from the putative ancestors than are present between species of *Perissitys*. Additional such alterations render these lineages recognizable as distinct genera. The possibility of proliferation of species at the margins of geographic ranges (Shuto, 1974) is suggested by the presence of perissityids in Japan. Thus, although the style of morphologic change in West Coast perissityids is predominantly gradual, apparent punctuation may be developed in other geographic areas.

Evolution of “specific” characteristics in the *Perissitys* lineage has sufficed to produce morphologic dissimilarity regardable as of “generic” degree, but the style of change remains gradual within and between species of *Perissitys* and the characteristics evolve independently. Individual specimens have some but not all features more advanced than do other specimens from the same locality. A collection from a single locality probably represents more than one generation of mollusks, resulting in variety of form, but the heterogeneous expression of the evolving characteristics suggests heterochronous spread through the populations of incremental alterations.

The changes within and between species of *Perissitys* are modest. The bucciniform *Perissitys cretacea* becomes slightly shorter spired, and the inner lip broadens posteriorly.

P. elaphia has one or two more strong peripheral ribs than does *P. cretacea*. Typically in *P. elaphia* the parietal lip expands to cover the apertural face of the last whorl, there is an additional medial denticle within the outer lip, the posterior growth-line sinus is diminished, the anterior canal is lengthened, and *P. elaphia* has a more pyriform shape. The earliest *P. elaphia* have, however, a bucciniform shape, a moderate expansion of the parietal lip, only a small additional medial denticle within the outer lip, and no notable change in the anterior canal. Although there is usually a third spiral rib about the periphery, it is weaker than the other two. The third peripheral rib is rapidly strengthened upsection and some late early Santonian *P. elaphia* (Figure 38) have four strong peripheral spirals. The parietal callus also expands adapically so that *P. elaphia* from the *Inoceramus schmidti* horizon of Mill Creek, the *Baculites capensis* Zone on Chico Creek and later Santonian localities of the Redding

area (e.g., UCLA loc. 4217 on Clover Creek) have callus up the apertural face of the spire (Figure 40). Additionally, these late Santonian *P. elaphia* are of more pyriform shape as the whorl becomes more strongly contracted immediately anterior to the abapical strong peripheral spiral. Finally, the youngest *P. elaphia* have weakly developed pseudofolds and denticulations. The species cannot, therefore, be considered to be in a state of stasis. Morphologic variation within each locality collection suggests that the changes are gradually acquired and not abruptly developed.

Perissitys brevirostris lacks the apertural ornaments of *P. elaphia*, has a longer, straighter canal, a shorter spire, no more than three strong peripheral ribs, and a more expansive parietal lip. The earliest Campanian *P. brevirostris* (Figure 43) differs from typical *P. brevirostris* and resembles late Santonian *P. elaphia* in having a relatively high ramp and a more angulate peripheral profile. Although specimens found through 600+ m of the Ten Mile Member of the Chico Formation on Chico Creek (area 5) are identified as *P. brevirostris*, typical *P. brevirostris* with the longer straighter canal and usually rounder whorl profile are found through the upper 427 m of this thickness (Figures 54, 56). Despite some variation of whorl profile, spacing of the peripheral ribs, and height of spire, *P. brevirostris* is morphologically relatively stable through this section, in contrast to the greater number of changes in *P. elaphia*, which has been found through only 200+ m of the Musty Buck Member (Figure 2).

The transition from *P. brevirostris* to *P. pacifica* involves shortening of the spire, crowding of the peripheral spirals to form a narrower and more angulate periphery, and increased coverage of the shell by the expanded callus. Many specimens from the Chatsworth Formation in Bell Canyon (area 17) have two strong peripheral spirals, typical of *P. pacifica*, but the rounder whorl profile of *P. brevirostris* (Figure 61). In the upper part of its stratigraphic range *P. pacifica* gradually acquires the characteristics of *P. colocara* applying increased callus over the shell and developing less prominent peripheral spirals and nodes.

So many specimens of *P. colocara* have been identified as *Cophocara stantoni* that the differences between *P. pacifica* and *P. colocara* might be expected to be much greater. The differences consist, however, mainly of the addition of more callus and the further reduction of peripheral spirals and nodes, trends which ultimately result in *P. stantoni*. The more enveloping callus on *P. colocara* is typically deposited, at intervals, thickly near the aperture. When further growth occurs, this lump of callus distorts the growth spiral and causes the shell to appear deformed. Some specimens of *P. colocara* (Figures 84, 85) either produced less of a callus coat or were interrupted before they completed their coating and in their seminudity resemble *P. pacifica*. Although an enveloping callus coat gives an impression of definite specific difference, the coat developed over a period of time during which more individuals are more callused and specimens with less coating are rarer in the collections.

P. colocara and *P. stantoni* are difficult to distinguish because both are coated with callus. The crowding of the peripheral spiral ribs reaches its ultimate in *P. stantoni*, and

only one rib is dominant; the callus coat is thicker and applied more evenly; the spire is consistently short, and the periphery less angulate.

Specimens from the late Maastrichtian beds at the base of the San Francisquito Formation on Warm Springs Mountain (area 19) (Figure 95) and from the Lower Laguna Seca Formation, UCB loc. A-3262 (area 8) (Figure 96) have characteristics intermediate between *P. stantoni* and *P. stewarti*, but are, unfortunately, poorly preserved. UCB loc. A-3262 has not yielded turrillellas, and *Perissitys* has not yet been recovered in association with *Turritella peninsularis adelaidana* Merriam. The oldest turrillellas with which *P. stewarti* is associated are late *Turritella quaylei* and *T. peninsularis* and are probably not older than late Danian (Saul, 1983), but specimens from UCB loc. A-3262 and some other localities in the Panoche Hills (area 8) may be from older horizons. *P. stewarti* differs most evidently from *P. stantoni* in having two well-developed peripheral spiral rows of nodes, giving it a blunt, biangulate periphery. It also has a shorter spire and a thinner callus coating.

Perissitys is well represented in the fossil record and changes within as well as between its species are documented by specimens. Of the four genera, *Perissitys* supplies most evidence for style and rate of change. Four of the *Perissitys* species have fossil records that are stratigraphically complete enough to give an indication of the pace of change.

RATE OF MORPHOLOGIC CHANGE

The range of *Perissitys* is Coniacian to early Selandian (Paleocene). The Coniacian age is based on ammonite zonation and the Selandian on turrillid zonation. Several time scales have been proposed recently for this interval. Stage lengths vary on the various time scales, and estimates of chronologic duration of *Perissitys* species and the rates of change within the lineage are dependent on the time scale chosen. The DNAG 1983 Time Scale (Palmer, 1983) for this interval is in close agreement with a 1984 version of Berggren et al. (1985b), Kent and Gradstein (1985), and Berggren et al. (1985b) except for the placement of the Danian–Selandian boundary. If this boundary is put at 62.3 Ma (Berggren et al., 1985a; Berggren et al., 1985b) rather than at 63.6 Ma (Palmer, 1983), *Perissitys stewarti* is probably mainly Danian in occurrence. The range of *P. stewarti* (Figure 3) is plotted with respect to its association with *Turritella peninsularis* and is independent of the position of the Danian–Selandian boundary. At the earlier end of the *Perissitys* lineage, *P. cretacea* ranges through the Pacific West Coast Coniacian Stage defined by ammonite correlations. The early Campanian marine magnetic anomaly 33–34, Chron 33r, encompasses approximately 260 m of the Ten Mile Member in the Chico Creek section (Ward et al., 1983) (see Figure 2). Early *P. brevirostris* is found through this part of the Chico Creek section and Chron 33r is coincident with the earlier part of the range of *P. brevirostris*. Chron 33r is considered to have begun shortly after the Santonian–Campanian boundary and to last for 3.5–5 Ma. It is dated at 78.53 to 82.93 Ma by Harland et al. (1982, p. 74) but is considered to be nearly 2 Ma older on the DNAG 1983 Time Scale (Palmer, 1983).

Based on these correlations and plotted against the DNAG 1983 Geologic Time Scale, *Perissitys* has a duration of roughly 26 Ma (Figure 3). Seven successive specific taxa are named in this lineage. Were a constant rate of change assumed each species would have a time span of 3.7 Ma, or slightly more than one-third the 10 Ma considered to be the mean species duration for gastropods (Stanley, 1985, p. 16). *Perissitys cretacea* (Cooper), however, has been recognized only from the Coniacian which may be no longer than 1 Ma (Obradovich and Cobban, 1975, p. 46). But, as *P. cretacea* may not be descended from the only pre-Senonian perissityid herein recognized, *Pseudocymia aurora* new species of early late Turonian age, the earliest possible appearance of *P. cretacea* remains undefined and its range may have extended into the Turonian and exceeded one million years. *Perissitys elaphia* new species occurs through the Santonian, which is estimated to represent about 3.5 Ma (Palmer, 1983). Specimens identified as *P. brevirostris* (Gabb) are of early to mid Campanian age, and the taxon ranges through approximately 6 Ma. *Perissitys pacifica* new species is of late Campanian age and thus has a duration of roughly 4 Ma. *P. pacifica* changes less dramatically and more slowly than does *P. elaphia* but more rapidly than *P. brevirostris*. Early Maastrichtian *P. colocara* new species also has a probable duration of 4 Ma. It is succeeded near the middle of the Maastrichtian by *P. stantoni* (Stewart), which has a duration of at least 3.5 Ma. Unfortunately specimens of *Perissitys* have not yet been found in deposits certainly recognized as earliest Paleocene and the biochron of *P. stantoni* (Stewart) is probably not completely known, nor is that of the Paleocene species *P. stewarti* (Zinsmeister).

The number of altered characteristics in the genus *Perissitys* are plotted against geologic time in Figure 4. Each of the above-mentioned differences between species is given equal weight. The slope of the line is an indication of the rate of change in *Perissitys*. Change is most rapid through the Coniacian–Santonian and slowest through the early to mid Campanian. Although *Pseudocymia aurora* may or may not be ancestral to *Perissitys cretacea*, there are essentially four morphologic changes between the two. *P. cretacea* has fewer denticles on its outer lip, a slightly longer canal, a deeper posterior sinus, and a periphery marked by two strong spirals. Had *Pseudocymia aurora* been included on Figure 4, the slope of line between it and *Perissitys cretacea* would have been similar to that between *P. cretacea* and *P. elaphia*. Forms intermediate between *P. aurora* and *P. cretacea* are, however, unknown.

The *Perissitys* lineage exhibits its most rapid accrual of morphologic change through the Coniacian and Santonian, but the other lineages, although not as well documented, do not evince equal degrees of evolution. The least change recognized for this same Coniacian–Santonian interval is in the *Murphytyss* lineage whose species *M. michaeli* ranges through the Coniacian and Santonian stages.

In the *Perissitys* lineage the varied pace of gradual change produces morphologic differences of generic degree, but the recognition of different genera has not occurred at times of relatively rapid evolution and between species of short temporal duration. Previous workers have identified *P. pacifica*

as *P. brevirostris* and *P. colocara* as *Cophocara stantoni*, thus recognizing a generic distinction between these two new species, each of which has a duration of approximately 4 Ma. Occasionally late *P. pacifica* has been identified as *Cophocara stantoni* and early *P. colocara* as *P. brevirostris* reflecting independent and unequal development of characteristics. Perceived generic differences are not, therefore, dependent on rapid evolution nor great morphologic change.

If the average duration of a gastropod species is 10 Ma (Stanley, 1985), the perissityids are evolving more rapidly than is usual for their class. Their morphologic changes do not appear to reflect major habitat changes, although the different lineages probably had somewhat different requirements. Judging from their occurrence in the geologic record, *Pseudocymia*, *Murphytys*, and *Christitys* were less widely adapted than *Perissitys*. The continuing direction of changes, such as the increasing envelopment of the spire by the inner lip callus and the lengthening of the anterior siphonal canal in *Perissitys*, produce the distinct morphologies of this group. That so much directional change occurred during the Late Cretaceous, a time of relative stability, suggests biological rather than physical pressure. Greater arthropod predation and increasingly infaunal habitat of bivalves (Vermeij, 1977) that may have been prey of the perissityids would both have promoted infaunal adaptations in these siphonate gastropods.

CLASSIFICATION

Gastropods that we propose to include in the family Perissityidae form a morphologically compact group in the Coniacian, and five species of that age could readily be assigned to a single genus (Figures 5–9). Lineages based on these five species, traced through the Late Cretaceous, evolve new forms by modifying species-defining characteristics to the extent that by the mid Campanian the three most complete lineages are represented by species—*Perissitys brevirostris* (Gabb), “*Fusus*” cf. “*F.*” *kingii* Gabb, and “*Hindsia nodulosa*” (Whiteaves) (Figures 10–15)—which have not been considered congeneric, nor assignable to the same family. Clearly the approach of the systematist will affect the ordinal, familial, generic and even specific placement of these fossils. The classification presented here has its basis in stratigraphically ordered specimens collected from Late Cretaceous and early Paleocene sequences of the Pacific Coast of North America. The successions of fossils assigned to the perissityids document a part of the Late Cretaceous siphonate gastropod radiation (Sohl, 1964; Taylor et al., 1980).

SPECIES

A paleontological species is a morphologic species, and if there are gaps in the record of a lineage, the preserved segments of the lineage may readily be recognized as species. If there are no gaps, or the gaps are short relative to the rate of evolution of the lineage, a grading continuum of morphologies may result. This is the case with *Perissitys*. Because of the range of variation present at any stratigraphic level, and the changes between levels, *Perissitys* specimens identified by comparison to those from super- and subjacent strata

are alike enough to be identified as being of the same species. If artificial gaps are created, however, by comparing specimens of early Campanian age to those of Coniacian or mid Maastrichtian age, three easily distinguishable species, sufficiently different to have been previously allotted to three genera (Figure 4), are apparent. The West Coast lineage of *Perissitys* is an evolutionary continuum, and its species are arbitrarily named segments, but arbitrary only in the sense that there are no abrupt morphologic changes in this continuum despite the distinctness of the end members. Each lineage has several characteristic features that vary and evolve independently, producing a cline rather than punctuational series of phenotypes. Species recognition is dependent upon an aggregate of changing features, and each remains recognizable for various lengths of time (Figures 3, 4).

Should these forms be considered to be species if speciation events are absent? This paper deals only with specimens from the West Coast of North America, but there are perissityids in Japan and possible perissityids in New Zealand and Chile. Although the present West Coast record is one of phyletic transitions, the lineages may have split near the geographic range margins of the species. The North American perissityids pass through sufficient morphologic changes that segments of these lineages must be considered to be species. Additionally, the named species have biostratigraphic integrity and are useful for correlating Late Cretaceous and Early Tertiary sections.

GENUS

If the genus *Perissitys* were narrowly restricted to those species having the apertural characteristics of the type species, *P. brevirostris* (Gabb), only it and *P. pacifica* new species could be included therein. Of the remaining species, *P. cretacea* (Cooper) could be placed in a new genus along with the four contemporary species of Figures 5–9; *P. elaphia* might constitute a new monotypic genus; and *P. colocara* new species, *P. stantoni* (Stewart), and *P. stewarti* (Zinsmeister) would make up *Cophocara* (Figure 4). Such genera are horizontal in that their distribution tends to lie along restricted time planes and resemble many Recent genera in which aggregations of similar but distinct species are recognized, but their phylogenetic relationships through time are not. The perissityid genera recognized are linear (or vertical) genera. Retaining a single generic name for each lineage organizes the species; recognizing successive chronospecies provides gnemons along the genetic line.

FAMILY

Perissityidae are, or are derived from, bucciniform gastropods that have two folds or pseudofolds on the columella, a parietal welt or denticulations near the posterior end of the aperture, a posterior sinus to the growth line, and strong median denticulations within the outer lip. The outer lip flares anteriorly and is thickened by a varix. Impressions of former outer-lip thickenings and denticulations are found on steinkerns, even though such varices may not be obvious on the shell exterior. Compared to turritellid lineages of the same period and time span, the perissityid lineages evolve rapidly

and divergently, each lineage following its own course and arriving at forms suggestive of disparate families. The apertures of early perissityids resemble those of columbellinids, and several late Jurassic columbellinid trends—constricted and then flared apertures, denticulate outer and inner apertural lips, inner lip callus expanded and covering one-half to the entire exterior of the shell (Taylor et al., 1980)—resemble those of perissityids. These suggest a columbellinid derivation, possibly within the Early Cretaceous.

Perissitys stewarti (Zinsmeister, 1983) from the Paleocene is pyriform in shape with a moderately long, nearly straight anterior canal, and lacks apertural pseudofolds and denticulations; it resembles Todiclidae. *Pseudocymia(?) kilneri* new species of early Maastrichtian age is subfusiform in shape with a short, flexed anterior canal, strong denticulations on the outer lip, and weak pseudofolds on the columella, and resembles tropical Buccinidae. *Christitys martini* new species of early Campanian age is pyriform in shape, has weak denticulations on the outer lip and a fold on the columella. Its form, except for that of its outer lip, is similar to some Vasidae. *Murphitys madonna* new species, of early Maastrichtian age, is angulate bucciniform in shape and has a thickened outer lip and two folds on the columella. Except for these columellar folds it resembles some Cymatiidae. Zinsmeister (1983, p. 1297) includes those forms with short to moderately elevated spire, i.e., *Perissitys*, *Cophocara*, and *Heteroterma*, in Todiclidae, and moves the higher spired *Nekewis* from the Turridae to the Todiclidae because of its similarities to *Heteroterma*. None of these genera have the tetriclid fold at the base of the columella; neither *Heteroterma* nor *Nekewis* has the characteristic expanded inner lip of *Tudicla spirillus* (Linnaeus), and all have an eye-shaped rather than a well-rounded aperture. The growth line of *Heteroterma* and *Nekewis* is sinused posteriorly and resembles that of *Christitys* (Figures 166 and 176) and “*Hindsia nodulosa* (Whiteaves)” (Figure 13), and these genera are closer to Perissityidae than to Todiclidae. *Tudiclana simulator* Findlay & Marwick, 1937, which resembles *Perissitys brevirostris* but lacks the subsutural welt, is described as having a low fold at the base of its columella, and it may belong with *Tudicla* as indicated by Finlay and Marwick (1937). Abbott (1959, p. 20–471) suggests that *Tudicla* is usually included in the Vasidae because its overall shape resembles that of *Tudicula* spp., although there is no anatomical evidence to support this placement. Thus Finlay and Marwick (1937) and Zinsmeister (1983) may well be correct in divorcing the Todiclidae from the Vasidae. Although we do not consider *Perissitys* to be a tetriclid, the Todiclidae and Perissityidae may be more closely related than either is to the Vasidae.

SUPERFAMILY

At the family level the perissityids are grouped together because of their early characteristics in common, several of these characteristics also serving to distinguish them from other families, but at the next hierarchical level we place them in the superfamily into which these diverging lineages appear to evolve. Placing them in Muricacea of Ponder (1973)

would be simplest as he includes within the Muricacea the Buccinacea and Volutacea of Wenz (1941). This large polymorphic superfamily grouping tends, however, to obscure a number of relationships. The families Muricidae, Thaididae, Magilidae, and Columbariidae, which constitute the Muricacea of Wenz (1941) and Taylor and Sohl (1962), form a distinct group within Ponder's Muricacea. With Muricacea constituted as of Taylor and Sohl (1962), and the Buccinacea and Volutacea of Wenz (1941) and Taylor and Sohl (1962) regarded as distinct, choice of superfamily placement for the Perissityidae is increased. The Perissityidae have little in common with Late Cretaceous muricaceans and more similarity to buccinaceans and volutaceans. Buccinaceans and volutaceans appear in the late Early Cretaceous and both are relatively common in the Late Cretaceous (Taylor et al., 1980). Wenz (1943) and Zinsmeister (1983) place *Perissitys* and *Cophocara* in the Volutacea, apparently because the pyriform shape resembles that of *Tudicla*, which was included in the Volutacea by Thiele (1929), Wenz (1943), and others, and presumably by Taylor and Sohl (1962) who, following Wenz, placed the Vasidae—in which *Tudicla* is often included—in the Volutacea. Clearly the earliest perissityids have neither a volutid shape nor columella folds similar to those of volutes, whereas volutes from the same beds already display characteristic volute morphology. *Perissitys* evolves toward a shape similar to that of some genera included by Wenz in the Vasidae [e.g., *Pyropsis* (Conrad, 1860; Sohl, 1964), *Tudicla* (Röding, 1798; Abbott, 1959), and *Tudiclana* (Finlay and Marwick, 1937)], but Sohl (1964) later moved the Vasinae, including *Tudicla*, to the Buccinacea, and it is within the Buccinacea that the Perissityidae are placed.

As already indicated perissityids resemble the Cymatiidae and the Columbellinidae. Cossmann (1904), Wenz (1940), and Sohl (1960) assigned the Columbellinidae to the Strombacea, but, because columbellinids lack the apertural sinuses characteristic of strombids and aporrhaidids, we concur with Fischer (1884) and Taylor et al. (1980) and include Columbellinidae in the Tonnacea. It is the earliest of the tonnacean families to appear; Taylor et al. (1980, p. 385) derive it from the Strombacea within the Jurassic. The tonnacean families Cymatiidae, Bursidae, and Cassididae are reported from the mid Cretaceous (Taylor et al., 1980, p. 387), but described forms are not compellingly similar to perissityids, and the similarity of some perissityids to cymatiids results from ancestry within the same family. The characteristics of perissityids are in many respects intermediate between those of columbellinids and buccinaceans.

Ponder (1973) argues that the neogastropods are derived from the Subulitacea rather than from the advanced tonnacean mesogastropods considered ancestral by Wenz (1938, p. 65; 1941, p. 1082) and others. Subulitaceans have, in the Paleozoic, already lost the median sinus of the outer lip (Ponder, 1973, p. 302), whereas early perissityids and volutes have a shallow notch which may be a posteriorly displaced remnant of the median sinus. Taylor et al. (1980, p. 385–386) suggest that instead of Subulitidae, the Purpurinidae are antecedent to neogastropods. The perissityids, however, appear to be derived from a columbellinid ancestor, probably

in advance of the cymatiids, and perhaps in consort with Tūclididae and Colubrariidae. These latter two families have been variously classified but are probable Buccinacea (Sohl, 1964; Ponder, 1973). The perissityids, thus, suggest derivation of buccinaceans from early tonnaceans.

ORDER

Cox (1960) considered the line between mesogastropods and neogastropods to be arbitrary and included both orders in Caenogastropoda, but Ponder (1973) separates mesogastropods and neogastropods. Much of the evidence for separation lies in the soft parts and includes differences in chromosome numbers (Patterson, 1969; Ponder, 1973, p. 296), whereas similarities of neogastropods and some mesogastropods (tonnaceans) are evident in the shell. Both the soft and hard part comparisons involve interpretations as to derivation of structures, possible parallel evolution, etc. Unfortunately, for most soft part evolution there is no geologic record, and parallel and diverging evolution of shell form make the geologic record of the hard parts difficult to interpret. Neither Ponder's anatomical nor conchological criteria can be used for separation of fossil mesogastropod cymatiids and bursids from neogastropod buccinaceans. The fossil record suggests that perissityids evolved during the Late Cretaceous from forms that resembled some cymatiid mesogastropods into forms that resemble some buccinacean and turrid neogastropods. The line between meso- and neogastropods is, of course, arbitrary, as it is drawn across evolving lineages irrespective of whether neogastropods derive from "primitive" or "advanced" mesogastropods. In shell form the perissityids appear transitional between Mesogastropoda and Neogastropoda, but in a hierarchical classification there is no place for transitional forms, and we include them in the Neogastropoda. The evolution of the Perissityidae suggests that most (perhaps all) neogastropods are derived from within the Columbellinidae, and that the superfamilies and families of the Neogastropoda arose both from different columbellinids and sequentially from columbellinid stocks.

SYSTEMATIC PALEONTOLOGY

Phylum Mollusca Linnaeus, 1758

Class Gastropoda Cuvier, 1797

Order Neogastropoda Wenz, 1938

Superfamily Buccinaceae Rafinesque, 1815

Family Perissityidae new family

DIAGNOSIS. Bucciniform gastropods with two folds or pseudofolds on the columella, a parietal welt or denticulations near the posterior end of the aperture, a posterior sinus to the growth line, and strong median denticulations within the outer lip. The outer lip flares anteriorly and is thickened by a varix. Impressions of former outer-lip thickenings and denticulations are found on steinkerns, even though such varices may not be obvious on the shell exterior.

The new family Perissityidae is proposed for several genera of gastropods that range from Late Cretaceous through Early Tertiary. The early Senonian species of these genera are of moderate size and bucciniform shape, with fine to coarse spiral ribs and short but strong axial ribs about the whorl periphery. All forms thus far studied have fairly large paucispiral protoconchs. The growth line has a shallow antisprial sinus adapical to the mid whorl. The outer lip is slightly thickened, rimmed, and flared, especially from mid whorl to the anterior siphonal constriction. The anterior sinus is nearly two-thirds as long as the eye-shaped aperture. The apertural armature, which is very characteristic in early Senonian forms, is ontogenetically intermittently developed and best displayed in the adult stage. Impressions of the typical outer lip denticles are found on natural casts, spaced as though indicating varices. Most characteristic is the strong denticle at mid whorl with commonly a lesser one anterior to it. This set of denticles is just anterior to the anterior end of the antisprial sinus and at the posterior end of the outer lip flare. The denticles oppose a pseudofold or fold on the columella. A moderately strong tubercle (or set of tubercles) in conjunction with similar tubular structures on the inner lip constricts the posterior end of the aperture. Additionally there are usually small tubercles on the outer lip adjacent to the anterior siphonal canal. The inner lip is clearly demarcated, fairly thick, and in some species forms a pseudoumbilicus at the anterior end of the anterior siphon with the siphonal fasciole. Medially on the columella there are two or three subequal pseudofolds or one or two folds.

Folds and pseudofolds do not differ in apertural view; both appear to be spirally elongate plicae on the columella. Folds spiral uninterrupted on the columella of the teleoconch (Figures 149, 152, 163), but pseudofolds are short, extending less than a quarter turn (Figure 20) into the shell anterior and are absent within earlier whorls (Figures 31, 117). Pseudofolds, like varices, are developed at growth halts, and shells that have not developed a thickened and denticulate outer lip do not show pseudofolds (Figures 17, 35), but folds are present even though the outer lip has not been thickened (Figure 170). The strongest folds occur, however, within apertures that have a well-developed varix, and folds are apparently enhanced by additional callus at growth halts.

Turonian and early Senonian perissityids resemble Columbellinidae in overall shape, in having a well-armed aperture, and in the position of the posterior sinus on the outer lip just adapical to the whorl periphery. The posterior sinus of perissityids is not as narrow and elongate as that of the columbellinids; later Senonian *Perissitys* spp. and *Christitys* spp. are of more pyriform shape than are columbellinids; and the anterior segment of the outer lip of perissityids flares.

Although many perissityids have varices, none has the regular varices of the Cymatacea. The range of shape in perissityids is similar to that in cymatiids, but cymatiids lack folds on the columella and do not cover the shell with callus.

Perissityidae, especially Turonian and early Senonian Perissityidae, resemble some members of the large and polymorphic family Buccinidae in shell shape, sculpture, and shape of aperture. Buccinids do not cover the shell with

callus, lack columellar folds, and do not have strong medial outer lip denticulations and an anteriorly flared outer lip.

Like Fasciolariidae, some perissityids have columellar folds, and some later Senonian perissityids develop a fusiform shape and/or a long anterior siphonal canal. Unlike fasciolariids some perissityids become strongly pyriform in shape and deposit callus over the shell.

Perissityids have been included in the Vasidae which some of them resemble in being pyriform and having folds on the columella. Perissityids do not have spinose sculpture, have an anteriorly expanded outer lip, and a typical pattern of outer lip denticulations which includes a strong medial denticle.

Tudiclididae differ from pyriform Perissityidae in having a round aperture and a columellar fold at the posterior end of the anterior canal.

The posterior growth-line sinus of some perissityids resembles that of some Turridae, but turrids lack apertural armaments, external callus deposits, and columellar folds.

GENERA INCLUDED. *Perissitys* Stewart, 1927 (including *Cophocara* Stewart, 1927), *Pseudocymia* new genus, *Murphytys* new genus, *Christitys* new genus, and *Pseudoperissitys* Nagao & Otatume, 1938. Probably *Heteroterma* Gabb, 1869, will prove to be a perissityid; possibly *Nekewis* Stewart, 1927, belongs here.

DISTRIBUTION. North Pacific (Japan, Sakhalin, Alaska Peninsula, British Columbia, Washington, Oregon, California, Baja California) and eastern South Pacific (Chile, New Zealand).

GEOLOGIC AGE. Late Cretaceous (Turonian) to Early Tertiary (mid Selandian and possibly into Oligocene).

Genus *Perissitys* Stewart, 1927

TYPE SPECIES. *Perissitys brevirostris* (Gabb, 1864), by original designation (Stewart, 1927, p. 426).

DIAGNOSIS. Bucciniform to pyriform gastropods of medium to moderately large size with a subangulate whorl periphery which is ornamented by fewer than five spiral ribs. The crossing of these spiral ribs by short axial ribs produces the characteristic noded periphery. The edge of the outer lip anterior to the periphery is fimbriated. With the exception of the geologically earliest species, *P. cretacea* (Cooper), all species have an expanded inner lip that is developed at growth halts and is the inner lip equivalent of a varix.

REMARKS. Stewart (1927) did not assign this genus to a family, and he mentioned only one other species, *Pyropsis hombroniana* (d'Orbigny) from the Quiriquina Formation of Chile (Wilckens, 1904, p. 213, pl. 18, figs. 8, 9), as possibly belonging to *Perissitys*. Plaster casts of specimens of this species sent to us by Dr. E. Perez d'A. of Chile have a rounded aperture indicating that *P. hombroniana* is not a *Perissitys*, nor can it be included in the Perissityidae. *Pyropsis* sp. indet. of Nagao (1939, p. 228, pl. 21, fig. 5-5b) from "Upper Ammonites bed" = Upper Yezo Group, Abeshinai-gawa, Teshio Pref., Japan, is probably a *Perissitys*.

Morphologic changes which develop in West Coast *Perissitys* of Coniacian through Danian age include shortening of

the spire and lengthening of the anterior canal so that the shell shape changes from bucciniform to pyriform, expansion of the inner lip over the apertural face and envelopment of the spire and most of the body whorl in a callus coat, and reduction and disappearance of pseudofolds from the columella and tubercles from the outer lip. The change from bucciniform to pyriform shape includes displacement of the noded periphery from mid whorl toward the base of the whorl. The rows of nodes on the periphery become reduced in prominence, although the number of rows of nodes initially increases and then decreases.

Coniacian *Perissitys*, *P. cretacea* (Cooper, 1896) resembles other Coniacian perissityids, but typical *Perissitys*, *P. brevirostris* (Gabb, 1864), differs from all other perissityid genera in having the inner lip expanded over the apertural face and spire of the shell. In pyriform shape *Perissitys* resembles *Tudicula* H. & A. Adams, 1863, *Tudiclana* Finlay & Marwick, 1937, *Tudicla* Röding, 1798, and *Pyropsis* Conrad, 1860. But none of these has the inner lip expanded onto the spire as in *Perissitys*. Except for *Tudiclana* all have an aperture posteriorly broadened resulting in a rounder aperture, and an inner lip which is folded onto the whorl. *Tudiclana* has a low fold at the base of the columella, and lacks the callus coat and the raised subsutural welt of *Perissitys*.

RANGE. Along the west coast of North America *Perissitys* is found in sandstones of Coniacian (Late Cretaceous) to early Selandian (middle Paleocene) age. The species are discussed in chronologic order from earliest to latest.

Perissitys cretacea (Cooper, 1896)

Figures 7, 16-26

Sistrum (Ricinula?) cretaceum Cooper, 1896, p. 330, pl. 47, figs. 1, 2; Coan, 1981, p. 161.

DIAGNOSIS. Bucciniform *Perissitys* with two strong spiral ribs about the periphery, the inner lip not markedly expanded, two pseudofolds on the columella, and denticles on the outer lip.

DESCRIPTION. Shell of medium size, bucciniform and thick walled; spire about one-third of total shell height, consisting of five or six whorls including a smooth, mammillate protoconch of nearly three whorls succeeded abruptly by a whorl strongly sculptured by raised spiral threads and axial ribs; next and succeeding whorls gently concave below the appressed suture, with strong double angulation about the mid whorl accentuated by two strong spirals crossing short strong axial ribs; last whorl concave below the median angulation, narrowing to form a sturdy anterior siphonal canal of moderate length, which is twisted to the left (apertural view) and backward at its tip; suture at the abapical peripheral angulation.

Sculpture above the peripheral angulation of eight to ten subequal spiral threads which on the last whorl are narrower than the interspaces; peripheral angulation accentuated by two strong spiral ribs which form nodes across 12-14 short but strong axial ribs; spiral ribs abapical to periphery slightly stronger than on ramp, strongest on whorl base, becoming finer toward anterior siphon.

Outer lip with shallow antisprial sinus adapical to the periphery and slight spiral antisinus abapical to the periphery; flaring moderately, flare thickened with callus deposit which continues around the posterior end of the aperture and rounds into the sharply demarcated inner lip; inner lip of nearly equal width from posterior to anterior end of aperture, forming a pseudoumbilicus along the anterior siphonal canal at the siphonal fasciole. Outer lip with one strong, medial denticle interior to the periphery, a moderate denticle or denticle pair adapical to the strong denticle, and a group of small denticles next to the anterior canal. Inner lip and columella with two nearly equal pseudofolds, the more adapical one opposite the strong denticle of the outer lip and a moderately strong denticle just abapical to the posterior end of the aperture.

NEOTYPE. UCLA 59588, here designated. Cooper (1896, p. 330) stated that he had four specimens, but Coan (1981, p. 161) was unable to find any of them.

HYPOTYPES. UCLA 59589–59594 from UCLA loc. 4104; UCLA 59601 from UCLA loc. 5990.

DIMENSIONS. Of neotype: UCLA 59588—height 30.5 mm (incomplete), diameter 19.9 mm, height of spire 11.2 mm; of hypotypes: UCLA 59590—height 19.4 mm (incomplete), diameter 13.8 mm, height of spire 6.7 mm; UCLA 59592—height 27.8 mm, diameter 17 mm, height of spire 9.9 mm; UCLA 59601—height 21.4 mm, diameter 14.1 mm (incomplete), height of spire 8.7 mm.

TYPE LOCALITY. Cooper (1896, p. 330) indicated only Morley, Shasta County, California, and the precise locality for his specimens is indeterminable. Morley School is shown in sec. 25, T33N, R2W, Millville Quadrangle (U.S.G.S., 1954), on the Oak Run Road more than 4 mi. northeast of UCLA loc. 4104 in sec. 16, T32N, R2W, Millville Quadrangle, Shasta Co., California. No outcrops yielding gastropods similar to *P. cretacea* have been found in the immediate vicinity of "Morley School," and Cooper's specimens may have come from the vicinity of UCLA loc. 4104.

DISTRIBUTION. Sandy beds of Member IV (Popenoe, 1943), CIT locs. 1007, 1289, and 1596, and UCLA locs. 4104 (= CIT loc. 1034) and 5990, Redding area, Shasta Co., California.

GEOLOGIC AGE. Coniacian.

REMARKS. None of Cooper's (1896, p. 330) four specimens is available (Coan, 1981), and it seems unlikely that Cooper's description and figures referred to any other species, but a neotype is designated to obviate confusion with other species of Perissityidae. His specimens probably came from outcrops of Member IV along Oak Run. More than 40 specimens are at hand, the largest of these, UCLA 59595 from UCLA loc. 4104, has a diameter of 21.2 mm. All specimens upon which the above description is based are from Redding area outcrops in Swede Basin, Oak Run, and Clover Creek, Millville Quadrangle, and along Old Cow Creek, Pine Timber Gulch, and Bear Creek, Whitmore Quadrangle (area 11). The species has not yet been recognized elsewhere; it is the earliest known of the inferred *Perissitys* lineage. It may possibly be derived from a Turonian form of the Redding area, *Pseudocymia aurora* new genus and new species, from the Frazier Siltstone below *Collignoniceras* sp. (Jones, et al., 1978, p. XXII.8).

Progressive changes within *P. cretacea* include shortening and broadening of the spire and adapical movement of the suture from anterior to the abapical strong peripheral rib to just covering this rib. The inner lip becomes slightly broader, especially on the body whorl, its outer edge becomes straighter, loses the angular bend, and rounds convexly to join the outer lip. The adapical edge of the inner lip moves from just touching the abapical strong peripheral rib to touching or covering the adapical strong peripheral rib. These are small changes, but the time period is apparently short.

Perissitys cretacea differs from *Pseudocymia aurora* in having its suture upon, rather than abapical to, the peripheral angulation, finer spiral ribs, a more contracted and concave base, a longer more twisted siphonal canal, and fewer denticulations on the outer lip. *P. cretacea* differs from all later species of the genus in having an inner lip callus which is of nearly equal width from posterior to anterior end of the aperture. The shape of *P. cretacea* is similar to that of *Cantharus occidentalis* (Gabb, 1864) of Cenomanian age (Murphy and Rodda, 1960, p. 845), but *C. occidentalis* lacks the pseudofolds and strong denticulations on the outer lip of *P. cretacea*. *C. occidentalis* resembles *P. cretacea* in having a flaring outer lip rather than the unflared lip of modern *Cantharus*.

Perissitys elaphia new species

Figures 27–41

DIAGNOSIS. Pyriform *Perissitys* with three to four strong spiral ribs about the periphery, an inner lip expanded to cover the apertural face of the last whorl, two columellar pseudofolds, and denticles along the outer lip.

DESCRIPTION. Shell of medium size, pyriform; spire about one-fourth of the height of the shell, comprised of 1.5 to 2 smooth, globose nuclear whorls, succeeded by two gently concave whorls, about twice as wide as high; last whorl three-fourths or more of the shell height, having a narrow tumid band just below the suture, a concave ramp and rounded periphery accentuated by three or four strong spiral ribs, and contracting abruptly abapically to form anterior siphonal canal; anterior siphonal canal about as long as the eye-shaped aperture, curving gently to the left (apertural view); suture at or just below the adapical strong spiral rib.

Sculpture on subsutural welt of fine spiral threads, on ramp of very fine distant spiral threads; strong ribs of periphery made nodular by 11–14 strong short axial ribs, interspaces of strong ribs having fine threads; base of whorl with three to five narrow riblets grading into threads and very fine threads on the anterior siphonal neck.

Outer lip with slight antisprial sinus adapical to the periphery and slight spiral antisinus at the periphery; flaring slightly especially at, and abapical to, the periphery, lip flare thickened with callus deposit that also fills the antisprial sinus and continues up onto the spire at the posterior end of the aperture, inner lip expanded posteriorly, overlapping the suture, then spreading roundly to cover the apertural face of the last whorl, curving at the most abapical strong rib back toward the anterior end of the siphonal canal and crossing at the siphonal fasciole to form a pseudoumbilical chink;



edge of expanded inner lip well demarcated. Outer lip with a strong median denticle interior to the adapical strong peripheral rib flanked by a moderately strong denticle on either side, and next to the anterior canal a group of small denticles. Inner lip and columella with two nearly equal pseudofolds, the more adapical one opposite the strong denticles of the outer lip and a moderately strong denticle just abapical to the posterior end of the aperture.

HOLOTYPE. UCLA 59606 from CIT loc. 1232.

PARATYPES. UCLA 59607–59608 from CIT loc. 1232, 59609–59610 from UCLA loc. 3298, 59612–59613 from CIT loc. 1227, 59614–59615 from CIT 1246; 59618 from UCLA loc. 4107; 59620 from UCLA loc. 3623; 59621–59622 from CIT loc. 1016, 59623–59624 from UCLA loc. 3624; 59633–59634 from CIT loc. 1017.

HYPOTYPES. UCLA 59638 from UCLA loc. 3633; 59639 from UCLA loc. 4217; CAS 31325.01 from CAS loc. 31325.

DIMENSIONS. Of holotype—height 31.4 mm, diameter 19.7 mm, height of spire 8.4 mm; of paratypes—UCLA 59609, height 31.2 mm (incomplete), diameter 20.7 mm, height of spire 7.8 mm; 59633, height 26.5 mm (incomplete), diameter 17.6 mm, height of spire 7.9 mm.

TYPE LOCALITY. CIT loc. 1232: Price Hollow, 2250 ft. N, 2000 ft. E of SW cor. sec. 2, T32N, R2W, Millville Quadrangle, Shasta Co., California.

DISTRIBUTION. Member V and lower Member VI in Oak Run, Price Hollow, and Clover Creek of the Redding area (area 11); Chico Formation on Antelope Creek (area 2); Kingsley Cave Member of Chico Formation on Mill Creek (area 2); Musty Buck Member on Chico Creek (area 5) from approximately 360 m to 600 m above the base of the Chico Formation; lower Forbes Formation on Buckeye Creek (area 21); lower *Bostrychoceras elongatum* Zone of the Haslam Formation on Elkhorn Creek (area 3) and Browns River (area 4).

GEOLOGIC AGE. Santonian.

REMARKS. More than 100 specimens are assigned to this

species. The largest of these, UCLA 59609 from UCLA loc. 3298, has a diameter of 20.0 mm. Geologically older specimens have rounder whorls (Figures 32, 36, 38), later ones have a longer, more concave ramp, narrower, more angulate peripheral swelling, and the parietal callus expanding farther up onto and around the spire (Figures 40, 41). A specimen (CAS 31325.01) from CAS loc. 31325 on Buckeye Creek in the Rumsey Hills (area 21) resembles those from UCLA loc. 3633 on Chico Creek (area 5), but it is more abruptly constricted abapical to the periphery, and has only the more abapical of the two pseudofolds on the columella. Specimens from UCLA loc. 3633 are not large. None has denticles on its outer lip, but two low pseudofolds are present on the columella. The absence of *Bostrychoceras elongatum* and *Inoceramus schmidti* from the Chico Creek section above this locality but below the earliest occurrence of *Baculites chicoensis* has led to the inference that the late Santonian is missing from the Chico Creek section (Ward et al., 1983; Haggart and Ward, 1984; Haggart, 1984). The specimen from Buckhorn Creek is from the lower Forbes Formation, and, if *B. elongatum* and *I. schmidti* Zone equivalents are missing from the Chico Creek section (Figure 2), it may be younger than those from UCLA loc. 3633 at which *Baculites capensis* is present.

The relative stratigraphic positions of *P. elaphia* and *P. brevirostris* are the same in the Chico Formation (area 5) and in the Nanaimo Basin (area 3). In the Nanaimo Basin *P. elaphia* occurs in the lower *B. elongatum* Zone and *P. brevirostris* occurs in the overlying *I. schmidti* Zone with *Canadoceras yokoyamai*; on Chico Creek *P. elaphia* occurs in the *Baculites capensis* Zone and *P. brevirostris* in the overlying *B. chicoensis* Zone with *Canadoceras yokoyamai*. On Mill Creek (area 2), *P. elaphia* occurs in the *I. schmidti* Zone of the Kingsley Cave Member. These *P. elaphia* from the *I. schmidti* Zone on Mill Creek and the *B. elongatum* Zone of the Nanaimo Basin resemble the *P. elaphia* of the upper *B. capensis* Zone on Chico Creek. *Inoceramus schmidti* and *C.*

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Figures 16–61. Three species of *Perissitys*: *P. cretacea* (Cooper), *P. elaphia* new species, and *P. brevirostris* (Gabb). All figures ×1 unless otherwise noted. Photos 19–23, 26–32, 35–36, 38, 40, 41, 48–50, 60, 61 by T. Susuki. As nearly as possible the figures are arranged from geologically oldest to youngest. Figures 16–26, *P. cretacea* (Cooper, 1896), Coniacian, 16–25, hypotypes; 16, 18, specimen with protoconch preserved, UCLA 59601 from UCLA loc. 5990, ×1.5; 17, young individual with unadorned aperture, UCLA 59494 from UCLA loc. 4104, ×1.5; 19, UCLA 59589 from UCLA loc. 4104; 20, specimen having aperture cut away to show pseudofolds evanescently, UCLA 59593 from UCLA loc. 4104, ×1.5; 21, 23, UCLA 59590 from UCLA loc. 4104, ×2; 22, 26, UCLA 59592 from UCLA loc. 4104; 24, varix on ablbral side of shell, UCLA 59591 from UCLA loc. 4104; 25, neotype, UCLA 59588 from UCLA loc. 4104. Figures 27–41, *Perissitys elaphia* new species, Santonian; 27–29, holotype, UCLA 59606 from CIT loc. 1232; 30, paratype, UCLA 59612 from CIT loc. 1227, ×1.5; 31, specimen cut to show pseudofolds at aperture and smooth columella of earlier whorls, paratype, UCLA 59607 from CIT loc. 1232; 32, paratype, UCLA 59614 from CIT loc. 1246, ×1.5; 33, ablbral view showing inner lip margin—compare to Figures 24 and 43, paratype, UCLA 59633 from CIT loc. 1017; 34, paratype, UCLA 59621 from CIT loc. 1016; 35, juvenile, paratype, UCLA 59614 from CIT loc. 1246, ×3; 36, 38, paratype, UCLA 59609 from UCLA loc. 3298; 37, paratype, UCLA 59623 from UCLA loc. 3624; 39, paratype, UCLA 59621 from CIT loc. 1016; 40, 41, hypotype, UCLA 59639 from UCLA loc. 4217. Figures 42–61, *Perissitys brevirostris* (Gabb, 1864), hypotypes; 42, 44, early Campanian, juvenile with complete anterior canal, UCLA 59649 from UCLA loc. 3637, ×1.5; 43, typical earliest Campanian profile resembling that of *P. elaphia*, UCLA 59648 from UCLA loc. 3637; 45–47, specimen figured by Stanton, 1896, USNM 21254 from near Pentz; 48–50, UCBMP 11069 from near Pentz; 51–53, LACMIP 7247 from UCLA loc. 3641; 54, 56, LACMIP 7248 from UCLA loc. 3643; 55, 59, 60, UCLA 59661 from CIT loc. 1400, 60, ×2; 57, 58, topotype, UCLA 59666, from UCLA loc. 4082; 61, mid Campanian form intermediate to *P. pacifica*, UCLA 28715 from CIT loc. 1158.

yokoyamai from the Dobbins Shale on Sand Creek (area 21) are below Chron 33r and of Santonian age (Ward et al., 1983); but in the Nanaimo Basin they occur with *P. brevirostris* and are undoubtedly of Campanian age. Early *P. brevirostris* occurs with *Baculites chicoensis* and *C. yokoyamai* within the early Campanian Chron 33r on Chico Creek (area 5); on Mill and Antelope creeks (area 2) *P. elaphia* similar to those of the *Baculites capensis* Zone on Chico Creek occurs in the *I. schmidti* Zone. Although *I. schmidti* Michael, 1899, has not yet been recognized in the Chico Creek section, other species that occur with it of both late Santonian and early Campanian age are present there, and the absence of *I. schmidti* is more probably a result of deposition in shallow water rather than indicative of a hiatus in the section.

If the late Santonian zones of *Bostrychoceras elongatum* and *Inoceramus schmidti* are missing from the Chico Creek section the evolution of *P. elaphia* must be more rapid in the early Santonian and slower in the late Santonian. *I. schmidti*, however, ranges from late Santonian through early Campanian (Haggart, 1984); its absence in the Chico Creek section may be related to ecologic factors rather than complete absence of strata of appropriate age, and the morphologic changes in *P. elaphia* were developed through the entire Santonian.

This species differs from *P. cretacea* in its more pyriform shape, expanded inner lip callus which covers the apertural face of the last whorl, and in typically having three denticles at the periphery on the outer lip. Although the growth line on the whorl has an antispiral sinus similar to that of *P. cretacea*, the edge of the outer lip is straightened by callus adapical to the periphery and the outer lip of *P. elaphia* has a straighter profile than that of *P. cretacea*. *P. elaphia* differs from *P. brevirostris* in having a weaker sutural welt which is not noded, denticulations in the aperture, and a more bent siphonal canal.

Pyropsis sp. indet. (Nagao, 1939, p. 228, pl. 2, figs. 5, 5a-b) is similar in shape to *Perissitys elaphia*, and the growth line description is similar, but no columellar pseudofolds or outer lip denticulations are mentioned. The specimen is small and "imperfect" (Nagao, 1939, p. 228) and may not yet have formed the characteristic structures. *Pyropsis* sp. indet. is probably a *Perissitys* new species; it is said to have about ten peripheral nodes whereas *Perissitys elaphia* has 11 to 14.

ETYMOLOGY. *Elaphos*, Greek, deer or stag, for its occurrence in the Musty Buck Member of the Chico Formation.

Perissitys brevirostris (Gabb, 1864)

Figures 10, 11, 42-61

Perissolax brevirostris Gabb, 1864, p. 91, pl. 18, fig. 43; Tryon, 1881, p. 104, pl. 30, fig. 67; Stanton, 1896, p. 1047, pl. 67, fig. 4; Whiteaves, 1903, p. 356, pl. 43, fig. 3; Arnold, 1909, p. 104, pl. 1, fig. 2; Grabau and Shimer, 1909, p. 769, fig. 1119; Arnold and Anderson, 1910, p. 274, pl. 23, fig. 2.

Tudicla (Perissolax) brevirostris (Gabb): Tryon, 1883, p. 141, pl. 51, fig. 59.

Tudicula (Perissolax) brevirostris (Gabb): Cossmann, 1901, p. 71, text-fig. 21.

Perissitys brevirostris (Gabb): Stewart, 1927, p. 426, pl. 20, fig. 4; Schenck and Keen, 1940, pl. 17, fig. 5; Popenoe, 1954, p. 17, fig. 4(5); Popenoe, 1973, p. 20, pl. 2, fig. 16; Saul and Alderson, 1981, p. 36, pl. 3, fig. 5.

Tudicla (Perissitys) brevirostris (Gabb): Wenz, 1943, p. 1304, abb. 3718.

Not *Perissitys brevirostris* (Gabb): Sundberg and Riney, 1984, p. 105, fig. 3.3 = *Murphitys madonna* new species.

DIAGNOSIS. Pyriform *Perissitys* with three strong spiral ribs about the periphery, a noded subsutural welt, inner lip expanded to cover all of the apertural face of the shell, and no apertural ornaments.

DESCRIPTION. Shell of medium to moderately large size, pyriform; spire about one-fifth of the height of the shell, comprised of 1.5 to 2 smooth, globose nuclear whorls, succeeded by 2-4 gently concave whorls, nearly three times as wide as high; last whorl about half of the shell height, having a noded, tumid band just below the suture, a concave ramp, a rounded periphery accentuated by three strong spiral ribs, and contracting abruptly to form anterior siphonal canal; anterior siphonal canal at least as long as the eye-shaped aperture, curving slightly to the left (apertural view); suture at the adapical strong rib.

Sculpture on noded subsutural welt of fine spiral threads, on margin of ramp of very fine distant spiral threads, mid ramp nearly smooth; strong ribs of periphery subequal, two adapical ribs equal and stronger, third (abapical) rib closer to second rib than second is to first; ribs made nodular by about 13 strong short axial ribs, interspaces of strong spiral ribs having fine threads; base of whorl with about four riblets; siphonal neck with faint distant spiral threads.

Outer lip nearly straight, with slight antisprial sinus and spiral antisinus, barely thickened; inner lip callus expanding up onto spire and covering most of apertural face of shell and lapping onto abapertural surface of siphonal neck. Aperture without denticles or pseudofolds.

HOLOTYPE. ANSP 4188 (Stewart, 1927, p. 426).

HYPOTYPES. USNM 21254 and UCBMP 11069 from near Pentz, Butte Co. (area 5); CGS 5792 from Sucia Island, Washington (area 18); UCLA 28715 from CIT loc. 1158, Bell Canyon (area 17), 59648-59649 from UCLA loc. 3637, Chico Creek (area 5), 59661 from CIT loc. 1400, Sucia Island (area 18), and 59666 from UCLA 4082, Tuscan Springs (area 2); LACMIP 7247 from UCLA loc. 3641, and 7248 from UCLA loc. 3643, both Chico Creek (area 5).

DIMENSIONS. Of hypotypes—UCBMP 11069, height 47 mm, diameter 30.3 mm, height of spire 10 mm; LACMIP 7247, height 33.7 mm, diameter 20.4 mm, height of spire 6 mm; LACMIP 7248, height 40 mm, diameter 27.2 mm, height of spire 8.6 mm; UCLA 59661, height 22 mm (incomplete), diameter 17.3 mm, height of spire 6 mm; UCLA 28715, height 41.5 mm, diameter 30.8 mm, height of spire 9.8 mm.

TYPE LOCALITY. Tuscan Springs, Tehama Co., California (area 2).

DISTRIBUTION. Chico Formation at Tuscan Springs (area 2); associated with *Submortoniceras chicoense* (Trask) in the Ten Mile Member, Chico Formation on Chico Creek and Butte Creek (area 5), and the Chico Formation at Pentz Ranch (area 5); upper Holz Shale Member of the Ladd Formation, Santa Ana Mountains (area 13); found below and with *Hoplitoplacenticeras vancouverense* (Meek) in the Cedar District Formation on Sucia Island (area 18); and in the upper *Inoceramus schmidti* Zone of the Haslam Formation at Blunden Point, on Brannan Creek, and the north shore of Departure Bay (area 3). Specimens from the lower Chatsworth Formation in Bell Canyon (area 17) are intermediate between *P. brevirostris* and *P. pacifica*.

GEOLOGIC AGE. Early and mid Campanian.

REMARKS. This is the most abundantly represented and most widely distributed species of *Perissitys*. The largest of the more than 100 specimens at hand is UCLA 59658 from UCLA loc. 3647, which despite lacking most of the shell on the last whorl, has a diameter of 44.6 mm. *Pyropsis* sp. indet. of Nagao (1939, p. 228, pl. 21, fig. 5-5b), which is of Coniacian or Santonian age (Hayami and Kase, 1977, p. 65), appears similar in shape to *P. brevirostris*, but, except that the inner lip is said to be expanded, the aperture is not described. The Alaskan specimens from the Chignik Formation listed as *Perissolax brevirostris* Gabb by Martin (1926, p. 304) are neither *brevirostris* nor *Perissitys*. Although they have a pyriform shape similar to *P. brevirostris*, they have a fold on the columella and other apertural denticulations, and they lack the widely expanded inner lip of *P. brevirostris*. They are described as *Christitys martini* new species.

The cowl of callus in *P. brevirostris* is usually deposited at intervals and its development probably records the onset of resting or non-growth periods, and, as it can be seen on the spire (Figures 55, 59), it is an inner lip equivalent of a varix. There is no apparent regularity to these growth halts.

Perissitys brevirostris remains a recognized taxon through a longer time (6 ± 1 Ma) than any other species of *Perissitys*, and its evolutionary changes are more subtle than those of its predecessor, *P. elaphia*. *P. brevirostris* differs from late *P. elaphia* in reaching a larger size, having the siphonal neck smoother and the subsutural welt more swollen and nodular, and in having a straighter anterior canal. The parietal lip is more expanded, but its margin is less distinct. No specimen assigned to *P. brevirostris* has denticulations or pseudofolds arming the aperture. In reducing apertural armaments Campanian *Perissitys* moves contrary to the apertural strengthening trend noted by Vermeij (1977), which he suggests helps to reduce shell breakage by arthropods. The enlargement of the callus to cover the apertural face may strengthen the shell, but it leaves the outer lip and at least half of the last whorl undefended. The callus becomes thicker and more enveloping in *P. pacifica*. *P. pacifica* and *P. brevirostris* are alike in providing the largest available specimens of *Perissitys*. In addition to the thicker callus, *P. pacifica* differs from *P. brevirostris* in having the three strong peripheral ribs closer together, the middle rib strongest and the apical rib weakest, and in having a better developed posterior siphonal notch.

Specimens identified as *P. cf. P. brevirostris* (Figure 43)

from the lower 100 m of the Ten Mile Member on Chico Creek (area 5) have a higher spire and more concave ramp than typical *P. brevirostris*. They are similar to the latest *P. elaphia* except for the apertural armaments. A specimen from UCLA loc. 3635, which is at the base of this interval, has a low pseudofold on the columella like that of the specimen (CAS 31325.01) from CAS loc. 31325, Buckeye Creek, Rumsey Hills (area 21). Specimens of *P. cf. P. brevirostris* from above the base of this 100-m interval have no pseudofolds.

Ammonites have not been found associated with *P. brevirostris* at its type locality at Tuscan Springs (area 2). The specimens of *P. brevirostris* from there resemble those from Pentz (area 5), where *Submortoniceras chicoense* is common and from the upper 500 m of the Chico Formation on Chico Creek (area 5). Outcrops of the Chatsworth Formation in Bell Canyon, Simi Hills (area 17), are believed (Saul and Alderson, 1981; Saul, 1983) to be older than the zone of *Metaplacenticeras pacificum*. *Perissitys* from Bell Canyon are intermediate between *P. brevirostris* and *P. pacifica* (Figure 61).

Perissitys pacifica new species

Figures 62–69

DIAGNOSIS. Pyriform *Perissitys* which have two strong and one weak spiral ribs about the periphery, a waved subsutural welt, the inner lip expanded to cover about half of the shell, and no apertural ornaments.

DESCRIPTION. Shell of medium to moderately large size, pyriform; spire about one-fifth of the height of the shell, comprised of 1.5 to 2 smooth, globose nuclear whorls, succeeded by 2–4 gently concave whorls more than three times as wide as high; last whorl about half of shell height, having a waved, tumid band adjacent to the suture, a concave ramp, and subangulate periphery accentuated by two strong and one weaker spiral ribs, contracting abruptly to form anterior siphonal canal; anterior siphonal canal slightly longer than the eye-shaped aperture, curving slightly to the left (apertural view) and abaperturally; suture at the adapical strong rib.

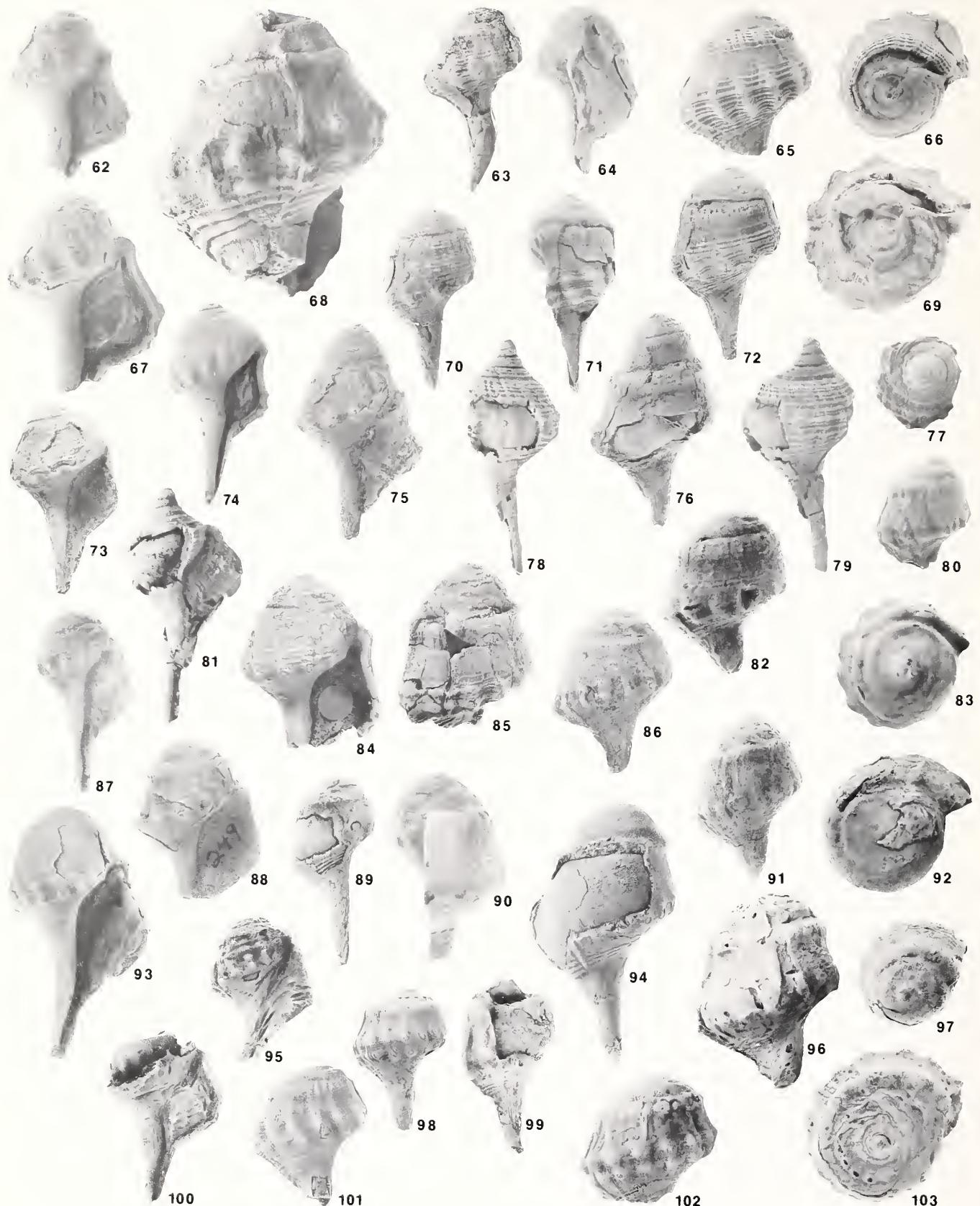
Sculpture on waved sutural welt of about five close-set spiral riblets, on ramp of distant spiral threads; peripheral spiral ribs made nodular by 12–13 strong, very short axial ribs, interspaces of peripheral spiral ribs having riblets; base of whorl with about four spiral riblets; siphonal neck with distant spiral threads.

Outer lip nearly straight with a slight posterior siphonal sinus at the sutural welt, a faint antiparallel sinus and spiral antisinus at the periphery, edge thickened by callus which coats a narrow strip of the outside of the whorl, expands up over the spire, and covers the apertural face of the whorl. Aperture without denticles or pseudofolds.

HOLOTYPE. UCLA 59691.

PARATYPES. UCLA 59692 from CIT loc. 1159; 59696–59698 from CIT loc. 974; 59712 from UCLA loc. 4207; 59715 from UCLA loc. 2415; 59719 from UCLA loc. 7110.

DIMENSIONS. Of holotype—height 30.5 mm (incomplete), diameter 24.4 mm, height of spire 6.5 mm; of paratype—UCLA 59719, height 33.8 mm, diameter 19 mm (in-



complete), height of spire 5.5 mm; UCLA 59696—height 36.5 mm (incomplete), diameter 29.5 mm, height of spire 9 mm.

TYPE LOCALITY. CIT loc. 1159, Dayton Canyon, Simi Hills, Los Angeles Co., California (area 17).

DISTRIBUTION. Associated with *Metaplacenticeras* cf. *M. pacificum* (Smith) in the Pleasants Sandstone Member of the Williams Formation, Santa Ana Mountains (area 13); the Chatsworth Formation in Dayton Canyon, Simi Hills (area 17); and the Tuna Canyon Formation in the Santa Monica Mountains (area 16). Also collected from near the top of the Debris Dam Sandstone, Agua Caliente Canyon (area 1), and an unnamed formation on the Salsipuedes arm of Santa Margarita Lake (area 15).

GEOLOGIC AGE. Late Campanian, *Metaplacenticeras pacificum* Zone.

REMARKS. A greater length of anterior siphonal canal is present on the specimen (Figure 63) from Garapito Creek, Santa Monica Mountains (area 16) than on any of the other 50+ available specimens.

The largest specimen, UCLA 59715 from UCLA loc. 2415, has a diameter of 51.5 mm. *P. pacifica* is very similar to *P. brevirostris* in shape and sculpture. It has a shorter, more callus-covered spire; the peripheral ribs are closer together; the subsutural welt is waved rather than noded; and the posterior siphonal notch is better developed. Steinkerns of the two species can be distinguished even if most of the shell is missing; those of *P. brevirostris* have a roundly convex profile, whereas those of *P. pacifica* are flattened to slightly concave adapical to the more angulate periphery. Some specimens of *P. pacifica* have less prominent peripheral nodes and are closer to *P. colocara* than to *P. brevirostris*.

ETYMOLOGY. *Pacifica*, for its occurrence in the *Metaplacenticeras pacificum* Zone.

Perissitys colocara new species

Figures 70–86

Cophocara n.sp. Popenoe, 1973, p. 24, fig. 39; Saul and Alderson, 1981, p. 36, pl. 3, figs. 6, 7; Sundberg and Riney, 1984, p. 105, fig. 3.1.

←

Figures 62–103. Four species of *Perissitys*: *P. pacifica* new species, *P. colocara* new species, *P. stantoni* (Stewart), and *P. stewarti* (Zinsmeister). All figures ×1 unless otherwise noted. Photos 72, 74–76, 84, 85, 88, 93, 94 by T. Susuki. As nearly as possible, the figures are arranged from geologically oldest to youngest. Figures 62–69, *P. pacifica* new species, late Campanian; 62, 64, holotype, UCLA 59691 from CIT loc. 1159; 63, paratype, UCLA 59719 from UCLA loc. 7110; 65, 66, paratype, UCLA 59712 from UCLA loc. 4207, ×1.5; 67, 69, paratype, UCLA 59696 from CIT loc. 974; 68, paratype, UCLA 59715 from UCLA loc. 2415. Figures 70–86, *P. colocara* new species, early Maastrichtian; 70, paratype, LACMIP 7252 from UCLA loc. 6534; 71, 74, holotype, LACMIP 7249 from LACMIP loc. 7962; 72, 73, paratype, UCLA 59082 from UCLA loc. 6534; 75, 76, paratype, LACMIP 7250 from UCLA loc. 6534; 77, juvenile with protoconch, paratype, LACMIP 7254 from LACMIP loc. 7792, ×4; 78, 79, 81, juvenile with protoconch, paratype, LACMIP 7253 from LACMIP loc. 7792, ×2.5; 80, 83, paratype, LACMIP 7255 from UCLA loc. 7149, 83, ×1.5; 82, paratype, CAS 463.01 from CAS loc. 463, ×1.5; 84, 85, paratype, LACMIP 7256 from UCLA loc. 3268; 86, hypotype, UCBMP 37992 from UCB loc. A-6618. Figures 87–95, *P. stantoni* (Stewart), hypotypes, late Maastrichtian; 87, 89, LACMIP 7259 from CIT loc. 1602; 88, UCBMP 37994 from UCB loc. 249; 90, 92, USNM 400974 from USGS loc. 7059; 91, UCBMP 37995 from UCB loc. A-3216; 93, 94, LACMIP 7258 from CIT loc. 1602; 95, LACMIP 7260 from UCLA loc. 1594. Figures 96–103, *P. stewarti* (Zinsmeister), hypotypes, early Paleocene; 96, UCBMP 37996 from UCB loc. A-3262; 97, 101, CAS 61617.01 from LSJU loc. I068, ×1.5; 98, 103, CAS 61619.01 from LSJU loc. 2245, 103, ×1.5; 99, 100, CAS 61616.01 from LSJU loc. 460; 102, CAS 61616.02 from LSJU loc. 460.

DIAGNOSIS. Pyriform *Perissitys* which have two to three closely spaced spiral ribs about the periphery, a strong wrinkled subsutural welt, inner lip expanded to cover at least two-thirds of the shell, and no apertural ornaments.

DESCRIPTION. Shell of medium to moderately large size, pyriform; spire variable but usually less than one-fourth of height to shell, comprised of 2–3 globose, smooth nuclear whorls, succeeded by two convexly rounded whorls commonly four times as wide as high, followed by 1–2 barely concave whorls of similar height to width, all callus coated; last whorl constituting half of shell height, having a tumid band just below the suture, a slight concavity to the ramp profile adjacent to the tumid band, and broadly expanded, subangulate periphery accentuated by 2–3 spiral ribs, contracting abruptly to form anterior siphonal canal; anterior siphonal canal longer than the triangulate aperture; suture adapical to the peripheral ribs, just abapical to the slight concavity of the ramp.

Sculpture on sutural welt of 2–5 spiral riblets, on ramp of distant spiral threads; peripheral spiral ribs made nodular by 10–14, extremely short, axial ribs; base of whorl commonly with four fine spiral riblets; siphonal neck with distant fine spiral threads.

Outer lip with posterior siphonal notch at the sutural welt, a slight antipiral sinus just adapical to the periphery and spiral antisinus at the periphery, edge slightly thickened by callus which covers at least two-thirds of the shell. Aperture without denticles or pseudofolds.

HOLOTYPE. LACMIP 7249.

PARATYPES. UCLA 59082 from UCLA loc. 6534, 59217 from UCLA loc. 3814; LACMIP 7253–7254 from LACMIP loc. 7792, 7256 from UCLA loc. 3268, 7250–7252 from UCLA loc. 6534, 7255 from UCLA loc. 7149, and 7257 from LACMIP loc. 2852; UCBMP 37992 from UCB loc. A-6618, 37993 from UCB loc. B-5321; and CAS 463.01 from CAS loc. 463.

DIMENSIONS. Of holotype—LACMIP 7249, height 36.7 mm, diameter 19 mm, height of spire 8 mm; of paratypes—LACMIP 7250, height 38.4 mm, diameter 24.8 mm, height of spire 12.3 mm; UCLA 59082, height 23.8 mm, diameter 14.3 mm, height of spire 5.6 mm; LACMIP 7256, height

31.2 mm (incomplete), diameter 25.4 mm, height of spire 9.7 mm; LACMIP 7255, height 20 mm (incomplete), diameter 17 mm, height of spire 5 mm; CAS 463.01, height 20.7 mm, diameter 16.5 mm, height of spire 4.8 mm.

TYPE LOCALITY. LACMIP loc. 7962, Carlsbad Research Park, San Diego Co., California (area 20).

DISTRIBUTION. Rosario Formation in Arroyo Santa Catarina (area 14), at Punta San Jose (area 10), near San Antonio del Mar (area 12), at Point Loma (area 9), and vicinity of Carlsbad (area 20); Chatsworth Formation on Lang Ranch, Simi Hills (area 17); upper Panoche Formation north of Coalinga, Fresno Co. (area 8); "Moreno Grande" Formation of Huey (1948) on Ortigalita Creek, Merced Co. (area 8).

GEOLOGIC AGE. Early Maastrichtian.

REMARKS. The greatest abundance of this species is from localities in Arroyo Santa Catarina (area 14), but specimens are also common at UCLA loc. 5902 north of Coalinga (area 8). Most are small, but a few medium-sized specimens are available and a large partial specimen from UCB loc. A-6618 has a diameter of 33.7 mm.

The sculpture on the sutural welt and the ramp is subdued, but the callus coating is applied so as to accentuate the spiral threads and riblets and *P. colocara* appears to have stronger spiral sculpture than does *P. pacifica*. On many specimens such a thick welt of parietal callus is applied at the growth pauses that the spiral curve of the shell is offset. The specimens look lumpy and distorted. *P. colocara* is unusually variable for this group in height of spire and peripheral ribbing. A few specimens have a spire height closer to one-third of the height of the shell (Figures 75, 76) rather than the more common under one-fourth proportion. Some specimens have peripheral ribs similar to those of *P. pacifica*, but most have finer ribs, more closely spaced, similar to those of *P. stantoni*. *P. colocara* is more callus coated than is *P. pacifica* and a little less so than *P. stantoni*. The subsutural welt of *P. colocara* is stronger than that of *P. pacifica*, is adapical to the peripheral nodes and less undulating than that of *P. pacifica*. The suture on adult *P. colocara* is more deeply channeled than it is on *P. pacifica* or *P. stantoni*, and the whorl of *P. colocara* is more angulate than is that of *P. stantoni*.

ETYMOLOGY. *Kolos*, Greek, docked, curtailed, shortened, stunted, and *kara*, Greek, head, top, referring to the usually short spire of the species.

Perissitys stantoni (Stewart, 1927)

Figures 87–95

Cophocara stantoni Stewart, 1927, p. 428, pl. 20, figs. 1–3; Saul, 1986, p. 27, fig. 21.

Tudicla (Cophocara) stantoni (Stewart): Wenz, 1943, p. 1305, fig. 3719.

Not *Cophocara stantoni* Stewart: Smith, 1975, p. 475, pl. 2, figs. 17, 18 = *P. stewarti* (Zinsmeister).

DIAGNOSIS. Pyriform *Perissitys* with one dominant spiral rib about the periphery, a weakly noded subsutural welt, the shell well coated with callus except for last quarter of last whorl, and apertural ornaments lacking.

DESCRIPTION. Shell of medium to moderately large size, pyriform; spire about one-fifth of height of shell, comprised of 3–4 post-nuclear whorls about four times as wide as high, all callus coated; last whorl about half of shell height, having a tumid band adjacent to the suture, a slight concavity to the ramp profile adjacent to the tumid band, and an expanded, subangulate periphery accentuated by 1–3 spiral ribs of which one is dominant; whorl contracting abapically abruptly to form anterior siphonal canal; anterior siphonal canal nearly as long as eye-shaped aperture; suture just abapical to the slight concavity of the ramp.

Sculpture nearly obliterated by callus coating except on last quarter of last whorl; sutural welt of large specimens slightly nodulose; peripherally spiral ribs made nodular by 15–17 extremely short axial ribs; base of whorl with about three spiral riblets.

Outer lip with posterior siphonal notch at the sutural welt; growth line strongly bent at the posterior notch, otherwise straight; inner lip expanded to cover all but last quarter of last whorl. Aperture without denticles or pseudofolds.

HOLOTYPE. USNM 73399.

PARATYPES. USNM 73400 and 73403 from USGS loc. 1258; whereabouts of the ANSP specimen figured by Stewart (1927, pl. 20, fig. 2) from near Martinez, Contra Costa Co. (area 7), is unknown (Elana Banamy, *in litt.*, 17 Oct. 1985).

HYPOTYPES. USNM 400974 from USGS loc. 7059 (area 8); UCBMP 37994 from UCB loc. 249 (area 7) and 37995 from UCB loc. A-3216 (area 8); LACMIP 7258–7259 from CIT loc. 1602 (area 7), and 7260 from UCLA loc. 1594 (area 19).

DIMENSIONS. Of holotype—height 42.2 mm (incomplete), diameter 26 mm, height of spire 17.5 mm; of hypotypes—USNM 400974, height 34.6 mm (incomplete), diameter 27.4 mm, height of spire 7.5 mm; UCBMP (37994), height 30.5 mm (incomplete), diameter 24 mm, height of spire 8.7 mm; LACMIP 7258, height 47.3 mm, diameter 27 mm, height of spire 9 mm.

TYPE LOCALITY. USGS loc. 1258, near Blum and Company's Pacheco warehouse, 1½ mi. north of Pacheco, Contra Costa Co., California (area 7).

DISTRIBUTION. Near or at the top of the Great Valley Series in the vicinity of Martinez, Deer Valley, and Riggs Canyon (area 7); Garzas and Volta Sands near Pacheco Pass, Merced and Stanislaus cos. (area 8); Asuncion Formation on Cantinas Creek, southern Santa Lucia Range, San Luis Obispo Co. (area 15); basal San Francisquito Formation on Warm Springs Mountain (area 19).

GEOLOGIC AGE. Late Maastrichtian.

REMARKS. The type species of *Cophocara* Stewart, 1927, is *C. stantoni*. As the most notable difference between it and *Perissitys pacifica* is the thicker, more enveloping callus layer on *C. stantoni*, we include *stantoni* in *Perissitys*. *P. stantoni* has fewer and weaker spiral ribs, weaker nodes and thicker callus covering than any other described species of *Perissitys*. It is very similar to *P. colocara*, but has a less concave whorl profile abapical to the sutural welt and more rounded whorl profile abapical to the periphery, more and smaller nodes on the periphery, a more nodulose subsutural band, and better

developed posterior siphonal notch. Although a few specimens of *P. colocara* are large, the average size of the 40+ specimens studied of *P. stantoni* is about twice that for specimens of *P. colocara*, and the largest specimen recorded was one of Gabb's, which was a diameter of 36 mm (Stewart, 1927, p. 428).

The specimens from UCLA loc. 1594 on Warm Springs Mountain are poorly preserved. They resemble *P. stantoni*, but may have had a more tumid subsutural welt and a spiral row of nodes on the ramp (Figure 95).

Perissitys stewarti (Zinsmeister, 1983)

Figures 96–103

Cophocara stantoni Stewart: Smith, 1975, p. 465, pl. 2, figs. 17, 18. Not *Cophocara stantoni* Stewart, 1927.

Cophocara stewarti Zinsmeister, 1983, p. 1298, fig. 3J; not fig. 3K = "Heteroterna trochoidea" Gabb" of Nelson, 1925, non Gabb, 1869.

DIAGNOSIS. Pyriform *Perissitys* with two spiral ribs about the periphery, a nodulose subsutural welt, the inner lip expanded to cover nearly two-thirds of the shell, and no apertural ornaments.

HOLOTYPE. UCR 6670/9.

HYPOTYPES. CAS 61619.01 from LSJU loc. 2245, CAS 61616.01 and 61616.02 from LSJU loc. 460, and CAS 61617.01 from LSJU loc. 1068; UCBMP 37996 from UCB loc. A-3262.

DIMENSIONS. Of holotype—height 28 mm (incomplete), diameter 29 mm, height of spire 5 mm; of hypotypes—LSJU 10240, height 25.9 mm, diameter 19.3 mm, height of spire 4.3 mm; LSJU 10241, height 23 mm (incomplete), diameter 24.5 mm, height of spire 5.9 mm; CAS 61617.01, height 16.9 mm (incomplete), diameter 4 mm, height of spire 3 mm.

TYPE LOCALITY. UCR loc. 6670, Simi Hills, Ventura Co., California (area 17).

DISTRIBUTION. Lower Santa Susana Formation, Simi Hills (area 17) (Zinsmeister, 1983, p. 1298); near the base of the Laguna Seca Formation, Panoche Hills, Fresno Co. (area 8) (Smith, 1975, p. 468); San Francisquito Formation on north side of East Fork Fish Canyon (UCLA loc. 1581) (area 19); Sepultura Formation at Punta Canoas (UCLA loc. 6368) (area 14).

GEOLOGIC AGE. Early Paleocene, late *Turritella peninsularis quaylei* (area 19) and *T. peninsularis* zones (area 17). Specimens from near the base of the Laguna Seca Formation (area 8) may be older; they are probably below localities with *T. peninsularis*, but the available collections have no associated turritellas. Misidentified as *Cophocara stantoni*, *P. stewarti* has been used to indicate Cretaceous age. Some of the localities are recorded as being from the Moreno Formation, others as being from the Laguna Seca Formation. The formation name seems in some cases to have been chosen on a faunal rather than lithologic basis: Moreno, if the fossils were considered to indicate Cretaceous age, Laguna Seca (or equivalent), if a Paleocene age seemed

indicated. Plotted on a map, the purported younger locality may appear to be downsection from the older, and stratigraphic range of *P. stewarti* cannot be inferred.

REMARKS. The spire makes up one-seventh to one-eighth of the height of the shell. Post-nuclear whorls are about six times as wide as high, and all are callus coated; about half of shell height is the last whorl. The two strong peripheral spirals are made nodose by 14–17 extremely short, axial ribs; and the base of the whorl has 4–5 spiral riblets adjacent to the siphonal neck. The growth line is strongly bent at the posterior notch but is otherwise straight. The aperture is without denticles or pseudofolds. The anterior canal is straight except for a backward bend near its tip.

P. stewarti is the youngest recognized *Perissitys*. It has the shortest spire of known species, and were its ancestry unknown, its classification in the Tudiclididae (Zinsmeister, 1983, p. 1298) would be apt. *P. stewarti* is very similar to, and easily confused with, *P. stantoni*, but has a thinner, less extensive callus, more strongly marked varices, a deeper posterior siphonal notch, and stronger nodes on the subsutural band. The peripheral nodes are in two nearly equal rows, whereas *P. stantoni* has one dominant row. The anterior siphonal canal is much shorter and has a stronger backward flexure near its tip. A virtually shell-less specimen from UCB loc. A-3262 has a diameter of 26.2 mm and, with shell, would be larger than the holotype.

Perissitys stewarti resembles *Heteroterna trochoidea* Gabb, 1869, in its two spiral rows of nodes and short spire, but *H. trochoidea* lacks the callus coating over the shell, the strong rounded welt at the suture, and has a more sloping ramp. *P. stewarti* resembles *H. gabbi* Stanton, 1896, in whorl profile, but *H. gabbi* lacks the callus coating and has longer axial ribs crossed by several spiral ribs. *H. striata* Stanton, 1896, lacks the sutural welt and the callus coating and has at least four spiral ribs about the periphery.

Genus *Pseudocymia* new genus

TYPE SPECIES. *Pseudocymia aurora* new species.

DIAGNOSIS. Small to medium sized, shortly fusiform gastropods with shouldered whorls having a concave ramp and base straightly sloping into an anterior siphonal neck of short to moderate length which is bent to the left and abaperturally, and has near its anterior end a well-developed siphonal fasciole. The shell appears to be out-of-round, a little flattened aperture-to-back and expanded laterally. It is ornamented by narrow spiral ribs which override strong, short axial ribs. The axial ribs are most pronounced on the periphery. The spire is less than half of the total shell height. The aperture is elongate oval with well-demarcated inner lip and flaring outer lip. The inner lip has two pseudofolds near the base of the whorl and another near the posterior end of the aperture. The outer lip is thickened and denticulated with the strongest denticulations opposite the base of the whorl.

RANGE. Turonian to Maastrichtian.

DISCUSSION. This genus is based on *P. aurora* of Turonian age. It resembles species of *Columbellina* but lacks the marked, oblique posterior sinus in the outer lip. The outer

lip denticulations are, however, separated into posterior and medial sets by a groove similarly placed to that of *Columbellina*'s posterior sinus. *P. aurora* has a remarkable resemblance to *Cymia tecta* (Wood, 1828) of the modern Panamic fauna, but lacks the medial columellar fold of that species and is slightly compressed. The aperture-to-back flattening of the shells is suggestive of Cymatiidae and Bursidae. Another group in the Perissityidae which shares this characteristic is that of "Fusus" kingii Gabb. *Pseudocymia* is uniangulate about the periphery rather than distinctly biangulate as is the "Fusus" kingii group. *Pseudocymia* remains fusiform rather than becoming pyriform as do *Perissitys* and *Christitys*. It lacks the columellar folds of *Christitys* and *Murphyts*.

The genus is named for its resemblance to the type species of *Cymia*, *C. tecta* (Wood, 1828).

Pseudocymia aurora new species

Figures 104–108

DIAGNOSIS. Thick-shelled *Pseudocymia* with a broad apical angle and an outer lip that is considerably thickened and internally strongly lirate.

DESCRIPTION. Shell of medium size, broadly fusiform, rather massive, somewhat compressed aperture-to-back; spire of about four whorls, convex-conical in outline; apical angle approximately 60°; whorl outline subangular, shouldered just abapical to the middle, ramp gently concave; last whorl with a fairly broad, steeply sloping, slightly concave ramp adapical to the shoulder, abapical to which the whorl contracts evenly to the anterior end; suture linear, impressed, sinuous; siphonal fasciole well developed, rounded, enclosing a very shallow umbilical pit.

Spiral sculpture of the body whorl consisting of about 12 moderately strong revolving round-topped ridges below the whorl shoulder, and two or three much weaker spirals above the whorl shoulder, separated by interspaces somewhat wider than the spirals, and generally with two or three very fine revolving lirae in the interspaces; axial sculpture of about 12 blunt rounded ribs on the shoulder, obsolete or absent adapically and abapically.

Inner lip with a moderately thick callus coating, concave parietally, nearly straight anteriorly to the narrow and twisted canal, ornamented near the posterior suture with a pronounced rounded swelling bearing three or four transverse denticulations, and near its mid-length by two low rather distantly placed pseudofolds of which the posterior is slightly stronger; outer lip much thickened and bearing internally a series of strong transverse wrinkles which increase in size progressively from anterior end to whorl shoulder; outer lip rather deeply notched internally opposite the whorl shoulder, posterior to which two smaller wrinkles oppose the swelling on the inner lip and enclose adapically a narrow anal gutter at the juncture of the lips.

HOLOTYPE. UCLA 59586.

PARATYPE. UCLA 59587 from CIT loc. 1532, Salt Creek, Millville Quadrangle (area 11).

DIMENSIONS. Of holotype—height 37.5 mm; height of last whorl 25 mm; diameter 23.5 mm; height of spire 14.4 mm.

TYPE LOCALITY. CIT loc. 1212, Salt Creek, Millville Quadrangle, Shasta Co., California (area 11).

DISTRIBUTION. Represented by two specimens, both from the upper half of the Frazier Silt on Salt Creek, Shasta Co., California.

GEOLOGIC AGE. Late Turonian, horizon of *Subprionocyclus neptuni*, below occurrences of *Collignonceras* sp. (Jones et al., 1978, p. XXII.8, figs. 5, 6).

REMARKS. The holotype is a nearly perfect shell, and is remarkably modern looking for a Turonian gastropod. It is very similar in shape and sculpture to *Cymia tecta*, type species of *Cymia*, from which it differs chiefly in its circum-apertural denticulations and lack of the strong fold about midway of the inner lip. The sculpture of *P. aurora* resembles that of *Murphyts michaeli*. *M. michaeli* has a longer anterior canal which lacks the well-developed fasciole of *P. aurora*. Although the outer lip of *P. aurora* is thickened, it is not rimmed like that of *M. michaeli*.

ETYMOLOGY. *Aurora*, Latin, dawn, morning.

Pseudocymia(?) aitha new species

Figures 5, 109–112

DIAGNOSIS. Small *Pseudocymia(?)* with three strongest spiral ribs on the periphery, two of which are clearly evident on the spire. Within, the outer lip has three strong denticles near the periphery and small denticles near the anterior canal.

DESCRIPTION. Shell shortly fusiform, small; spire about half of height of shell, comprised of four post-nuclear whorls, each about twice as wide as high; apical angle approximately 42°; whorl outline angulate with shallowly concave ramp, peripheral angulation accentuated by three strong spiral ribs, base sloping straight to the anterior siphonal fasciole; anterior canal short, bent to the left and abaperturally; suture coincident with the abapical peripheral spiral cord.

Sculpture of narrow spiral ribs, weak posterior to the periphery, moderately strong on the periphery and base; interspaces wider than the ribs; peripheral spiral ribs made nodulous by about ten short but strong axial ribs.

Aperture broad posteriorly; outer lip expanded and thickened, with a posterior siphonal notch nearly midway between the suture and the periphery, bearing a posterior denticle just anterior to the siphonal notch, two strong denticles at the periphery, the posterior of which is the stronger, and three small denticles at anterior end of aperture; inner lip well marked, bearing two wrinkle-like denticles near anterior end of aperture, two pseudofolds anterior to the mid-point and three small denticles at beginning of anterior siphonal canal.

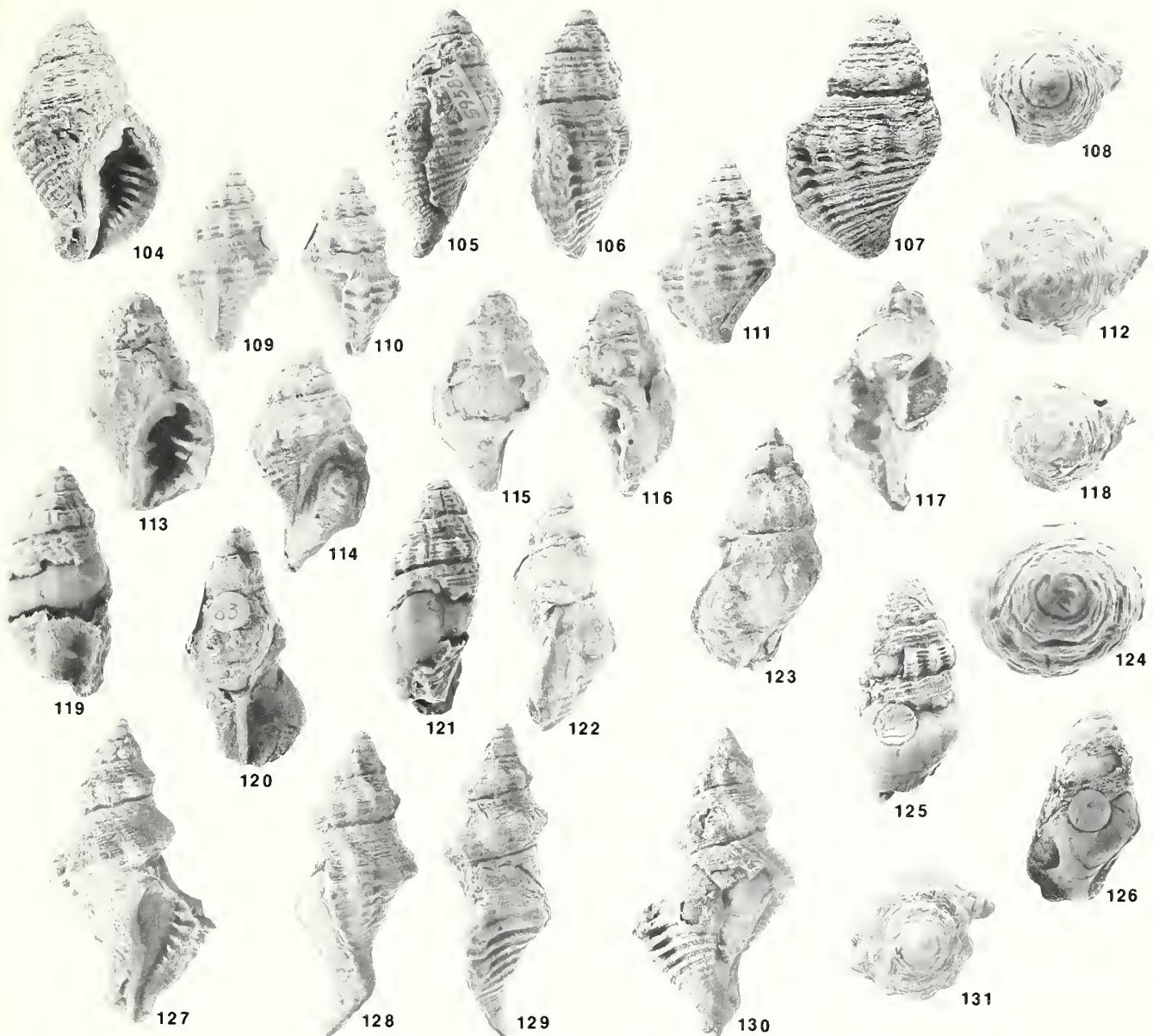
HOLOTYPE. UCLA 39440.

DIMENSIONS. Of holotype—height 28 mm (incomplete); diameter 18 mm; height of spire 14 mm.

TYPE LOCALITY. CIT loc. 1007, Oak Run, Millville Quadrangle, Shasta Co., California (area 11).

DISTRIBUTION. One specimen from Member IV of the Redding Formation in Oak Run, Millville Quadrangle (area 11) and a poorly preserved specimen from Member V, Bear Creek, Whitmore Quadrangle (area 11).

GEOLOGIC AGE. Coniacian.



Figures 104–131. Species of *Pseudocymia* new genus. All $\times 1$ unless otherwise noted. **Figures 104–108.** *Pseudocymia aurora* new species, Turonian, holotype, UCLA 59586 from CIT loc. 1212; 104 and 108 photos by T. Susuki. **Figures 109–112.** *Pseudocymia(?) aitha* new species, Coniacian, holotype, UCLA 39440 from CIT loc. 1007; 112, $\times 1.5$. **Figures 113–118.** *Pseudocymia(?) cf. P.(?) aitha* new species, Santonian, hypotypes, $\times 2$, from UCLA loc. 6496; 113, 115, 116, 118, LACMIP 7261; 114, 117, LACMIP 7262; 117, the back of the last whorl is broken off and the pseudofolds and median outer lip denticulation are visible. **Figures 119–126.** *Pseudocymia(?) cahalli* new species, Campanian; 119, 121, 124, 125, the anterior canal is broken off and the outer lip is crushed, holotype, LACMIP 7263 from UCLA 2324; 124, $\times 1.5$; 120, 122, 123, paratype, UCLA 39473 from CIT loc. 83; a badly leached shell preserving only remnants of sculpture but more of the anterior canal including part of the anterior siphonal fasciole, breakage of the posterior end of the outer lip gives a false impression of its posterior outline; 126, paratype, CAS 61618.01 from LSJU loc. 1860 with posterior end of outer lip preserved. **Figures 127–131.** *Pseudocymia(?) kilmeri* new species, early Maastrichtian, holotype, UCBMP 37997 from UCB loc. B-5323, edge of outer lip broken posterior to the periphery.

REMARKS. The holotype is well preserved and nearly complete, lacking part of the nucleus and the anterior end of the anterior siphonal canal. Although the growth line has an antispiral sinus, this sinus is not as sharply bent and deep as the posterior siphonal notch suggests that it should be. The

notch may, therefore, have been deepened by an injury, and so definite a notch may not be characteristic of the species. Despite this deeper siphonal notch and the less fortified aperture, the species is included in *Pseudocymia* because of its overall shape and well-developed anterior fasciole.

Pseudocymia(?) aitha differs from *P. aurora* in its more angulate whorl profile, slightly more concave ramp, and fewer denticles on the outer lip. It is very similar to *Perissitys cretacea*, from which it differs in being less expanded about the periphery, having slightly stronger and fewer spiral ribs and longer axial ribs, more than one median denticle on the outer lip, and the most posterior portion of the inner lip abapical to the peripheral spirals rather than lapping over them.

ETYMOLOGY. *Aitha*, Greek, burnt, fiery, reddish-brown, for its occurrence near Redding, California.

Pseudocymia(?) cf. P.(?) aitha new species

Figures 113–118

HYPOTYPES. LACMIP 7261–7262 from UCLA loc. 6496.

DIMENSIONS. Of LACMIP 7261—height 16.8 mm, diameter 9.6 mm, height of spire 7 mm; of LACMIP 7262—height 17.4 mm, diameter 10 mm, height of spire 7 mm; both specimens are incomplete.

DISTRIBUTION. Two specimens from the Panoche Formation, Howard Ranch Quadrangle, Merced Co., California (area 8).

GEOLOGIC AGE. Santonian.

REMARKS. Two small incomplete specimens resemble *P.(?) aitha*, but are slightly more slender, have a less angulate whorl profile, and one or two more axial ribs per whorl. The posterior section of the outer lip is sulcate, but the notch is broader than that of *P.(?) aitha*. As in *P.(?) aitha* there is a posterior denticle just anterior to the siphonal notch and two strong denticles at the periphery, the posterior of which is stronger. These specimens are superficially similar to *M. michaeli*, but they are more slender, have fewer axial ribs per whorl, and the denticles on the outer lip are placed as in *P.(?) aitha*.

Pseudocymia(?) cahalli new species

Figures 119–126

DIAGNOSIS. Elongate *Pseudocymia(?)* with the outer lip ornamented by two strong denticles at the periphery, a posterior denticle of moderate size and small denticles near the anterior siphon.

DESCRIPTION. Shell of medium size, fusiform; spire of about five post-nuclear whorls, each about twice as wide as high; apical angle approximately 30°; whorl outline subangular with shallowly concave ramp, peripheral angulation accentuated by short axial ribs; suture just abapical to the periphery.

Sculpture of narrow subequal spiral ribs; interspaces wider than the ribs; periphery made nodulose by about ten short but strong axial ribs.

Aperture widest posteriorly; outer lip expanded and thickened by varix, bearing a pair of strong denticles opposite the periphery, a posterior denticle, and at least two smaller ones near the anterior siphon; inner lip of moderate width, thick, with a strong pseudofold opposite the periphery, a lesser one

near the anterior siphon, one or two denticles at the anterior siphon, and one or two denticles near the posterior end.

HOLOTYPE. LACMIP 7263.

PARATYPES. UCLA 39473 from CIT loc. 83 and CAS 61618.01 from LSJU loc. 1860.

DIMENSIONS. Of holotype—height 35.7 mm (incomplete); maximum diameter 18.3 mm (incomplete); height of spire 17 mm.

TYPE LOCALITY. UCLA loc. 2324, Santa Ana Mountains, Orange Co., California (area 13).

DISTRIBUTION. Cedar District Formation, Sucia Island (area 18); and uppermost Holz Shale Member of Ladd Formation, Santa Ana Mountains (area 13).

GEOLOGIC AGE. Mid Campanian.

REMARKS. The above description is based upon three incomplete specimens; one from Sucia Island and two from the Santa Ana Mountains. None of the specimens retains the anterior siphonal canal, but there is an indication of a well-developed siphonal fasciole. The spiral ribs appear to be strongest anterior to the periphery. The short axial ribs are most numerous on the spire (about 14) but are reduced to about ten stronger ones on the ultimate whorl. The outer lip is poorly preserved on a paratype (UCLA 39473). Denticles within the outer lip are described from impressions on the infilling of the holotype and the second paratype (CAS 61618.01).

P.(?) cahalli is most similar to *P.(?) kilmeri*, from which it differs in having a less strongly angulate whorl profile, the suture closer to the noded periphery, and stronger pseudofolds on the columella.

ETYMOLOGY. The species is named for C.A. Hall.

Pseudocymia(?) kilmeri new species

Figures 127–131

DIAGNOSIS. Elongate *Pseudocymia(?)* expanded peripherally and contracted suturally, with six evenly spaced linear denticles within the outer lip between the periphery and the anterior canal. There are two weak pseudofolds on the columella.

DESCRIPTION. Shell medium sized, subfusiform with backward flexed short open anterior canal and small pseudoumbilicus; spire almost half of height of shell, comprised of five post-nuclear whorls, each about twice as wide as high; apical angle approximately 38°; profile of last three whorls concave adapical to the periphery, prior whorls convex; base sloping straight into constriction adapical to the siphonal fasciole; suture abapical to the periphery; shell broadened by indistinct varices at about 180°.

Overall sculpture of spiral riblets strongest on the peripheral angulation, progressively weaker from periphery to both sutures with weakest riblets on the sutural ramp and three or four strongest on the angulation, one to three threads between the riblets; about ten axially elongated nodes per whorl on the periphery; suture on fourth abapical strong rib.

Aperture widest posteriorly; outer lip thickened by varix, expanded medially, and bearing a strong denticle plus one or two smaller ones near the posterior end, two strong den-

ticles at the periphery and four of decreasing strength anteriorly; inner lip of moderate width and thickness with small denticles bordering the posterior notch, two faint pseudofolds just anterior to the midpoint and a low welt near the anterior end.

HOLOTYPE. UCBMP 37997.

DIMENSIONS. Height 47.4 mm; diameter 24.9 mm; height of spire 22.4 mm; height of penultimate whorl 10.3 mm; diameter of penultimate whorl 16 mm.

TYPE LOCALITY. UCB loc. B-5323: Punta San Jose, Baja California (area 10).

DISTRIBUTION. Rosario Formation, Punta San Jose (area 10).

GEOLOGIC AGE. Early Maastrichtian.

REMARKS. The above description is based upon the only known specimen, the nearly complete holotype. The outer lip is broken along the sutural ramp; the tip of the anterior canal is chipped; some shell is missing from the back of the body whorl, and the apex is eroded.

P.(?) kilmeri has much more subdued apertural ornament than *P. aurora*, but the denticulations are similarly placed. *P.(?) kilmeri* is also much more elongate, has a more fusiform shape, and slightly longer anterior canal. In sculpture and shape of base it resembles *P.(?) aitha*, but it is also more fusiform than *P.(?) aitha*, has a more abapical suture, and has stronger spiral ribs adapically to the three prominent ones on the periphery.

In shape and sculpture *P.(?) kilmeri* bears a strong resemblance to *Solenosteira* spp., especially *S. gatesi* Berry, 1963, of the modern Panamic fauna. It differs from *S. gatesi* most notably in the flare of its outer lip and the strength of the denticles within.

ETYMOLOGY. The species is named for F.H. Kilmer who collected the holotype at Punta San Jose, Baja California, Mexico.

Genus *Murphitys* new genus

TYPE SPECIES. *Murphitys michaeli* new species.

DIAGNOSIS. Plumply bucciniform gastropods of small to medium size which have a rounded to doubly subangulate whorl profile. Whorls are ornamented by spiral ribs, two of which predominate, and short axial ribs. Outer lip expanded to form a rim which is thickened at its edge and has posterior, medial, and anterior denticles within. Parietal lip is roundly expanded. Columella has two folds. Anterior canal is moderately long, slightly curved, and has a fasciole near its tip.

DISCUSSION. Characteristic of this genus is the rimmed outer lip with its inner surface rolled outward. The parietal lip is roundly expanded, although that of the earliest species, *M. michaeli*, is only slightly more expanded than the parietal lip of *Perissitys cretacea* or *Pseudocymia aurora*, both of which it resembles in shape and sculpture. The parietal lip is more roundly expanded in later species of *Murphitys* but is not as expansive as the parietal lip of *Perissitys* spp. *Murphitys* differs from *Perissitys* and *Pseudocymia* in having folds on the columella. The folds are faint on *M. michaeli* but

become strong on *M. madonna*. Additional trends in this lineage lead to the loss of the posterior sinus on the outer lip and to a more angulate whorl profile.

The illustration of *Fusus* (s.l.) *volutodermoides* Nagao, 1939 (p. 231, pl. XXII, fig. 5) from the upper Yezo Group, Abeshinai, Teshio Prov., Japan, resembles *M. michaeli*, but that species is described as having a smooth columella.

RANGE. Coniacian to early Maastrichtian.

ETYMOLOGY. The name is a compound of Murphy (for M.A. Murphy) and *itys*, Greek, rim or felly of a wheel.

Murphitys michaeli new species

Figures 9, 132-147

DIAGNOSIS. Small *Murphitys* which have a rounded whorl profile and peripheral spirals that are scarcely stronger than the other spirals. The outer lip bears a strong medial denticulation. The two columellar folds are, although distinct, not strong.

DESCRIPTION. Shell small, bucciniform; spire about one-third of total shell height, consisting of about five whorls including a smooth mammillate protoconch of one whorl succeeded by whorl sculptured by raised spiral threads and axial ribs; all whorls roundly convex; base of whorl narrowing to form a sturdy anterior siphonal canal of moderate length and twisted to the left (apertural view) and backward at its tip; suture adapical to the whorl mid-point.

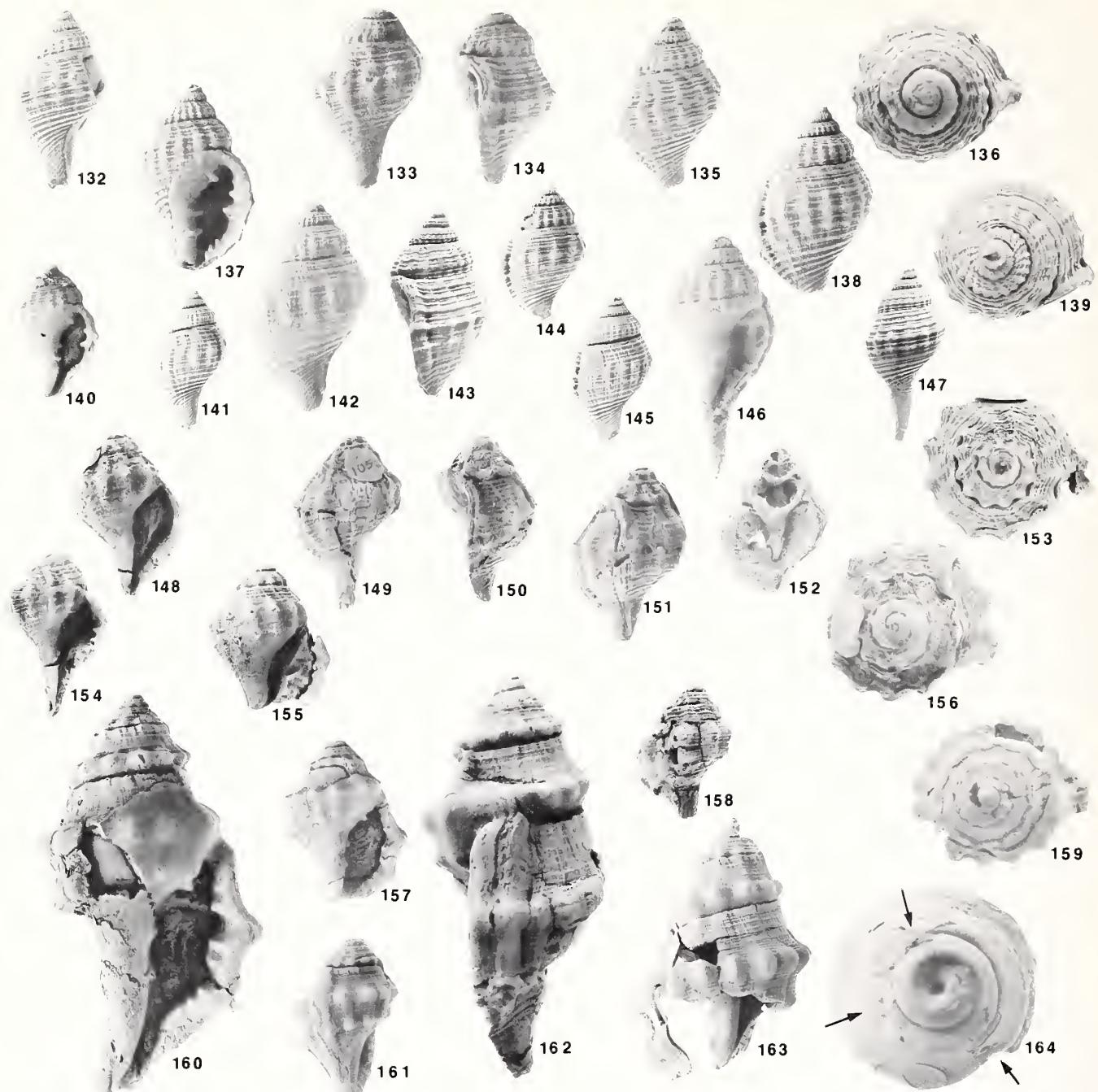
Sculpture of alternating spiral ribs and threads with inter-spaces usually a little wider than the ribs; two or three peripheral ribs slightly stronger and the suture on the most anterior of these; spiral sculpture undulated by arcuate colabral ribs which decrease in number to about 15 and in regularity and strength on the last whorl.

Outer lip thickened and slightly expanded to form a rimmed aperture with shallow antispiral sinus adapical to the periphery and slight spiral antisinus anterior to the periphery; inner lip fairly broad and thin, parietal portion roundly expanded onto the body whorl. Outer lip with two posterior denticles, a strong medial denticle and a clump of small denticles just posterior to the anterior canal; inner lip with a posterior denticle and two folds, the posterior one opposite the strong median denticle of the outer lip and the anterior one just posterior to the clump of outer lip denticles; an additional denticle sometimes present at the posterior end of the anterior canal.

HOLOTYPE. LACMIP 7264.

PARATYPES. LACMIP 7265-7269 from UCLA loc. 4106, 7270 from CIT loc. 1247, and 7271-7272 from CIT loc. 1230.

DIMENSIONS. Of holotype—height 19.7 mm, diameter 13.0 mm, height of spire 7.7 mm; of paratypes—LACMIP 7265, height 28.4 mm, diameter 13.2 mm, height of spire 8.6 mm; LACMIP 7267, height 22.0 mm, diameter exclusive of outer lip flare 12.6 mm (including outer lip flare 14.3 mm), height of spire 8.0 mm; LACMIP 7270, height 23.0 mm, diameter 12.9 mm, height of spire 7.8 mm; LACMIP 7271, height 19.6 mm, diameter 13.7 mm, height of spire 5.4 mm;



Figures 132–164. Species of *Murphitys* new genus. All $\times 1$ unless otherwise indicated. As nearly as possible the figures are arranged from geologically oldest to youngest. **Figures 132–147.** *Murphitys michaeli* new species. 132–136, Coniacian; 137–147, Santonian; 132, 135, paratype LACMIP 7272 from CIT loc. 1230, $\times 1.5$; 133, 134, 136, paratype, LACMIP 7271 from CIT loc. 1230; 133, 134, $\times 1.5$; 136, $\times 2$; 137–139, 143, holotype, LACMIP 7264 from UCLA loc. 4106; 137, 138, 143, $\times 1.5$; 139, $\times 2$; 140, paratype with more of anterior canal preserved, LACMIP 7268 from UCLA loc. 4106; 141, 145, paratype with subdued axial sculpture, LACMIP 7270 from CIT loc. 1247; 142, paratype, LACMIP 7266 from UCLA loc. 4106, $\times 1.5$; 144, paratype with moderate axial sculpture, LACMIP 7267 from UCLA loc. 4106; 146, paratype with part of last whorl cut away and columellar folds exposed, LACMIP 7269 from UCLA loc. 4106, $\times 1.5$; 147, paratype with nearly complete anterior canal, LACMIP 7265 from UCLA loc. 4106. **Figures 148–156.** *Murphitys corona* new species, early Campanian, all from CIT loc. 1053. 148–151, 156, holotype, LACMIP 7273; 156, $\times 1.5$; 152, paratype with back cut away and columellar folds exposed, LACMIP 7275; 153, 155, paratype with more fully developed outer lip, LACMIP 7274; 153, $\times 1.5$; 154, paratype with nearly complete anterior canal and anterior siphonal fasciole, LACMIP 7276. **Figures 157–164.** *Murphitys madonna* new species, early Maastrichtian. 157, 161, paratype, SDSNH 25942 from SDSNH loc. 3162A; 158, paratype, LACMIP 7277 from LACMIP loc. 4898, $\times 1.5$; 159, 163, paratype with last whorl broken and columellar folds exposed, SDSNH 27871 from SDSNH loc. 3162A; 160, 162, holotype, SDSNH 25958 from SDSNH loc. 3161A; 164, paratype, steinkern with impressions of outer lip armaments at varices (arrows), LACMIP 7278 from UCLA loc. 5431.

LACMIP 7272, height 19.3 mm, diameter 11.9 mm; height of spire 7.4 mm.

TYPE LOCALITY. UCLA loc. 4106, hillside north of Clover Creek, Millville Quadrangle, Shasta Co., California (area 11).

DISTRIBUTION. Member IV along Oak Run (area 11) and Members V and VI along Clover Creek (area 11); ?Kingsley Cave Member of the Chico Formation on Mill Creek (very poor specimens) (area 2).

GEOLOGIC AGE. Coniacian and Santonian.

REMARKS. *Murphytys michaeli* resembles *Perissitys cretacea* but differs from it in having a more convexly rounded whorl profile with a concave ramp only on the last third of the last whorl. The first and second post-nuclear whorls of *M. michaeli* are virtually indistinguishable from those of *Perissitys elaphia*. Juvenile specimens of the two species then become distinguishable as *P. elaphia* develops a concave ramp. *M. michaeli* does not have as expanded an inner lip as *P. elaphia* nor as long an anterior canal. *M. michaeli* is similar to *Pseudocymia aurora* in its apical profile and sculpture but differs in being more constricted anterior to the periphery, having a rounded whorl profile and a broader, thinner, roundly expanded inner lip, lacking a pseudoumbilicus, and having fewer denticles on the outer lip.

Strength of spiral ribbing is variable in *M. michaeli*. Peripheral spirals are in some specimens scarcely stronger than those anterior and posterior, but in other specimens two peripheral spirals are strong enough to give the whorl a subangulate profile.

In apertural view the anterior fold is the more prominent one, its outer end being farther out on the inner lip, and the posterior fold is much less noticeable, its outer end being well within the aperture. The posterior is the more prominent fold away from the aperture within the spire. Both are, however, not strong except at varices.

ETYMOLOGY. The species is dedicated to Michael A. Murphy in recognition of his work on the Cretaceous of the Ono area, Shasta Co., California.

Murphytys corona new species

Figures 146–156

DIAGNOSIS. Plump *Murphytys* which have a doubly subangulate periphery demarcated by the two strongest spiral ribs. The outer lip bears about five nearly equal denticulations.

DESCRIPTION. Shell of medium size, roundly bucciniform; spire less than one-third of total shell height, consisting of about four post-nuclear whorls; protoconch unknown; whorls roundly convex with slightly concave ramp and double angulation at the periphery; last whorl narrowing to form a sturdy, nearly straight, anterior canal of moderate length; suture between the peripheral angulations.

Sculpture of alternating spiral ribs and threads with interspaces about twice as wide as the ribs; two slightly stronger ribs on the two angulations; ribbing anterior to the periphery a little stronger than that posterior to the periphery; spiral sculpture undulated by slightly arcuate, broadly rounded collabral ribs that number 11–14 on the last whorl; angulations noded at intersections with collabral ribs.

Outer lip thickened, slightly expanded, and somewhat re-curved to form a rimmed aperture with shallow antipiral sinus adapical to the periphery and slight spiral antisinus anterior to the periphery; inner lip broad and thin, roundly expanded onto the body whorl. Outer lip with about five nearly equal denticles and 2–3 denticulations adjacent to the anterior canal; columella with two folds and a parietal denticle, the stronger fold at the base of the previous whorl, the weaker one near the posterior end of the anterior canal.

HOLOTYPE. LACMIP 7273.

PARATYPES. LACMIP 7274–7276 from CIT loc. 1053.

DIMENSIONS. Of holotype—height 26.8 mm; diameter 18 mm, height of spire 7.5 mm.

TYPE LOCALITY. CIT loc 1053: spur north of Santiago Creek, El Toro Quadrangle, Santa Ana Mountains, Orange Co., California (area 13).

DISTRIBUTION. Ladd Formation, upper Holz Shale Member, Santa Ana Mountains (area 13); and Chatsworth Formation, Bell and Dayton canyons, Simi Hills (area 17).

GEOLOGIC AGE. Early Campanian, associated with *Canadoceras* cf. *C. yokoyamai* (Jimbo) (Matsumoto, 1960, p. 102), zone of *Turritella chicoensis holzana* Saul, 1983, through late Campanian *Metaplaeoceras pacificum* Zone.

REMARKS. The double corona of distinct nodes at the periphery distinguishes this species from all other perissityids. The species is based on nine specimens from CIT loc. 1053. A poorly preserved specimen from CIT loc. 94, Ladd Formation, uppermost Holz Shale Member, *T. chicoensis* Zone, of Williams Canyon, Santa Ana Mountains, and juvenile specimens from Bell (CIT loc. 1158) and Dayton canyons (CIT loc. 1159), Chatsworth Formation, *T. chicoensis* and *Metaplaeoceras pacificum* zones, Simi Hills (area 17) are also probably this species.

The more posterior of the two columellar folds appears weaker in apertural view because it begins farther back within the aperture, whereas the stronger appearing anterior fold not only begins farther out toward the inner lip but is also at its strongest at that point and weakens within the whorl.

Juveniles of *Perissitys brevirostris* and *P. pacifica* are similar to *M. corona*, but the latter is more distinctly bicoronate. Adult *M. corona* lack the sutural welt of adult *P. brevirostris* and *P. pacifica*.

ETYMOLOGY. *Corona*, Latin, both for its corona of nodes on the periphery and its occurrence in the old Corona Quadrangle.

Murphytys madonna new species

Figures 157–164

Perissitys brevirostris (Gabb) Sundberg & Riney, 1984, p. 105, fig. 3.3. Not *Perissolax brevirostris* Gabb, 1864.

DIAGNOSIS. Moderately large, biangulate *Murphytys* which have four subequal denticulations along the outer lip and two strong folds on the columella.

DESCRIPTION. Shell large, doubly angulate about the broad periphery; spire about one-third of the total shell height, consisting of about six post-nuclear whorls; protoconch apparently smooth and relatively large; whorls concave on the

ramp with double angulation at the periphery; last whorl narrowing to form a sturdy, slightly backward deflected anterior canal, bent abaperturally at its tip, longer than the height of the last whorl, and having a siphonal fasciole at its tip; suture at or just abapical to the adapical angulation, on the first four post-nuclear whorls, dropping to just above the abapical angulation on the last whorl.

Sculpture of fine alternating spiral ribs and threads with interspaces about three times as wide as the ribs; ribbing anterior to the abapical peripheral angulation a little stronger than that posterior to the abapical peripheral angulation; on third post-nuclear whorl about nine short collabral ribs forming strong nodes at their intersections with the two peripheral angulations, increasing to 16 on sixth whorl.

Outer lip thickened, forming a rimmed leaf-shaped aperture; inner lip broad and of moderate thickness, parietal portion roundly expanded onto the body whorl. Outer lip with a pair of denticles posterior to the notch at the adapical angulation, a pair of denticles between the angulations and three to four smaller denticles between the abapical angulation and the anterior canal; columella with two folds and a parietal denticle, the stronger fold at the base of the previous whorl, the weaker one near the posterior end of the anterior canal.

HOLOTYPE. SDSNH 25958.

PARATYPES. LACMIP 7277 from LACMIP loc. 4898, 7278 from UCLA loc. 5431, 7279 from UCLA loc. 7137, 7280 from LACMIP loc. 1215, and 7281 from LACMIP loc. 8159; SDSNH 25942 and 27871 from SDNH loc. 3162-A.

DIMENSIONS. Of holotype—height 64.5 mm, diameter 35.1 mm, height of spire 23.6 mm.

TYPE LOCALITY. SDSNH loc. 3162-A, Carlsbad Research Park, San Diego Co., California (area 20).

DISTRIBUTION. Chatsworth Formation on Lang Ranch, Simi Hills (area 17); Pleasants Sandstone Member of Williams Formation, Bean Creek, east of San Juan Capistrano (area 24); Rosario Formation near Carlsbad (Point Loma Member) (area 20), at Punta Banda (area 22), near Punta San Jose (area 10), near San Antonio del Mar (area 12), and at Arroyo Santa Catarina (area 14).

GEOLOGIC AGE. ?Latest Campanian and early Maastrichtian.

REMARKS. Although more than 20 specimens of this species are at hand, most are poorly preserved. The best specimens are from the Carlsbad Research Park. Small specimens are roundly inflated like *Murphyia corona*, but have fewer and stronger nodes about the periphery. Large specimens are much more angulate and resemble stout "*Fusus*" *kingii* Gabb, 1864. They have, however, the rimmed aperture and roundly expanded inner lip of *Murphyia*. As in many other perissityids, steinkerns of the species have at intervals impressions of the outer lip denticles (Figure 164) left by the irregular development of the varices.

A medium-sized specimen (LACMIP 7281) from LACMIP loc. 8159, east of San Juan Capistrano (area 24) occurs with *Baculites* cf. *B. subanceps pacificus* Matsumoto & Obata, 1963. This baculite is considered to be of late Campanian age (Matsumoto with Miyauchi, 1984, p. 75), but some other mollusks from LACMIP loc. 8159 are not typical of late

Campanian faunas: *Calva peninsularis* (Anderson & Hanna, 1935), *Paleomoera dyskritos*, Dailey & Popenoe, 1966, and a large undescribed parallelodontid have all been found in beds of early Maastrichtian age.

ETYMOLOGY. From Madonna Hill on El Camino Real, east of Carlsbad, San Diego Co., California.

Genus *Christitys* new genus

TYPE SPECIES. *Christitys medica* new species.

DIAGNOSIS. Compactly turricate to pyriform gastropods of small to moderate size with an angulate whorl periphery made nodose by short axial ribs. Aperture deltoid in shape with a broad posterior sinus adapical to the whorl periphery. Outer lip with posterior and medial denticulations. Columella with a fold near the base of the previous whorl and posterior and anterior denticulations.

DISCUSSION. *Christitys* resembles *Murphyia* in having a columellar fold but is more sharply angulate about the periphery and has fewer denticulations on the outer lip. The outer lip denticulations are weaker in the geologically younger *C. martini* than they are in *C. delta* or *C. medica*. Conversely, the posterior denticulations of the inner lip are stronger in *C. martini* than in *C. delta*. *C. martini* has a shorter spire and more pyriform shape and resembles *Heteroterna* Gabb, 1869. *Heteroterna* differs from *Christitys* in lacking columellar folds. *Cominella? praecursor* Wilckens, 1907, from the late Senonian of southern Patagonia was placed in *Heteroterna* by Finlay and Marwick (1937), but the aperture is not described (Wilckens, 1907, p. 117). The figures of *C.? praecursor* are suggestive of *Christitys*. The lack of columellar folds in *Heteroterna* is not considered by us to preclude a close relationship to *Christitys*.

ETYMOLOGY. The generic name is a compound of Christie (for J.M. Christie), and *itys*, Greek, rim or felly of a wheel.

Christitys delta new species

Figures 8, 165–168

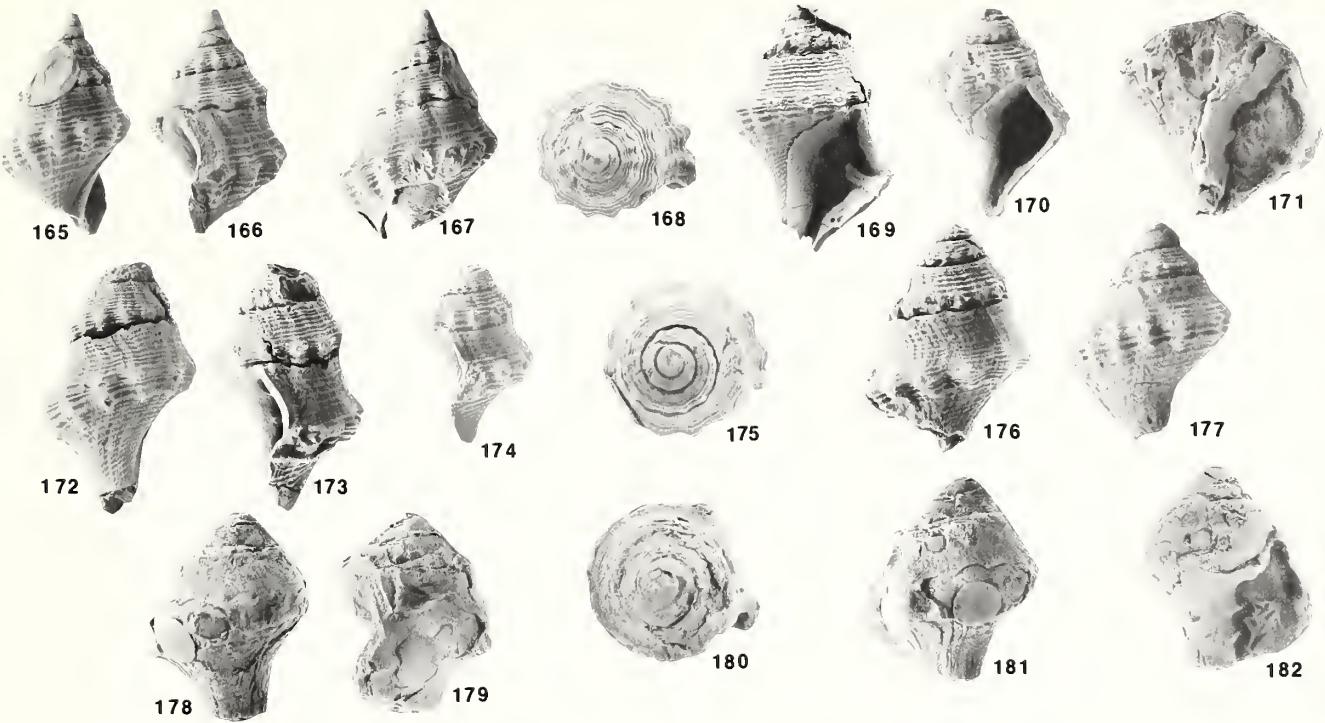
DIAGNOSIS. Compactly turricate *Christitys* which have a sharply angulate periphery.

DESCRIPTION. Shell small, compactly turricate; spire consisting of about four whorls and a smooth, mammiform protoconch of one and a half whorls succeeded by a whorl sculptured by raised spiral threads; first two whorls roundly convex; others concave on the ramp, angulate at the periphery, and abruptly contracted abapically.

Sculpture of spiral ribs narrower than the interspaces, strongest on the angulate periphery, weakest on the ramp; periphery made nodose by 14 very short axial ribs.

Outer lip with a shallow antipodal sinus adapical to the periphery and moderate spiral antipodal sinus anterior to the periphery; inner lip well demarcated and of moderate and nearly constant width. Outer lip with two tiny posterior denticles and a moderately strong coalesced pair just anterior to the peripheral angulation; inner lip with a moderate parietal denticle, a fold on the columella just at the base of the previous whorl and an anterior pseudofold.

HOLOTYPE. UCLA 39455.



Figures 165–182. Species of *Christitys* new genus. All $\times 1.5$ unless otherwise noted. Figures 165–168. *Christitys delta* new species, holotype, Coniacian, UCLA 59455 from UCLA loc. 4209. Figures 169, 170, 172–177. *Christitys medica* new species, Santonian, all from UCLA loc. 4106; 169, 172, 173, holotype, LACMIP 7282; 170, paratype, LACMIP 7286, $\times 2$, a juvenile; 174, paratype LACMIP 7284, a young specimen with nearly complete outer lip; 175, 176, paratype LACMIP 7283; 177, paratype LACMIP 7285, $\times 2$. 171, 178–182. *Christitys martini* new species, Campanian, all from USGS 5795, $\times 1$; 171, paratype USNM 400976; 178–182, holotype, USNM 400975.

DIMENSIONS. Height 20.2 mm; diameter 14.9 mm; height of spire 10.2 mm.

TYPE LOCALITY. UCLA loc. 4209, north side of Clover Creek valley, Millville Quadrangle, Shasta Co., California (area 11).

DISTRIBUTION. Known only from the type locality in Member IV on Clover Creek (area 11).

GEOLOGIC AGE. Coniacian.

REMARKS. The above description is based upon the holotype and only known specimen. The spire is very well preserved, but unfortunately the anterior canal is broken off. This specimen is higher spired, more sharply angulate at the periphery, and more coarsely sculptured than any specimen assigned to *C. medica*. It differs from *Perissitys cretacea* and *Murphyia michaeli* in having its suture very close to its angulate whorl periphery, which produces a nearly triangular spire.

ETYMOLOGY. The species is named *delta*, fourth letter of the Greek alphabet, for its triangular spire.

Christitys medica new species

Figures 169, 170, 172–177

DIAGNOSIS. Compactly turricate *Christitys* which have an angulate periphery broad enough to display three to four spiral ribs.

DESCRIPTION. Shell small, compactly turricate; spire consisting of about four whorls (protoconch not observed), first whorl convexly rounded and spirally sculptured; second whorl with flat ramp, spiral sculpture and angulate, noded periphery; third and fourth whorls with slightly concave ramp; angulate noded periphery abruptly contracted anteriorly, produced into siphonal neck of moderate length.

Sculpture of spiral ribs narrower than the interspaces, three to four strongest on the angulate periphery made nodose by about 13 very short axial ribs.

Outer lip with a shallow antisprial sinus between the suture and the periphery and moderate spiral antisinus anterior to the periphery, slightly flared anterior to the periphery; inner lip well demarcated and of moderate and nearly constant width. Outer lip with small denticle posterior to the periphery, a strong bifid denticle just anterior to the periphery, abapically a moderate denticle, and tiny denticles adjacent to the anterior canal; inner lip with a well-developed parietal denticle, a fold opposite the periphery, and an anterior pseudofold, all of apparently equal strength.

HOLOTYPE. LACMIP 7282.

PARATYPES. LACMIP 7283–7286, all from UCLA loc. 4106.

DIMENSIONS. Of holotype—height 21.8 mm (incomplete), diameter 15.2 mm; height of spire 9.3 mm (incomplete); of paratypes—LACMIP 7283, height 20.2 mm (in-

complete), diameter 15.2 mm, height of spire 9.7 mm; LACMIP 7286, height 8.6 mm, diameter 9.9 mm, height of spire 4.2 mm.

TYPE LOCALITY. UCLA loc. 4106, hillside north of Clover Creek, Millville Quadrangle, Shasta Co., California (area 11).

DISTRIBUTION. All specimens are from the type locality in Member VI on Clover Creek, Shasta Co., California.

GEOLOGIC AGE. Santonian.

REMARKS. None of the seven specimens is complete. *C. medica* differs from *C. delta* in its slightly broader periphery and in having the suture slightly more abapical to the periphery, giving the spire a slightly more turritulate shape. Except for the stronger peripheral ribs, the ribbing is overall of more even strength on *C. medica*. The denticulations of the outer lip, especially the large bifid denticle, resemble those of the "Fusus" *kingii* lineage (Figures 6, 14). In external shape and sculpture the species is most similar to Santonian age "*Hindsia nodulosa*," but *C. medica* has a shorter spire, appears to have had a shorter anterior canal, and has the large bifid denticle within the outer lip rather than the two denticles present in "*H. nodulosa*" (Figure 12).

ETYMOLOGY. The specific name is from Latin, *medica*, clover from Media, for its occurrence on Clover Creek.

Christitys martini new species

Figures 171, 178-182

DIAGNOSIS. Pyriform *Christitys* which have a bluntly angulate periphery defined by two spiral ribs.

DESCRIPTION. Shell of moderate size, apparently pyriform; spire consisting of about four whorls (protoconch unknown); last whorl with slightly concave ramp, bluntly angulate periphery, contracted abruptly anterior to the periphery to form an anterior canal of unknown length.

Sculpture of spiral riblets narrower than the interspaces and two strong ribs defining anterior and posterior sides of the periphery; periphery made nodose by about 12 very short axial ribs.

Outer lip with a shallow antisiphonal sinus between the suture and the anterior side of the periphery and slight spiral antisinus anterior to the periphery, not flared; inner lip well demarcated, a little expanded posteriorly. Outer lip thickened with denticle about midway along the ramp, a moderately strong bifid? denticle at the anterior side of the periphery, and abapically a moderate denticle; inner lip with a thick tripartite parietal denticle, a fold opposite the periphery, and an anterior pseudofold.

HOLOTYPE. USNM 400975.

PARATYPES. USNM 400976-400977 from USGS loc. 5795 and 400978 from USGS loc. 5796.

DIMENSIONS. Of holotype—height 27 mm (incomplete), diameter 25 mm, height of spire 8.5 mm.

TYPE LOCALITY. USGS loc. 5795, Whalers Creek, near Chignik Lagoon, Alaska Peninsula, Alaska (area 23).

DISTRIBUTION. Lower member of Chignik Formation, *Inoceramus schmidti* Zone near Chignik Bay, Alaska Peninsula.

GEOLOGIC AGE. Early Campanian. Ward et al. (1983) place the *Inoceramus schmidti* Zone in the Santonian because magnetic anomaly 33-34 occurs above *I. schmidti* in the Great Valley Series of California. Jones (1963, p. 432), however, records *Canadoceras newberryanum* throughout the Chignik Formation, and *C. newberryanum* occurs above magnetic anomaly 33-34 on Chico Creek (area 5). The Chignik Formation specimens may be of early Campanian age.

REMARKS. The species is based on four specimens from the Chignik Formation listed by Martin (1926, p. 304) as *Perissolax brevirostris*. These specimens are worn and broken, but the apertural characteristics are those of *Christitys*. *C. martini* differs from *C. medica* in having a broader periphery, shorter spire, and more expanded inner lip; from *Perissolax brevirostris* in having apertural decorations, and a much less expanded inner lip; from *P. elaphia* in having a fold on the columella, a deeper antisprial sinus to the growth line, two rather than three or four strong spirals at the periphery, and a much less expanded inner lip. The strong outer lip denticles of *C. martini* are at and abapical to the periphery as in *C. delta* and *C. medica* rather than at and adapical to the periphery as in *P. cretacea* and *P. elaphia*. *C. martini* resembles *Murphytyss corona* in shape, but has a more pronounced antisprial sinus to the growth line; the outer lip is not rimmed, and the inner lip is less expanded.

Christitys martini resembles *Pseudoperissolax bicarinata* Nagao & Otatume, 1938 (pl. 4, fig. 3-5a), but *P. bicarinata* lacks columellar folds and outer lip thickening. It is said to be of Campanian or Maastrichtian age, and may be closely related to *Christitys*. In shape *C. martini* also resembles *Heterotera trochoidea* Gabb, but the latter is without apertural ornament and has a thin inner lip, is from the Paleocene "Martinez Stage," and is considerably younger. The apertural ornaments, which appear to be reduced in *C. martini*, could have been lost by Paleocene time, and *Heterotera* may be related to *Christitys*. The relationships of these three apparently similar genera need further study.

ETYMOLOGY. The species is named for G.C. Martin who recorded the specimens from the Chignik Formation.

ACKNOWLEDGMENTS

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LOCALITIES CITED

Approximately one-third of the cited localities have been previously published; these are cited briefly with a reference. The italicized number to the left refers to the locality to an area of Figure 1.

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| | | | White. Laguna Seca Formation. ?Late Danian or ?early Selandian. |
| 17 | 1158 | CIT (= UCLA 6020): SE slope of Simi Hills, N bank Bell Canyon, 1.15 mi. due W of Los Angeles–Ventura Co. line on boundary (extended) between T1 and 2N, Calabasas Quad., Ventura Co., Calif. Coll.: W.P. Popenoe, June 18, 1935. Chatsworth Formation. Late mid Campanian. | |
| 17 | 1159 | CIT: Prominent fossil bed on crest of spur between forks of Dayton Canyon, about 400 ft. E of Los Angeles–Ventura Co. line, approx. 400 ft. N, 2350 ft. W of SE cor. sec. 28, T2N, R17W, Calabasas Quad., Los Angeles Co., Calif. Chatsworth Formation. Late Campanian. (Popenoe et al., 1987, p. 98.) | |
| 11 | 1212 | CIT: Little Cow Creek, Millville Quad., Shasta Co., Calif. Frazier Siltstone (= Member II), hard sandy concretions, in shale. Late Turonian. (Popenoe, 1983, p. 765.) | |
| 14 | 1215 | LACMIP: Mollusks and echinoid from Arroyo Santa Catarina, approx. 6 km N, 6 km E of mouth of Rio Santa Catarina, Baja California, Mexico. Coll.: H. Dushane, July, 1958. Rosario Formation. Early Maastrichtian. | |
| 11 | 1227 | CIT (= UCLA 3296): Massive sandstone interbedded with conglomerate on S side of high E–W trending ridge, S side Oak Run Valley, 3275 ft. S 54°50'W of SE cor. sec. 10, T32N, R2W, Millville Quad., Shasta Co., Calif. Coll.: Popenoe & Ahlroth, 1936. Member V. Early Santonian. | |
| 11 | 1230 | CIT: SE side Oak Run valley, SE of Dry Creek, S side of hill on section line between sections 11 & 14, 200 ft. S, 1750 ft. E of NW cor. sec. 14, T32N, R2W, Millville Quad., Shasta Co., California. Coll.: Popenoe & Ahlroth, 1936. Member V. Coniacian. | |
| 11 | 1232 | CIT: Price Hollow, Millville Quad., Shasta Co., Calif. Member V, cross-bedded sandstones interbedded with thick conglomerate. Early Santonian. (Saul, 1978, p. 56.) | |
| 11 | 1246 | CIT: Clover Creek, loose boulder on hillslope on E side of 1000 ft. hill, about 0.3 mi. NE of Reinicke's Ranch house, SE 1/4, NE 1/4 sec. 13, T32N, R2W, Millville Quad., Shasta Co., Calif. Coll.: Popenoe, 1936. Member V. Santonian. | |
| 11 | 1247 | CIT: N side Clover Creek, Millville Quad., Shasta Co., Calif. Member V. Santonian. (Matsumoto, 1960, p. 104.) | |
| 7 | 1258 | USGS: Near Blum and Company's Pacheco warehouse, about 1 1/2 mi. N of Pacheco, Contra Costa Co., Calif. Coll.: T.W. Stanton, 1894. Great Valley Series. Late Maastrichtian. | |
| 11 | 1289 | CIT: Bear Creek, at stone culvert on road to Aldridge's, SW of Bonnie Crags, about 1/2 mi. | |
| 13 | 83 | CIT (= UCLA 2949): Fine ss just above shale, section line fence gate on old road, 1/4 mi. W of Schultz Ranch, S side of Williams Canyon, approx. 435 ft. S of NW cor. sec. 20, T5S, R7W, El Toro Quad., Santa Ana Mts., Orange Co., Calif. Coll.: B.N. Moore, 1926. Ladd Formation, uppermost Holz Shale Member. Mid Campanian, <i>Turritella chicoensis</i> Zone. | |
| 13 | 94 | CIT: Sandstone just above shale about 300 ft. E of section line on ridge N of Williams Canyon, 500 ft. N, 300 ft. E of SW cor. sec. 17, T5S, R7W, El Toro Quad., Santa Ana Mts., Orange Co., Calif. Coll.: B.N. Moore, 1928. Ladd Formation, uppermost Holz Shale Member. Mid Campanian, <i>Turritella chicoensis</i> Zone. | |
| 7 | 249 | UCB: ½ mi. W of Muir Station, ¼ mi. N of Franklin Creek, Concord Quad., Contra Costa Co., Calif. Coll.: J.C. Merriam. Great Valley Series. ?Late Maastrichtian. | |
| 8 | 460 | LSJU: 300 ft. S, 650 ft. W of NE cor. sec. 24, T14S, R11E, Chouhet Ranch Quad., Panoche Hills, Fresno Co., Calif. Basal Laguna Seca Formation, 300 ft. below base of Domengine. ?Late Danian. | |
| 8 | 463 | CAS (= CAS 2362): Center E side sec. 4, T20S, R14E, north side Los Gatos Creek, Coalanga Quad., Fresno Co., Calif. Coll.: F.M. Anderson. Panoche Formation, "Ragged Valley Shale Member." Early Maastrichtian. | |
| 13 | 974 | CIT: Aliso-Santiago Creek divide, El Toro Quad., Orange Co., Calif. Williams Formation, Pleasants Sandstone Member. Late Campanian. (Matsumoto, 1960, p. 99.) | |
| 11 | 1007 | CIT: Oak Run, Millville Quad., Shasta Co., Calif. Member IV. Coniacian. (Matsumoto, 1960, p. 100.) | |
| 5 | 1016 | CIT: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, Musty Buck Member. Santonian. (Matsumoto, 1960, p. 101.) | |
| 5 | 1017 | CIT: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, Musty Buck Member. Santonian. (Matsumoto, 1960, p. 101.) | |
| 11 | 1034 | CIT: See UCLA 4104. | |
| 13 | 1053 | CIT (= UCLA 4191): N of Santiago Creek, El Toro Quad., Orange Co., Calif. Ladd Formation, upper Holz Shale Member. Early Campanian. (Matsumoto, 1960, p. 102.) | |
| 8 | 1068 | LSJU: S of Chaney Ranch Canyon, W 1/2, SW 1/4 sec. 19, T14S, R12E, Chouhet Ranch Quad., Panoche Hills, Fresno Co., Calif. Coll.: R.T. | |

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| | | W of Aldridge's and 1.3 mi. E of road forks and 2 mi. E of road crossing of N fork Bear Creek, 2000 ft. S, 500 ft. E of NW cor. sec. 18, T31N, R1E, Whitmore Quad., Shasta Co., Calif. Coll.: W.P. Popenoe & H.V. Church, August 17, 1936. Member V. Coniacian. | | Harding Canyon, NW $\frac{1}{4}$, NW $\frac{1}{4}$ sec. 29, T5S, R7W, El Toro Quad., Santa Ana Mts., Orange Co., Calif. Coll.: W.P. Popenoe, 1946. Ladd Formation, uppermost Holz Shale Member. Mid Campanian. |
| 18 | 1400 | CIT: Sucia Island, Orcas Island Quad., San Juan Co., Wash. Cedar District Formation. Mid Campanian, <i>Hoplitoplacenticeras</i> Zone. (Matsumoto, 1960, p. 107.) | 13 2415 | UCLA: Spur NW side Bee Canyon, El Toro Quad., Orange Co., Calif. Williams Formation, Pleasants Sandstone Member. (Saul, 1978, p. 56.) |
| 18 | 1402 | CIT: Float from base of cliffs on S side of Fossil Cove near W end, Sucia Island, sec. 26, T38N, R2W, Orcas Island Quad., San Juan Co., Wash. Cedar District Formation. Mid Campanian. | 14 2852 | LACMIP: West side Arroyo Santa Catarina, Estado de Baja California, Mexico. Rosario Formation. Early Maastrichtian. (Webster, 1983, p. 1096.) |
| 11 | 1532 | CIT: Salt Creek, Millville Quad., Shasta Co., Calif. Frazier Siltstone (= Member II), near top. Turonian. (Matsumoto, 1960, p. 107.) | 20 3162A | SDSNH: Carlsbad Research Center, gently dipping (3–5° SW), locally faulted sequence of blue-gray sandy claystone with interbedded, well-cemented sandstones exposed during development of industrial park, fossils collected through a 70+ ft. section, stratigraphic horizons denoted by letter "A" being lowest, section was best exposed along Palmer Way approx. 2000 ft. W of intersection with El Camino Real (no longer accessible), 33°8'2"N lat., 117°16'41"W long., San Luis Rey Quad., Carlsbad, San Diego Co., Calif. Coll.: B.O. Riney, May 1982, with permission of Koll Company. Rosario Formation, Point Loma Member. Early Maastrichtian. |
| 19 | 1581 | UCLA: N side East Fork Fish Canyon, Warm Springs Mountain Quad., NW San Gabriel Mts., Los Angeles Co., Calif. San Francisquito Formation. Late Danian. (Saul, 1983, p. 112.) | 8 A-3216 | UCB: In banks along Los Baños Creek, SE $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$ sec. 12, T11S, R9E, Volta Quad., Merced Co., Calif. Moreno Formation, Volta Sands. Mid Maastrichtian. |
| 19 | 1594 | UCLA: N side Warm Springs Mt., Warm Springs Mountain Quad., Los Angeles Co., Calif. San Francisquito Formation. Late late Maastrichtian. (Saul, 1983, p. 113.) | 8 A-3262 | UCB: W branch of small draw a short distance N of large unnamed gully about 3.5 mi. S of Ortigalita Creek near intersection of S border sec. 1 and meridian 120°50'W, approx. 700 ft. E of SW cor. sec. 1, T12S, R10E, Charleston School Quad., Merced Co., Calif. Coll.: A. Bennington, December, 1939. Laguna Seca Formation. Danian. |
| 11 | 1596 | CIT: Forks of Snow and North Bear creeks, 2750 ft. S, 1250 ft. E of NW cor. sec. 7, T32N, R1E, Whitmore Quad., Shasta Co., Calif. Coll.: W.P. Popenoe & W.M. Tovel, September 10, 1941. Member V. Coniacian. | 14 3268 | UCLA: Olive silts exposed along banks of small gully about 3 mi. NE of Santa Catarina Landing and $\frac{1}{4}$ mi. S of the channel of Arroyo Santa Catarina, 5.9 km N, 5.9 km E of Santa Catarina stream at Pacific Ocean, N 18° W of Punta Canoas, Baja California, Mexico. Coll.: W.P. Popenoe & party, February, 1949. Rosario Formation. Early Maastrichtian. |
| 7 | 1602 | CIT: NW side of crest of ridge just W of prominent bend in highway between Martinez and Crockett, 500 ft. NW of CIT 1601, approx. 1.8 mi. N 75° W of shore end of ferry pier at Martinez, and S of Benicia city wharf, Benicia Quad., Contra Costa Co., Calif. Coll.: W.P. Popenoe, Nov. 14, 1944. Great Valley Series, upper sandstone just below Martinez. Late Maastrichtian. | 11 3298 | UCLA (= CIT 1006): Between Basin Hollow and Clover creeks, Millville Quad., Shasta Co., Calif. Member V. Santonian. (Popenoe, 1957, p. 448.) |
| 18 | 1860 | LSJU: South end of Sucia Island also northwest islet of Sucia Group, Puget Sound, Orcas Island Quad., San Juan Co., Wash. Coll.: F.L. Cole, 1893. Cedar District Formation. ?Mid Campanian. | 5 3623 | UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, Musty Buck Member. Early Santonian. (Matsumoto, 1960, p. 155.) |
| 8 | 2245 | LSJU: Between Marca Canyon and Chaney Ranch Canyon, 100 ft. S, 700 ft. W of NE cor. sec. 24, T14S, R11E, Chouhet Ranch Quad., Panoche Hills, Fresno Co., Calif. Coll.: R.A.C. Brown, S. Muller, M. Payne & H.G. Schenck, 1940. Basal Laguna Seca Sand, 300 ft. below base of Domengine. ?Late Danian or ?early Sealandian. | 5 3624 | UCLA: First ravine to S of Mickey's Place on W side of Chico Creek about 500 ft. upstream |
| 13 | 2324 | UCLA: Just E of Santiago Creek, S of Williams Canyon and N of Modjeska Canyon, limey ss at top of Holz exposed in abandoned road cut in large gully, 4200 ft. N 70° W of mouth of | | |

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| 5 | 3633 | from UCLA 3622 and 100 ft. below fork in ravine, 800 ft. N, 900 ft. E of SW cor. sec. 1, T23N, R2E, Paradise Quad., Butte Co., Calif. Coll.: L.R. & R.B. Saul, 1952. Chico Formation, Musty Buck Member. Early Santonian. | 4400 ft. W of Hunt Ranch House and just downstream from old ruined iron bridge over creek, 1700 ft. S, 2100 ft. W of NE cor. sec. 17, T31N, R2W, Millville Quad., Shasta Co., Calif. Coll.: W.P. Popenoe, 1954. Member V. Santonian. |
| 5 | 3633 | UCLA: E of Chico Creek county road, Paradise Quad., Butte Co., Calif. Chico Formation, top of Musty Buck Member. ?Late Santonian, <i>Baculites capensis</i> Zone. (Matsumoto, 1960, p. 15, 156.) | UCLA (= CIT 976): S side Williams Canyon, El Toro Quad., Santa Ana Mts., Orange Co., Calif. Williams Formation, lower Pleasants Sandstone Member. Late Campanian. (Matsumoto, 1960, p. 99.) |
| 5 | 3635 | UCLA: On E bank of Chico Creek W from ^H _B House and approx. 400 ft. S of twin meadows, 1800 ft. S, 400 ft. E of NW cor. sec. 13, T23N, R2E, Paradise Quad., Butte Co., Calif. Coll.: L.R. & R.B. Saul, 1952. Chico Formation, basal Ten Mile Member. Early Campanian. | UCLA: N side of Clover Creek valley along SW slope of NE trending hill, 1300 ft. N, 500 ft. W of SE cor. sec. 31, T32N, R2W, Millville Quad., Shasta Co., Calif. Coll.: W.P. Popenoe, 1954. Member IV, siltstone with interbedded fossiliferous concretionary sandstone slabs. Coniacian. |
| 5 | 3637 | UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, Ten Mile Member. Early Campanian. (Matsumoto, 1960, p. 15, 156.) | UCLA: Clover Creek Millville Quad., Shasta Co., Calif. Member VI. Late Santonian. (Popenoe et al., 1987, p. 99.) |
| 5 | 3641 | UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, Ten Mile Member. Early Campanian. (Saul, 1983, p. 121.) | LACMIP: Near base of east-facing road cut opposite Madonna Hill Guest Home, 5392 El Camino Real, 0.85 mi. N of Palomar Airport Road, San Luis Rey Quad., San Diego Co., Calif. Coll.: G.L., C.B. & L.M. Kennedy & W. & L. Hindes, 1973. Rosario Group, Point Loma Formation. Early Maastrichtian. |
| 5 | 3643 | UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. Chico Formation, middle Ten Mile Member. Early Campanian zones of <i>Submortoniceras chicoense</i> and <i>Turritella chicoensis holzana</i> . (Saul, 1974, p. 1093.) | UCB: S side Punta San Jose, next promontory eastward from one on which old fish camp is located and at end of road on point; promontory at UCB B-5322 blocks travel along beach except at lowest tides, approx. 2 m strat. below UCB B-5322 and farther E along beach, Baja California, Mexico. Coll.: E.C. Allison & F.H. Kilmer, 1957. Rosario Formation. ?Early Maastrichtian. |
| 5 | 3647 | UCLA: E side Chico Creek up ravine which is 1.7 mi. from Ten Mile House site by Chico Creek county road, leached fossils in ss approx. 150 ft. up ravine from county road and near large block of basalt, 1750 ft. S, 2750 ft. E of NW cor. sec. 35, T23N, R2E, Paradise Quad., Butte Co., Calif. Coll.: L.R. & R.B. Saul, 1953. Chico Formation, Ten Mile Member. Late early Campanian zones of <i>Submortoniceras chicoense</i> and <i>Turritella chicoensis</i> . | 10 B-5323 |
| 17 | 3814 | UCLA: Dark gray calcareous ss stringers in buff ss in gully channel 250 ft. N of private road on Lang Ranch, 2800 ft. N, 175 ft. W of SE cor. sec. 26, T2N, R19W, Thousand Oaks Quad., NW end Simi Hills, Ventura Co., Calif. Coll.: D.H. Dailey, 1958. Chatsworth Formation. Early Maastrichtian. | UCLA: Siltstone and sandstone exposed in littoral zone and 10 to 20 ft. above high tide, S side Punta San Jose, about ½ mi. E of the point and 30 mi. airline S of Ensenada, Pacific coast of Baja California, Mexico. Coll.: W.P. Popenoe & W.V. Sliter, 1965. Rosario Formation. Early Maastrichtian. |
| 2 | 4082 | UCLA (= CIT 1038): Tuscan Springs, Tuscan Springs Quad., Tehama Co., Calif. Chico Formation. Early Campanian. (Saul, 1978, p. 57.) | 23 5795 |
| 11 | 4104 | UCLA (= CIT 1034): Hard, cemented ss slabs weathering out of siltstone in pasture a little W of N of Hathaway Ranch house, about 1500 ft. S, 1400 ft. E of NW cor. sec. 16, T32N, R2W, Millville Quad., Shasta Co., Calif. Coll.: W.P. Popenoe, 1959. Member IV. Coniacian. | USGS: Whalers Creek, about 2 mi. from Chignik Lagoon. Series of sandstones about 100 ft. below the coal. Alaska Peninsula. Coll.: W.W. Atwood, 1908. Chignik Formation, Lower Member (Martin, 1926, p. 304). Campanian, <i>Inoceramus schmidtii</i> Zone. |
| 11 | 4106 | UCLA: Clover Creek, Millville Quad., Shasta Co., Calif. Member VI. Early Santonian. (Popenoe, 1983, p. 760, 765.) | 23 5796 |
| 11 | 4107 | UCLA: Ss in bed of South Cow Creek, about | USGS: North side of Chignik Bay 1 mi. N of base of sand spit, Alaska Peninsula. Coll.: W.W. Atwood, 1908. Chignik Formation, Lower Member (Martin, 1926, p. 304). Early Campanian, <i>Inoceramus schmidtii</i> Zone. |
| 8 | 5902 | | UCLA: In gullies tributary to Oil Canyon at its source, just W of center of sec. 7, T19S, R15E, Joaquin Rocks Quad., Fresno Co., Calif. Coll.: |

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| W.P. Popenoe, 1949. Panoche Formation, "Ragged Valley Shale," about 200 ft. above contact with Joaquin Rocks Member. Early Maastrichtian, <i>Pachydiscus (Neodesmoceras) catarinae</i> Zone and Goudkoff's E Zone. | | | Coll.: R.W. Pack & R. Anderson, 1910. Moreno Formation, within 100 ft. of base of lower gray sandstone. Mid Maastrichtian. |
| 11 5990 UCLA: Sandstone cropping out in bed of small NW-ward-flowing gully tributary to French Creek, near S end of Swede Basin, 300 ft. S, 1800 ft. E of NW cor. sec. 9, T33N, R2W, Millville Quad., Shasta Co., Calif. Coll.: W.P. Popenoe, 1959. Member IV. Coniacian. | 16 7110 | UCLA: N side of Garapito Creek just above 1300 ft. contour, 900 ft. N, 725 ft. E of SW cor. sec. 33 (proj.), T1N, R16W, San Vicente y Santa Monica Grant, Topanga Quad., Santa Monica Mts., Los Angeles Co., Calif. Coll.: J.M. Alderson, 1983. Tuna Canyon Formation, upper sandstone. Late Campanian, zones of <i>Metaplacenticeras pacificum</i> and <i>Turritella chicoensis pescaderoensis</i> . | |
| 14 6368 Blocks fallen from bluffs, first large point N of Punta Canoas, about 3 mi. S of Santa Catarina Landing, Baja California, Mexico. Coll.: Weir, Gugnian & Stager, Feb. 14, 1948. Sepultura Formation. Early Selanian. | 22 7137 | UCLA: Fossiliferous, hard calcareous concretion from ss beds in graben(?) (<i>Coralliochama</i> beds in sea cliff on both sides of graben?), about 200 ft. eastward along shore from sandy ravine with road to beach, N side Punta Banda Peninsula, Baja California, Mexico. Coll.: J.M. Alderson, 1984. Rosario Formation. Early Maastrichtian. | |
| 8 6496 UCLA: Approx. 1½ mi. SW of Howard Ranch and ½ mi. N of Romero Creek, 2700 ft. N, 2160 ft. W of SE cor. sec. 21, T9S, R8E, Pa-checo Pass Quad., Merced Co., Calif. Coll.: F.A. Schilling, Jr., 1958. Panoche Formation, boulder in conglomerate 8200 ft. below top. Santonian. | 12 7149 | UCLA: Fossils at beach level from sea cliff exposure approx. 2 km S of San Antonio del Mar, Baja California, Mexico. Coll.: Victor Miller, 1984. Rosario Formation. Early Maastrichtian. | |
| 14 6534 UCLA: S side of short cul de sac having prominent bare vertical outcrop on N side, W side Arroyo Santa Catarina almost opposite road into Arroyo, approx. 8.1 km N, 4.2 km E of mouth of stream NW side Arroyo Santa Catarina, N 19° W of S tip Punta Canoas, Baja California, Mexico. Coll.: L.R. Saul, R.L. Saul & W.P. Popenoe, 1968. Rosario Formation, buff silts below gritty sands with fossils, cobble conglomerate above. Early Maastrichtian. | 20 7792 | LACMIP: 5 m from base of a temporary cut bank which has exposed 17 m of section, N side Faraday Ave., E of intersection with Rutherford Road, approx. 3570 ft. N, 9730 ft. W of SE cor. San Luis Rey Quad., Carlsbad Research Park, Agua Hedionda Grant, San Diego Co., Calif. Coll.: James Loch, spring 1984. Rosario Formation, Point Loma Member. Early Maastrichtian. | |
| 8 A-6618 UCB: Moreno Grande concretionary sandstone along road in S bank of Ortigalita Creek in SW¼, NE¼, NW¼ sec. 28, T11S, R10E, Ortigalita Peak Quad., Merced Co., Calif. Coll.: L.I. Briggs, 1948–49. Moreno Formation. Early Maastrichtian. | 20 7962 | LACMIP: Carlsbad Research Park, cut bank N side of Faraday Ave. W of intersection with Rutherford Road, W of fault of unknown offset, approx. 3575 ft. N, 9770 ft. W of SE cor. San Luis Rey Quad., Agua Hedionda Grant, San Diego Co., Calif. Coll.: James Loch, spring 1984. Rosario Formation, Point Loma Member. Early Maastrichtian. | |
| 17 6670 UCR: E side Meier Canyon, 3030 ft. SW 20° from hill 1314, Calabasas Quad., Simi Hills, Ventura Co., Calif. Coll.: W.J. Zinsmeister, 1974. Santa Susana Formation. Early "Martinez" probably = early Selanian. | 24 8159 | LACMIP (= CIT 1824): Shales in canyon back of mine office of Gladding McBean Co. North Mine. This is the foot wall of fault by mine, N½, NE¼ sec. 1, T8S, R7W, Cañada Gobernadora Quad., Orange Co., Calif. Coll.: C.R. Stauffer, 1945. Williams Formation, Pleasants Sandstone Member. ?Late Campanian–?early Maastrichtian. | |
| 18 7003 UCLA: East end of Little Sucia (SW islet of Sucia Is.) approx. 200 ft. S from N side of islet and at base of northern E-facing cliff outcrop, sec. 26, T38N, R2W, Orcas Island Quad., San Juan Co., Wash. Coll.: R.B. Saul, 1972. Cedar District Formation, ? just below <i>Hoplitoplacenticeras</i> . Mid Campanian. | 21 31325 | CAS: Head of Buckeye Creek, north branch of creek SE of Lee Bow Well, sec. 22, T12N, R3W, Rumsey Quad., Rumsey Hills, Yolo Co., Calif. Basal Forbes?, float from lower conglomerate. Late Santonian or early Campanian. | |
| 8 7059 USGS: Foothills between Ortigalita and Little Panoche creeks, about 4 mi. SE of mouth of Ortigalita Creek, on hilltop in NW¼, NE¼ sec. 12, T12S, R10E, about 1500 ft. SW of 875 ft. hill, Ortigalita Peak Quad., Merced Co., Calif. | | | |

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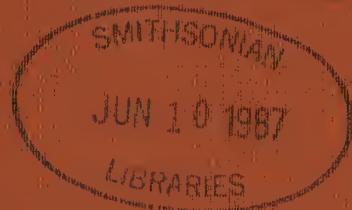
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CONTRIBUTIONS IN SCIENCE

A NEW SPECIES OF *BARISIA* (SAURIA, ANGUIDAE)
FROM OAXACA, MEXICO

John P. Karges and John W. Wright



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

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A NEW SPECIES OF *BARISIA* (SAURIA, ANGUIDAE) FROM OAXACA, MEXICO

John P. Karges and John W. Wright¹

ABSTRACT. A new species of *Barisia* from the cloud forest of the Sierra Juarez, Oaxaca, Mexico, has both paired postmental scales and complete series of superciliary scales and therefore is assigned to the *gadovi* species group. It differs from the other species of this group (*gadovi* and *antauges*) by having distinctly barred labial regions. It also has two or more subocular scales and smooth dorsal scales (only one subocular and distinct keeling in *B. gadovi*) and a dorsal color pattern with at least traces of dark, posteriorly directed chevrons (absent in *B. antauges*). With a maximum snout-vent length of 77 mm (N = 95), this is the smallest member of the *gadovi* species group and previously has been confused in collections with the sympatric, similar-sized *B. viridiflava* of the *moreletii* group. All members of the *moreletii* group have single postmental scales and *B. viridiflava* has acutely keeled dorsal scales. Like congeners, *B. juarezi* new species is viviparous.

RESUMEN. Una nueva especie de *Barisia* del bosque nebuloso de la Sierra Juárez, Oaxaca, México, tiene escamas postmentales paraleadas y una serie completa de escamas superciliares; y por lo tanto, es asignada al grupo *gadovi*. Esta difiere de las otras especies de este grupo (*gadovi* y *antauges*) por tener las regiones labiales distintivamente barreadas. Esta también tiene dos o más escamas suboculares y escamas dorsales sin quillas (solamente una escama subocular y quillas distintivas en *B. gadovi*) y el patrón del color dorsal con por lo menos trazas oscuras en forma de cheurones (galones) oscuros, dirigidas posteriormente (ausentes en *B. antauges*). Con una longitud hocico-cloaca máxima de 77 mm (N = 95), este es el miembro más pequeño del grupo *gadovi* y en colecciones anteriores, ha sido confundido con *B. viridiflava*, una especie del grupo *moreletii*, que es simpática y de tamaño similar. Todos los miembros del grupo *moreletii* tienen solamente una escama postmental y *B. viridiflava* tiene escamas dorsales agudamente aquilladas. Como sus congéneros, *B. juarezi* nueva especie, es vivípara.

INTRODUCTION

As generally understood, the anguid lizard genus *Barisia* consists of seven species arrayed in three species groups (Tihen, 1949). These species occur from northern Mexico southward to western Panama. Some species have comparatively wide distributions, such as *Barisia imbricata*, which occurs over

a broad area including the Sierra Madre Oriental, Sierra Madre Occidental, Mesa Central, and Sierra Madre del Sur; others are restricted to single mountains or isolated ranges (*B. viridiflava*, *B. levicollis*, and *B. antauges*). The habitats occupied by *Barisia* are primarily seasonally wet montane llanos, and forest-edge grassland in pine and/or oak woodlands or cloud forest. These habitats have been relatively poorly explored by biologists, in large part due to inaccessibility, and may remain poorly known owing to the rapid deforestation and habitat alterations by man. The extensive highlands of southern Mexico are not contiguous and consist of isolated mountain ranges and intervening valleys that constitute effective ecological barriers for montane organisms. These areas have a high level of species endemism. We describe here a new species of *Barisia* endemic to the Sierra Juarez in northern Oaxaca that was independently discovered by each of us. We name it in honor of one of Mexico's greatest heroes, Benito Juarez, a man who was also indigenous to the region.

Barisia juarezi new species

Figures 1-5

HOLOTYPE. University of Texas at Arlington (UTA) R-8485, an adult male, from the northern slope of the Sierra Juarez between 6.1 and 11.6 km (3.8 and 7.2 mi.) N crest of Cerro Pelon, Ixtlan District, Oaxaca, Mexico, 7 April 1979, by J.A. Campbell, L.S. Ford, J.E. Joy, Jr., and J.P. Karges at approximately 2500-2700 m elev. (original number, JAC-3708).

PARATYPES. Ninety-four, see Specimens Examined, below.

DIAGNOSIS AND DEFINITION. *Barisia juarezi* is a member of the *gadovi* species group as defined by Tihen

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Figure 1. Dorsolateral view of an adult male (LACM 130277, 77 mm SVL), paratype of *Barisia juarezi* new species photographed in life.

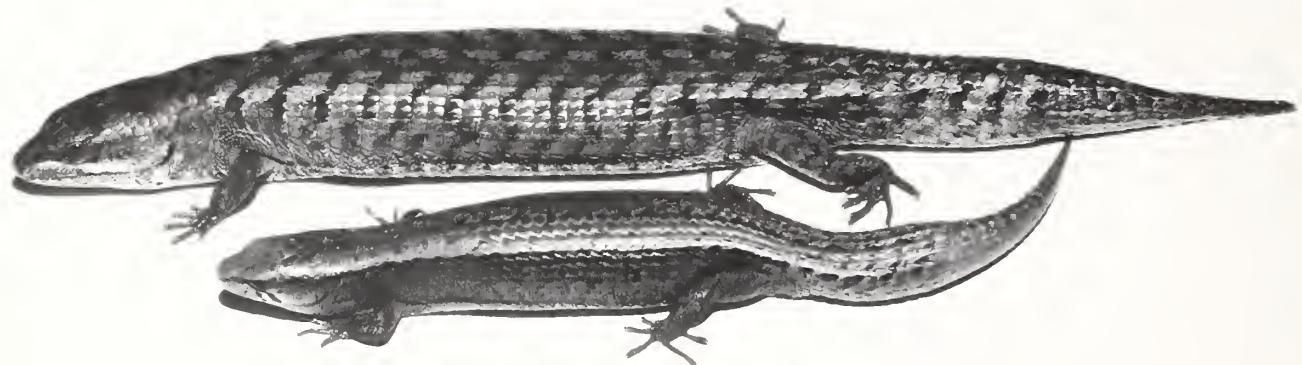


Figure 2. Dorsolateral views of adult female *Barisia gadovi* (upper, LACM 129612) and paratype of *B. juarezi* new species (lower, LACM 129615) photographed in life. The differences in facial markings, dorsal color pattern, and size are conspicuously illustrated.

(1949), with both paired postmental scales and complete series of superciliary scales. It is the smallest member of the group (maximum observed snout-vent length, 77 mm) and differs from the other species of the group, *B. gadovi* and *B. antauges* (here including *B. modesta*), by having two distinct dark diagonal labial bars with an intervening white bar, extending from the posterior supralabials to the orbit and along the lower border of the subocular (Figs. 1 and 2). The much

larger (to 102 mm SVL, Tihen, 1949) *B. gadovi* has a single, horizontal light supralabial stripe, and *B. antauges* has dark and light mottled supralabials but no stripes or bars. In addition, *B. juarezi* differs from *B. antauges* by the presence of at least traces of dark, posteriorly directed chevrons (Fig. 3), a characteristic shared with *B. gadovi* where the chevrons are generally more distinct (Fig. 4). *Barisia juarezi* and *B. antauges* both differ from *B. gadovi* in the presence of two or

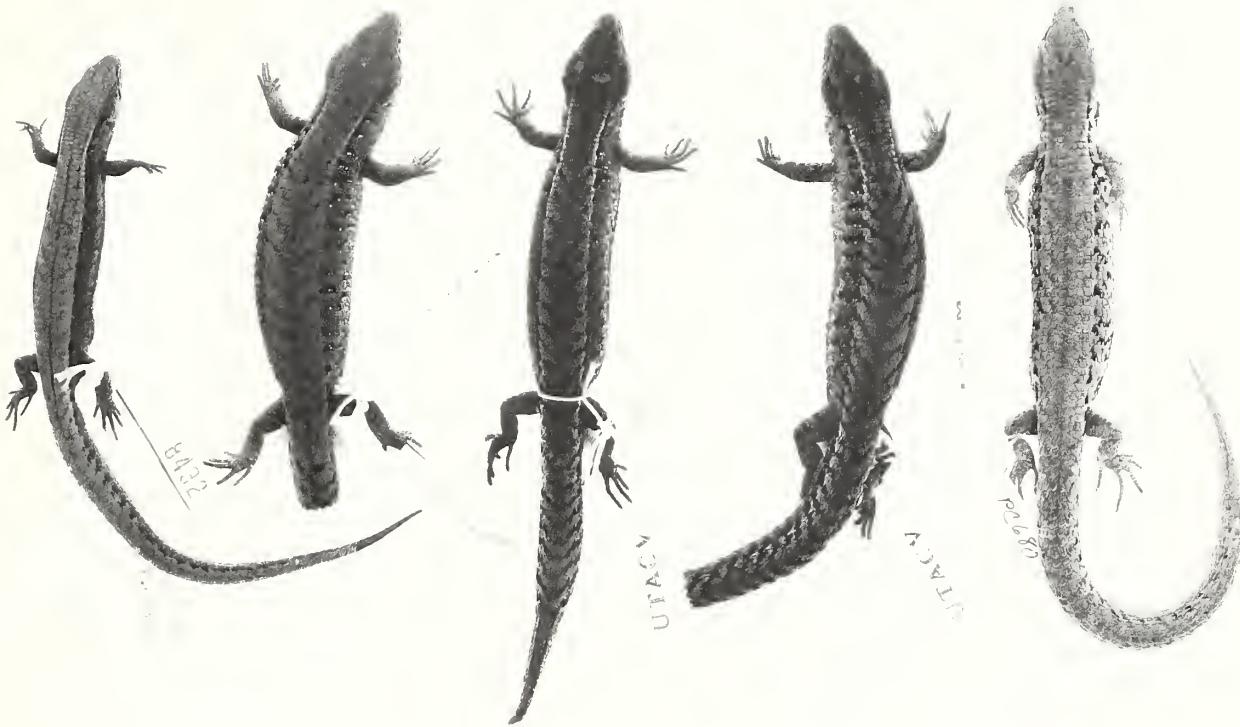


Figure 3. Variation in dorsal color pattern of male *Barisia juarezi* new species. Specimens (all paratypes) range in snout-vent length from 53 mm to 71 mm and are UTA R-8432, 8425, 5806, 8489, and LACM 130277 from left to right.

more suboculars (only one in *B. gadovi*) and smooth dorsal scales (distinctly keeled in *B. gadovi*).

DESCRIPTION OF HOLOTYPE. An adult male, 65 mm snout-vent length, with complete tail (89 mm) and total length (154 mm) to tail ratio of 0.58; head width, 9.75 mm; head length to anterior auricular margin, 13.0 mm; greatest head depth, 7.35 mm; horizontal length of right orbit, 2.45 mm; axilla-to-groin length, 39.5 mm; longest toe (fourth) on right hind foot, 5.92 mm, on right front foot, 4.57 mm.

Three anterior internasal scales, right side with large median and smaller lateral scale, occupying same amount of space as single left internasal (Fig. 5); two anterior internasals in medial contact posterior to rostral; rostral, first supralabial (by small lateral internasal on right side), nasals, posterior internasals, and supranasals in contact with anterior inter-

nasals; no postrostral; supranasals longer than wide, not in medial contact; right posterior internasal longer than wide and in medial contact with anterior element of divided left posterior internasal; anterior element of left posterior internasal generally rhomboidal and slightly larger than posterior element, effectively forming an anterior canthal; two left internasals equal in size to right; two postnasals on each side, lower nearly twice size of upper and more than half as large as nasal; single large loreal on each side, contacting third and fourth supralabials, both postnasals, posterior internasals (posterior element on left), single preocular, first superciliary, and narrowly contacting first medial supraocular on right side; frontonasal rhomboidal, about as long as wide, contacting both posterior internasals and both prefrontals; paired prefrontals in medial contact posteriorly, about as large as



Figure 4. Dorsal views of representative pairs of adult specimens of members of the *Barisia gadovi* species group. From left to right the specimens are *B. antauges*—BMNH 1903.9.30.122, 72 mm SVL and MBS 3685, 82 mm; *B. juarezi* new species—LACM 130277, 71 mm and UTA R-8489, both paratypes, 67 mm; and *B. gadovi*—LACM 121921, 93.5 mm and UTA R-5794, 74 mm.

frontonasal, abutting frontal; frontal large, twice as long as wide; five medial supraoculars and two small lateral supraoculars on each side; six superciliaries over each eye, first largest; frontoparietals rhomboidal, much smaller than adjacent frontal and parietals; supralabials 9/9, antepenultimate largest and last to reach orbit at posterior margin of second subocular; two elongate suboculars and three discrete postoculars on each side; primary temporals 4/4, lowest narrowly contacting posterior subocular on each side; secondary temporals 5/5; tertiary temporals 4/4, with small azygous scale on right between uppermost tertiary temporal and right paraoccipital; rosette of scales around interoccipital, including two parietals, interparietal (containing parietal eye in posterior half), two paraoccipitals and medially paired pos-

toccipitals; infralabials 8/7; sublabials 5/5, extending in series anteriorly to second infralabial and second pair of chinshields; five pairs of chinshields posterior to mental, first being medially paired postmentals; second pair of chinshields only other pair in medial contact; single medial gular scale between second and third pairs of chinshields.

Eight smooth nuchal scales across narrowest part of nape; granular scales extending from auricular opening posteriorly along lateral surfaces of neck and along lateral fold; dorsal and ventral body scales in parallel, regular (not oblique) rows both transversely and longitudinally; transverse dorsal scale rows from postoccipitals (inclusive) to level of posterior margin of thigh, 48; all dorsal scales smooth, in 14 longitudinal rows and of uniform size across midbody; an additional row

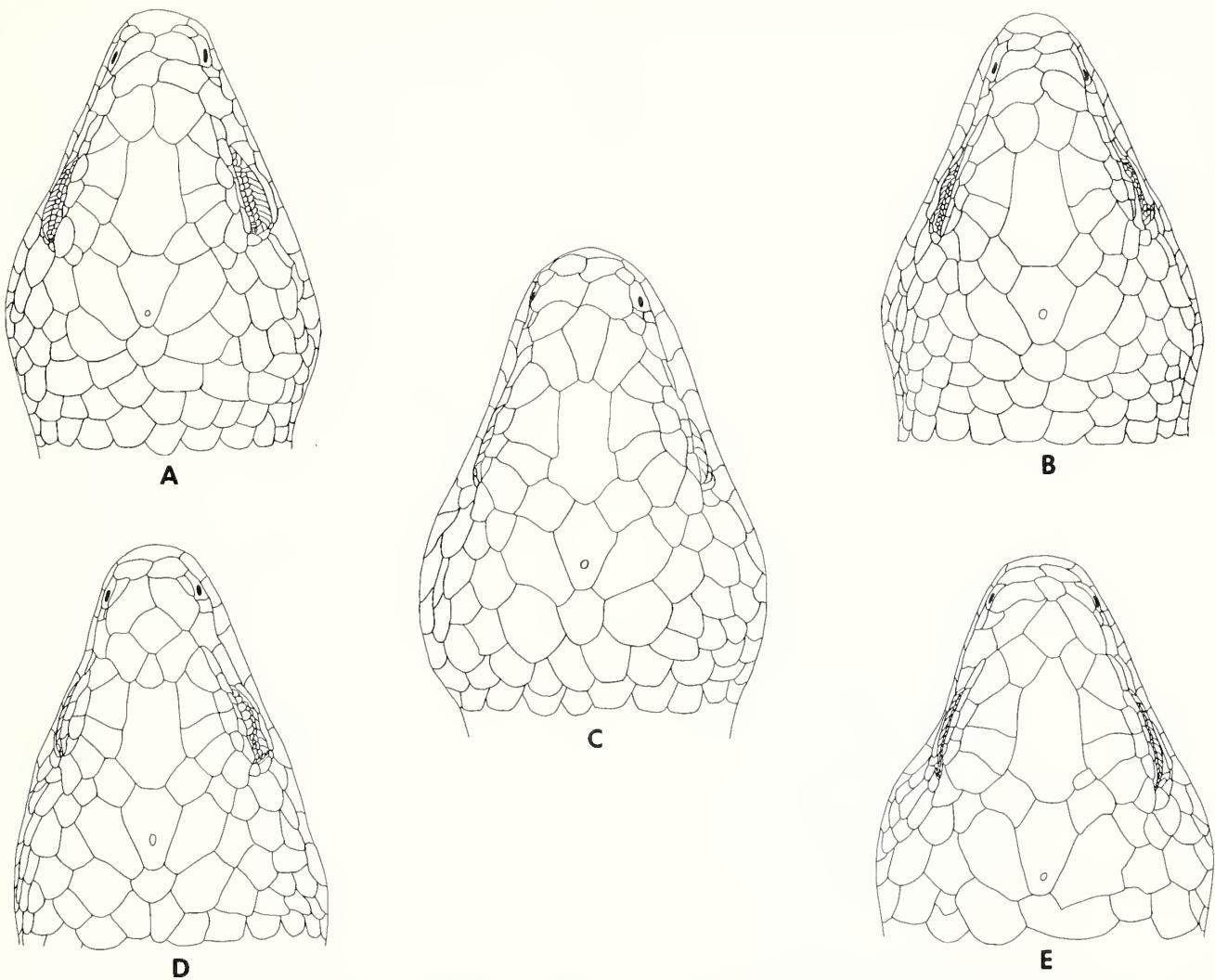


Figure 5. Variation in head scutellation of representative *Barisia juarezii* new species. Specimens (all paratypes) from A to E are: UTA R-4317, 8456, 8488, 4315, and 5806. See text for descriptions and terminology.

of slightly smaller scales along dorsolateral border of lateral fold on each side; ventral scales across midbody in 12 longitudinal rows; ventrals smooth, in 55 transverse rows from first gular to anterior edge of vent; tail complete with 70 caudal whorls and 23 scales around base; caudal scales arched transversely near base of tail, giving tail a longitudinally keeled texture.

Adpressed limbs separated by 11 transverse dorsal scale rows; enlarged, smooth, imbricate scales on anterior and dorsal surfaces of forelimbs and anterior and ventral surfaces of hind limbs, posterior surfaces with granular scales; toes clawed except for clawless second toe (injured) and freshly severed third toe on hind foot; 16 subdigital lamellae under fourth toe of right hind foot.

Dorsum above third and fourth longitudinal dorsal scale rows with uniform longitudinal pale brown stripe with darker brown spots on several middorsal scales; sides, between lat-

eral fold and third longitudinal scale row, darker brown than dorsum, with irregular, non-continuous dark brown bars (Figs. 1–3), consisting of dark brown individual scales, some white spots on lower posterior margins; individual dark brown scales scattered along dorsolateral portion of body, from nape onto tail, forming spotted line along body; dark brown spots scattered along middorsum and onto tail; ground color of dorsal surfaces of limbs and tail similar to dorsum; venter dark and mottled, individual scales usually containing much more dark pigment than pale; ventral surfaces of tail and limbs similar to venter; lighter areas of ventral scales metallic silver-blue in life and preservative; top of head and posterior part of jaws with pale reddish-brown ground color; preorbital region of face dark brown, including first superciliary scales, upper part of loreal and preocular scales above white suborbital stripe; suborbital stripe an anterior extension of diagnostic white labial bar, covering posterior half of sixth and anterior

third of seventh supralabial; dark brown diagonal bar, posterior to white bar (also diagnostic) on posterior half of seventh and anterior half of eighth supralabial; anterior five and posteriormost supralabials pale brown; anterior half of sixth supralabial also brown, completing diagnostic pattern of two dark diagonal bars with intervening pale bar on upper jaw; lateral surfaces of neck uniform brown.

VARIATION

We attempted to select from the type series a holotype specimen that was modal in as many features as possible. The following analysis of variation is thus focused on departures from these modal conditions in the same sequence as contained in the preceding description of the holotype. The analysis is based on all 95 specimens contained in the hypodigm (see Specimens Examined, below).

SIZE AND BODY DIMENSIONS

The largest specimen is a female (77 mm in SVL) but there is no significant difference between the mean sizes (Mann-Whitney $U = 81.82$, $P \ll 0.05$) of the 15 largest females ($\text{mean} \pm \text{SE}$, 70.1 ± 0.90) and 15 largest males (69.6 ± 0.79). Adult male *B. juarezi* have wider heads and larger jaws than females. In 43 individuals with SVL greater than 60 mm (21 ♂♂ and 22 ♀♀) there is a highly significant difference between the sexes in the snout-vent length/head-width ratio (Mann-Whitney $U = 208.72$, $P \ll 0.01$, ♂♂ 6.48 ± 0.12 , 5.77–7.83 and ♀♀ 7.52 ± 0.09 , 6.64–8.30). There is also a significant difference in relative tail lengths between the sexes ($|Z|$ —transformed Mann-Whitney $U = 4.334$, $P \ll 0.01$) calculated for 30 specimens greater than 50 mm SVL, with complete, unregenerated tails (♂♂ 1.38 ± 0.02 , 1.23–1.50, $N = 17$ and ♀♀ 1.33 ± 0.03 , 1.09–1.50, $N = 13$). The relatively longer tail of males results in a mean difference of one percent between males (57%) and females (58%).

SCUTELLATION

In general, we use the scale terminology of Tihen (1949) with modifications proposed by Waddick and Smith (1974). Occasionally we have found it necessary to redefine some conditions as they pertain to *B. juarezi*. The standard positions of several scales (e.g., frontal, nasals, rostral) of gerrhonotines provided reference points for identifying other scales.

The anterior internasals are most frequently paired (45 of 95 specimens); occasionally single (22 specimens including the holotype) or one or both (21 specimens) are divided to form three or four discrete scales (Fig. 5C). In four specimens, a single medial scale is present between the anterior internasals and constitutes a postrostral scale. In animals with four scales (both anterior internasals divided) in a lateral series behind the rostral, the medial pair of scales is best termed the medial internasals rather than medially paired postrostrels, since the postrostral is defined as a single medial azygous scale (Waddick and Smith, 1974), or if two postrostrels are present, they form a longitudinal series. We have not observed a longitudinal series of anterior and posterior

postrostrels in *B. juarezi*, but one specimen (UTA R-6096) does have a postrostral scale posterior to a nearly medial element of a divided anterior internasal. When divided into lateral and medial elements, the medial scale is usually larger than the lateral. The anterior internasals of each side contact medially behind the rostral in most specimens (85 of 94, 90.5%); in four specimens the medial contact of the anterior internasals is precluded by the contact of the rostral and enlarged supranasals (Fig. 5A); and in two others, medial anterior internasal contact is precluded by the rostral-postrostral suture.

The supranasals are separated from medial contact by the anterior internasals, posterior internasals, and postrostrels when present, in 72 specimens (77.4%). Individual supranasal scales are roughly triangular and usually longer than wide, although an individual specimen may have one supranasal wider than long on one side. Both supranasals are longer than wide in 53 (57%) specimens, both wider than long in 22 (23.6%), and one longer than wide and the other wider than long in 18 (19.4%). The number of animals with medial contact of the supranasals (21) approximately equals the number of specimens with both supranasals wider than long (22). On the dorsal surface of the snout, the paired scales posterior to the anterior internasals, postrostral, and supranasals are the posterior internasals, among the most variable head scales. Anterior contacts of the posterior internasals variously include the anterior internasals (rarely, Fig. 5D), postrostral (if present), the supranasals (if expanded, Figs. 5A, B), and anterior medial contact of the two posterior internasals (Fig. 5D). The posterior internasals vary in size relative to adjacent scales, and are often asymmetrical, with the scale on one side larger than its counterpart (Fig. 5C). Occasionally one of the posterior internasals is divided into anterior and posterior elements, the anterior element effectively forming a postrostral and the posterior element forming a canthal.

The frontonasal scale is either present (55 specimens), absent (37), or partially fused with the prefrontals (1). The frontonasal is bordered by the postrostral (if present and posteriorly placed), the posterior internasals, and prefrontals. The frontonasal is usually rhomboidal and about as long as wide (Fig. 5D), but sometimes longer than wide (Fig. 5C). The frontonasal varies from one-half to equal in size to the adjacent prefrontals. When the frontonasal is absent, the prefrontals are large and occupy the area where the frontonasal would be on other individuals (Figs. 5A, B). In six of the 37 specimens lacking a frontonasal scale, the prefrontals are partially fused, usually along the anterior half of the medial contact. The remaining 31 specimens lack frontonasals, and the paired posterior internasals and paired, fully divided prefrontals form a linear pattern of paired scales, medially divided, which in some cases also includes the enlarged supranasals and anterior internasals (Figs. 5A, B). There are usually five, occasionally four, medial supraoculars and usually two or three lateral supraoculars but rarely none, one, or four.

The scales on the side of the head of *B. juarezi* are also variable and their definitions require some clarification. Im-

mediately posterior to the nasals are the postnasals. These are usually divided into upper and lower elements but occasionally are fused to a single scale, or, more rarely, divided into three small elements. Usually, a single loreal is present on each side but occasionally there are two on one or both sides of the head. When divided, the loreal is usually divided horizontally into upper and lower elements. The upper element is usually the smaller scale and owing to its position it forms what others (Waddick and Smith, 1974; Campbell, 1982) have called an anterior canthal or cantholoreal. Rarely, the upper or lower loreal elements may be further divided into anterior and posterior elements; in these cases (four specimens) there are three loreal scales. Between the loreals and the orbit is a single preocular (rarely divided into upper and lower elements).

The complete series of supraciliary scales extends from the canthus to the posteriormost medial supraocular. Most specimens (91 of 94, 95.8%) have six supraciliaries in both series (68 specimens) or in at least one series (923 specimens). Twenty-one animals have five in one or both series, four have seven in one or both series, and one specimen has only four on one side. The anteriormost supraciliary scale extends anterior to the eye and is somewhat expanded. In this respect, it could be called the posterior canthal (see Waddick and Smith, 1974, fig. 3 for *Gerrhonotus liocephalus*), but we prefer to include it in the supraciliary series as did Bogert and Porter (1967, fig. 5) for *Abronia mixteca*.

In decreasing frequency, there are two, three, or four suboculars, of which the posteriormost is occasionally in contact with the lowest primary temporal. The small but discrete postocular scales occur in a vertical series of two, three, or rarely four scales bordering the posterior margin of the eye.

There are typically four primary temporals, sometimes three or five, in a linear series extending from the supralabial-subocular margin upward to and abutting the frontoparietals. The four secondary temporals, sometimes five, are posterior to the primary temporals. The two uppermost tertiary temporals are in medial contact across the back of the head, forming the postoccipitals (and the first row of transverse dorsal scale rows, see below).

Most specimens have either nine or 10 supralabials on at least one side, but 38 (40.4%) have 10/10, 20 (21.3%) have 9/9, and 26 (27.7%) have nine on one side and 10 on the other. Ten specimens have 11 supralabials on at least one side, and two specimens have 11 on both sides. The most frequent number of infralabials is eight on at least one side (85.1%), and the modal class (41 specimens) has eight on both sides. Other specimens have nine on at least one side (33 specimens, 35.1%), nine on both sides (seven specimens), seven on one or both sides (13 specimens), and a single specimen (LACM 130277) has five infralabials on one side.

We began the counts of transverse rows with the row immediately behind the occipital scale and ended at the level of the posterior edge of the hind limbs. The count was made along the middorsal row. The range for all 95 specimens was 42–55 ($x = 47.34 \pm 2.20$). The number of longitudinal dorsal scale rows, counted at midbody, was usually 14 enlarged scales of similar size (84.21%, 80 of 95 specimens). There

was frequently an additional row of slightly smaller scales on each lateral border. In fact, 62 specimens (65.3%), including the holotype, have this extra row on both sides, or rarely on only one side. Nineteen specimens have only 14 discrete longitudinal scale rows, 14 specimens have 16 rows, and 59 specimens have 14 discrete rows and two additional lateral rows of smaller scales. Two specimens have 14 rows and an additional row only on one side, and one specimen has 12 rows and a lateral row of reduced scales on each side.

The ventral scales are arranged in parallel rows in both longitudinal and transverse series. The transverse series was counted from the most anterior medial gular scale behind the postmentals (wedged between enlarged chinshields) to and including the scale row lining the anterior margin of the vent (preanals). This count was possible on 93 specimens and the number ranged from 50 to 59 ($x = 54.3 \pm 1.92$). The number of ventral rows, counted at midbody between the lateral folds, was 12 in 91 specimens (95.79%), 13 in one specimen, and 14 in three. The preanal margin consists of four, rarely three, large scales with smaller scales lining the lateral edges of the vent. Fifteen specimens have complete, unregenerated tails, with 69–77 (71.0 ± 0.59) caudal whorls. There are 16 to 19 subdigital lamellae under the fourth toe of the hind foot.

COLOR AND PATTERN VARIATION

In life, the dorsum is uniformly light brown, but varies from reddish-brown to tan, often with a bronze tint. The dark brown posteriorly directed dorsal chevrons form a "herringbone" pattern, which may be bold or faint (Figs. 1–3). This pattern is the predominant dorsal pattern of *B. juarezi* and occurs in both sexes (23 of 35 males; 26 of 39 females). Less frequently, the dorsal pattern is obscured to such an extent that the middorsum is entirely uniform (10 males; 12 females), contrasting with the darker, barred dorsolateral surface. In five specimens, a distinct narrow, dark middorsal stripe is present, extending from the occipital or nuchal region posteriorly onto the tail. Frequently, the middorsal area is dark, forming an indistinct stripe through the centers of the chevrons, particularly distinct posteriorly and onto the tail.

The sides of the body are darker than the dorsum, especially in subadult and juvenile specimens. Dark brown scales mark the dorsolateral border from the nape posteriorly onto the tail. In adults, the sides have dark erratic bars from the dorsum to the lateral fold, consisting of dark brown scales, some with white or cream-colored flecking along the posterior scale margin. The lateral bars are most distinct in adult males and much less distinct or occasionally absent in females. The lateral pattern is obscured in juveniles by the entirely dark lateral surface. The ground color of the lateral fold and granular scales on the sides of the neck is gray-brown, with some scattered white flecks, sometimes covering entire scales.

The ventral color pattern is sexually dichromatic. In males, the venter is darkly mottled, with limited patches of pale pigmentation usually confined to the posterior edges of individual scales. In life, and to a lesser extent in preservative,

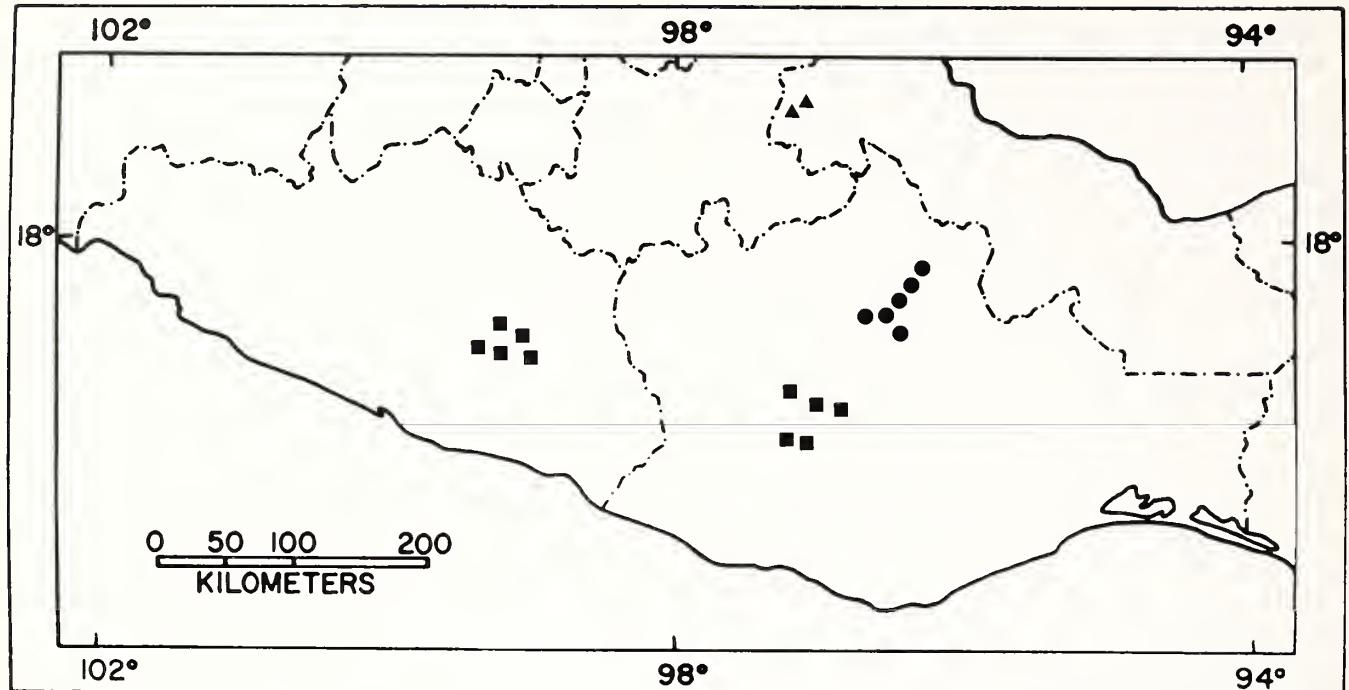


Figure 6. The geographical distribution of the three members of the *Barisia gadovi* species group (*antauges*—▲, *gadovi*—■, and *juarezi* new species—●). All three species occur principally in pine-oak habitats in portions of the Sierra Madre del Sur in Guerrero, Oaxaca, and Veracruz, Mexico.

the paler areas have an iridescent, metallic blue tinge. Rarely, a male will have more pale ventral pigment than dark. Females, on the other hand, have much paler iridescent blue-gray or cream venters, with mottling so diffuse that the venter is nearly uniform. Some dark mottling occurs in the gular region of some females, and occasionally large dark blotches occur on individual scales. In juveniles, the venter is dark brown, like the lateral surfaces, with heavy mottling. The gular region of juveniles is paler than the remainder of the venter, with distinct sublabial stripes, contiguous with the diagnostic supralabial bars.

In all individuals, the dorsal surfaces of the limbs and tail are the same as the dorsal ground color, and the ventral color of the appendages is that of the venter. Regenerated portions of autotomized tails are a much lighter brown or tan than the original portions of the tail, and the tail is frequently enlarged into a bulbous swelling at the point of regeneration.

COMPARISONS

The two species most similar to *B. juarezi* are the two other members of Tihen's (1949) *gadovi* group, *B. gadovi* Boulen-ger and *B. antauges* Cope [here including *B. modesta* (Cope) *fide* H.M. Smith, *in litt.*]. The *gadovi* group was defined by Tihen (1949) as *Barisia* having paired postmental scales and complete superciliary series. The other two species groups, *moreletii* and *imbricata*, have either single postmentals or incomplete superciliary series. The *gadovi* group occurs west of the Isthmus of Tehuantepec in the highlands of south-

central Mexico (Fig. 6). Within the group, *B. juarezi* is most similar to *B. antauges* in size, color pattern of the head, and squamation. The following comparisons are based on the seven known specimens of *B. antauges* (see Specimens Examined, below). The maximum snout-vent length in *B. juarezi* ($N = 95$) is 77 mm (UTA R-8696) whereas the largest *B. antauges* (USNM 30221, holotype) is 85 mm. The number, placement, and variation in head scales are similar in both *B. juarezi* and *B. antauges*. There is a rosette of apparently homologous scales surrounding the interoccipital scale in both species. A postrostral scale is present in all specimens of *B. antauges* but is absent as a discrete medial scale in more than half (55.5%) of the specimens of *B. juarezi*. The presence of a single medial frontonasal and an anterior canthal on one or both sides is variable in both species. Additional shared similarities in head scales include: eight to 10 supralabials on each side; five or six superciliaries per side; two or three lateral supraoculars; five or six medial supraoculars; four or five primary and secondary temporals; and five to seven tertiary temporals (see Variation, above). In *B. juarezi*, the preocular is usually a large scale extending from the upper anterior portion of the orbit forward to the distinct loreal(s) and downward to the supralabials. The preocular in *B. antauges* is less distinct and usually fused with the lower and posteriormost loreal. The smooth dorsal scales are arrayed in 14 to 16 longitudinal rows.

The presence of smooth dorsal scales easily distinguishes both *B. antauges* and *B. juarezi* from the other group member, *B. gadovi*, which has acutely keeled middorsal scales.

Additional scale characteristics which differentiate *B. juarezi* from *B. gadovi* are: usually six (range 4–7) superciliaries in *B. juarezi* and usually four (range 3–5) in *B. gadovi*; the loreal is usually single on each side in *B. juarezi* and paired (upper and lower elements, with upper forming an anterior canthal) in *B. gadovi* (and *B. antauges*); *Barisia juarezi* has two or three suboculars, whereas *B. gadovi* has a single, elongate scale; and the longitudinal dorsal scale rows of *B. juarezi* number 14 (sometimes 16, see Variation, above) whereas there are usually 18 (occasionally 16) in *B. gadovi*. The differences in color pattern of the side of the head (cheek) between *B. juarezi* and *B. gadovi* are distinct. In *B. gadovi*, there is a long, horizontal, white stripe on the supralabials extending from the angle of the jaw to the nostril. The face stripes are both light and dark and diagonal in *B. juarezi*. The most conspicuous similarity between *B. juarezi* and *B. gadovi* is the otherwise unique dorsal color pattern of posteriorly directed dark chevrons, most distinct in adult males (Fig. 4). These are not present in *B. antauges*.

Two other species of *Barisia*, each allocated to different species groups (Tihen, 1949), occur in the highlands of north-central Oaxaca. *Barisia imbricata* (of the *imbricata* species group) is known from several localities in the region (Guillette and Smith, 1982), including the Sierra Juarez. *Barisia viridiflava*, member of the *moreletii* group (Tihen, 1949), and *B. juarezi* are sympatric (see Habitat, below). *Barisia imbricata* is easily distinguished from *B. juarezi* by its large size (maximum SVL approximately 140 mm), low number (2–4) of superciliaries in incomplete series, rugose head scales deeply indented at sutures, acutely keeled middorsal scales in less than 45 transverse rows, and the lack of diagonal face stripes. More similar to *B. juarezi* is *B. viridiflava*, as borne out by the presence of many specimens of *B. juarezi* masquerading as *B. viridiflava* in some collections. Overall sizes of *B. juarezi* and *B. viridiflava* are similar (maximum SVL of *viridiflava*, 75 mm). The differences in color and pattern are distinct; *B. viridiflava* usually has at least one (middorsal) or three prominent longitudinal dark stripes in the paler brown dorsal area, whereas *B. juarezi* has dark chevrons. The light jaw stripe in *B. viridiflava* is horizontal and extends posteriorly from the loreals across the suboculars to the lower temporals. The middorsal scales of *B. viridiflava* are distinctly keeled, unlike *B. juarezi*. Most important of the scale differences is the single postmental, a character which is diagnostic for separating the *moreletii* and *gadovi* groups.

HABITAT AND BIOLOGY

Barisia juarezi occurs in cloud forest at elevations from 2000 to approximately 2800 m on the northern slopes of the Sierra de Juarez (Fig. 6). The cloud forest merges with pine-oak forest at elevations from 2800 to 3000 m on the summits and adjacent ridges. The dominant forest plant species are oaks (*Quercus* sp.), some pine (*Pinus ayacahuite* and *Pinus* sp.), madrone (*Arbutus xalapensis*), sweetgum (*Liquidamber* sp.), and a tree fern (*Cyathea mexicana*). Epiphytic mosses, bromeliads, ferns, and orchids are abundant and dense on trees, and unlike the higher more open pine-oak forest, there

is a dense understory consisting of small trees, shrubs, vines, and herbs. Second growth is dense in areas of fallen trees and lumbered clearings. Rain occurs in the habitat in all months but is heaviest during the period of June through October or November. Most of the precipitation comes from moisture-laden winds from the Gulf of Mexico.

Barisia juarezi is almost strictly terrestrial, occurring on the forest floor and in clearings, seeking refuge under rocks, logs, and in the leaf litter. Specimens caught on the surface were sunning or actively foraging in the patches of dappled sunlight penetrating the canopy.

Like congeners, *Barisia juarezi* is viviparous. A pregnant female (UTA R-8488) collected 7 April 1979, had three well-developed, pigmented embryos in the oviducts. The degree and pattern of pigmentation and size of these embryos was similar to those of the smallest field-collected individuals (25, 27, 28.5 mm SVL), indicating that they were nearly full-term. Additionally, several *B. juarezi* have given birth in captivity in our laboratory.

The female reproductive cycle apparently involves over-winter gestation, with parturition occurring in late spring, immediately prior to the summer monsoon season. Females attain sexual maturity at approximately 60 mm SVL, and enlarged ovarian follicles were present in a single female collected 2–3 April and seven collected in June and early July. Oviductal eggs (embryologic stage not determined but still largely yolk masses) were found in four females preserved in mid-July and August. A female collected in winter (early January) also contained large oviductal eggs. The smallest field-collected juveniles were obtained in early April, further corroborating pre-monsoon natality. Young-of-the-year, between 30 and 40 mm SVL, have been collected throughout the summer months.

Rainfall appears to modify substantially the seasonal activity of *B. juarezi*. Most specimens were collected during the wet season. In April 1979, a normal dry season, they were common in leaf litter and under surface rocks and logs. The soil was moist, indicating some recent rain. Following a severe drought across southern Mexico and a delayed monsoon in the winter of 1982–83, we found no specimens in early June 1983, and the soil was dry, even under surface objects.

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SPECIMENS EXAMINED

Barisia juarezi (paratypes, 94). MEXICO: Oaxaca; Ixtlan District; 51 km (by rd.) N Ixtlan de Juarez, LACM 15158; 54 km N Guelatao on Mex. Hwy. 175, 2510 m, LACM 122496; 60.3 km (34.7 mi. by rd.) NE Guelatao, Mex. Hwy. 175, 2316.5 m (7600 ft.), LACM 125365; 52.2 km (32.4 mi. by Hwy. 175) N Guelatao, 2515 m, LACM 129614–15; 55.6 km (34.5 mi. by Hwy. 175) N Guelatao, 12.6 km (7.8 mi. by rd.) NE jct. of rd. to Comaltepec, LACM 130271; 17.9 km (11.1 mi. by rd.) S Vista Hermosa, LACM 130272–84; 7.2 km (4.5 mi. by rd.) N Cerro Pelon, UTA R-3409–15, CAS 142597; 3.2 km (2 mi.) N Cerro Pelon, UTA R-3832; 9.4 km (5.8 mi.) N crest Cerro Pelon, UTA R-4309–17; 9.8 km (6.1 mi.) N crest Cerro Pelon, UTA R-4305–07, 4863–64; 10.5 km (6.5 mi.) N crest Cerro Pelon, UTA R-5803–06; 11.4 km (7.1 mi.) N crest Cerro Pelon, UTA R-5807–09; 9.7 km (6 mi.) N crest Cerro Pelon, UTA R-60996–100; 11 km (6.8 mi. by rd.) N Cerro Pelon, UTA R-7741, 7879, 8695–96; 10.2 km (6.3 mi.) N crest Cerro Pelon, UTA R-8425, 8430–32; 8.1–11.6 km (5–7.2 mi.) N Cerro Pelon, UTA R-8464; 6.1–11.6 km (3.8–7.2 mi.) N crest Cerro Pelon, UTA R-8484, 8486–95; 11.6 km (7.2 mi.) N crest Cerro Pelon, UTA R-8503–04, 8512–15; 12.1 km (7.5 mi.) N crest Cerro Pelon, UTA R-8511; ca. 16.1 km (10 mi.) SE Llano de las Flores, 2819.4 m (9250 ft.), AMNH 100711; 9.7 km (6 mi.) NE Cerro Pelon, 2194.6 m (7200 ft.), AMNH 100719; 61 km NE (by Mex. Hwy. 175) Guelatao, MVZ 112393; 52 km NE (by Mex. hwy. 175) Guelatao, MVZ 112394; Cerro Juarez, TCWC 36536–37; 10 km (6.2 mi.) NE Cerro Pelon, 52.4 km (32.5 mi.) SSW Valle Nacional, UMMZ 134015; 11.3 km (7 rd. mi.) NE Cerro Pelon, 2133.6 m (7000 ft.), UNM 25505; 4.8 km (3 mi.) E Cerro Pelon, UNM 30770–71; 11.9 km (7.4 mi.) E Cerro Pelon, UNM 30772–73; Vista Hermosa, Comaltepec, UCM 49305.

Barisia antaages (including *B. modesta*, 7). MEXICO: Veracruz; Pico de Orizaba, USNM 30221 (holotype), USNM 7084A–C (syntypes of *B. modesta*), CAS 98681, BMNH 1903.9.30.122, MBS 3685.

Barisia gadovi levigata (54). MEXICO: Oaxaca; Vic. Tejocotes, AMNH 102658–72, 102674–83, UNM 22756, 22781–82, UTA R-5793–98, LACM 102984–86, 121917–24, 121926; 13.2–15.5 km W (by rd.) San Vicente Lachixio,

LACM 125366–67; 10.4 km WSW (by rd.) San Vicente Lachixio, LACM 129613, MVZ 164778; Sierra de Cuatro Venados, LACM 125368–69; 25–25.3 km (15.5–15.7 mi. by rd.) W Zaachila, LACM 129611–12.

Barisia gadovi gadovi (46). MEXICO: Guerrero; Omilteme (and vicinity), MCZ 42703–15, 96804, UNM 6016, 26444, TCWC 9900–08; Chilpancingo, KU 23792–94; 7.2 km (4.5 mi.) W Mazatlan, TCWC 9897–99, 11383–84, 11536; Aso-leadero, 45 km (airline) WNW Chilpancingo, KU 105837–39; 6–12 km SW Filo de Caballo, KU 182656–64.

Barisia viridiflava (217). MEXICO: Oaxaca; Sierra de Juarez; Cerro Pelon, LACM 109296–99, 109384, 121931–37, CM 41256; 1.1 km (0.7 mi.) NE Cerro Pelon, LACM 121939–40, UTA R-5812–13, 7996, 8481–82; E Cerro Pelon, AMNH 98043; 49 km (by rd.) N Ixtlan de Juarez, LACM 15157; 49 km (by Mex. Hwy. 175) NE Guelatao, CAS 139904; 37 km (by rd.) N Guelatao, LACM 122500; 11.3 km (7 mi.) NNW Ixtlan de Juarez, CAS 87286, 87290; 14.5 km (9 mi.) NNE Guelatao, UTEP 5167; Cerro Humo Chico, UCM 38782–85, 44347–49; Llano de Las Flores, UMMZ 118808–09, 119631 (6), 124093, 125876 (4), AMNH 89647–51, 89827–30, 98044–45, UIMNH 60152–61, KU 70805–14; Llano de English, UIMNH 60137–51; 6.4 km (4 mi.) S Llano de las Flores, AMNH 89641–43, 90992–93, 90995, 100720; 11.8 km (7.3 mi.) NE Cerro Pelon, AMNH 102716; 8.7 km (5.4 mi. by rd.) N El Carrizal, AMNH 100717; 8.1 km (5 mi.) N El Carrizal, AMNH 102718–19, 102721–25; Cerro San Felipe, LACM 122497–99, 125372–77, UCM 41061–62, 48327–29, USNM 113220, UMMZ 126256 (5), 126257, 126258 (3), FMNH 99023–36, 112026, MVZ 112389–92, 140643–48, 162291–98, AMNH 90982–91, 103703, UMM 15495–504, UIMNH 60122–36; 12.9 km (8 mi.) W Cumbre del Estudiante, AMNH 97211; 2.4 km (1.5 mi.) N Campo Conchal, 27.4 km (17 mi. by rd.) NW Tamazulapan, LACM 131525–26; Mt. Zempoaltepec, LACM 15154–56, 62446, 130790, AMNH 90096, USNM 47184–85, 47599.

Barisia moreletii (5). MEXICO: Chiapas; 11 km (6.8 mi.) SE San Cristobal de las Casas, LACM 58102–04; 12.6 km (7.8 mi.) SE San Cristobal de las Casas, LACM 61209; 1.6 km (1 mi.) S San Cristobal de las Casas, LACM 74284.

Barisia imbricata (5). MEXICO: Oaxaca; 1 km (0.6 mi. by rd.) N Machin, 41.9 km (26 mi. by Mex. Hwy. 175) N Guelatao, LACM 130125; Veracruz; Pico de Orizaba, LACM 121929, 131443, 131445–46.

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AN EARLY MIocene Pinniped OF THE GENUS
DESMATOPHOCA (MAMMALIA: OTARIIDAE)
FROM WASHINGTON

Lawrence G. Barnes

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AN EARLY MIocene PINNIPED OF THE GENUS *DESMATOPHOCa* (MAMMALIA: OTARIIDAE) FROM WASHINGTON

Lawrence G. Barnes¹

ABSTRACT. The extinct otariid pinniped genus *Desmatophoca* Condon, 1906, is represented by two rare sea lion-like species that are relatively large and highly derived, in comparison with most other contemporaneous fossil otariids. The type and only previously described species of the genus is *Desmatophoca oregonensis* Condon, 1906, which was known only by the holotype skull and a questionably referred humerus from late Early to early Middle Miocene rocks referred to the Astoria Formation in Oregon, U.S.A. Another partial skull from the same formation is referred here to the same species.

A new species of *Desmatophoca*, *D. brachycephala*, has been discovered in slightly older rocks of Early Miocene age, also referred to the Astoria Formation, that are exposed on the north side of the Columbia River in Washington, U.S.A. *Desmatophoca brachycephala*, like *D. oregonensis*, is known by a skull of a male. It is distinguished from the latter species by having a relatively wider skull with a shorter rostrum, larger diameter canines, more derived cheek tooth structures, wider interorbital region, and larger mastoid processes. These and other differences make *D. brachycephala* a more derived species than *D. oregonensis*, and indicate that the distinctive otariid subfamily Desmatophocinae existed earlier in time than has previously been documented and must have had a significant early evolutionary history. The group is only known by fossils from the eastern North Pacific margin. Contrary to some previously published statements, there are enough substantial morphological differences between the Desmatophocinae and another fossil subfamily, the Allodesminae, to continue to classify them separately.

INTRODUCTION

Desmatophoca oregonensis Condon, 1906, was one of the first fossil otariid pinnipeds described in the scientific literature, and was for many years also the geologically most ancient one known. This sea lion-like animal has been discussed by many subsequent writers, and has figured in discussions of the origin of the family Otariidae (*sensu lato*; including sea lions, fur seals, walruses, and fossil taxa), yet it is still relatively poorly understood. It appears to be a rare species and is known in the previously published literature only by the holotype cranium (associated with an undescribed mandible fragment and some incomplete postcranial bones; see Packard and Kellogg, 1934:20) and a subsequently

referred isolated humerus (Packard, 1947). These fossils are all from rocks in the Newport Embayment that have been referred to the Astoria Formation (late Early to early Middle Miocene age), and are exposed on the coast of Oregon near Newport, Lincoln County (Howe, 1926; Packard and Kellogg, 1934:5–19, fig. 1; Moore, 1964; Ray, 1976). I consider the identity of the humerus to be tenuous, and shall not make further reference to it in this study.

Desmatophoca oregonensis has been the subject of widely differing taxonomic opinions. Condon (1906) believed that it had features of the family Otariidae as well as of the Phocidae (true seals). Wortman (1906) made the same claim. He correctly interpreted the species as the most primitive fossil pinniped then known, but gave its age as probably Oligocene and, citing characters he interpreted as similar to those of *Patriofelis* Leidy, 1870, reiterated his earlier (1894) theory that the pinnipeds evolved directly from oxyaenid creodonts. Kellogg (1922), while incorrectly concluding that *D. oregonensis* was younger geologically than another early species, *Allodesmus kernensis* Kellogg, 1922, stated unequivocally (1922:62) that it was a true otariid and not related to phocids. Packard and Kellogg (1934:24) later concluded that *D. oregonensis* was geochronologically older than *A. kernensis*, a currently held view (Barnes, 1972). Mitchell (1966) suggested that *D. oregonensis* was in some ways a suitable ancestor of later true sea lions, or (1968:1888, fig. 16) of all the Otariidae (*sensu lato*), but later, after the discovery of enaliartines, he considered it to be an early and aberrant offshoot of the otariid lineage (Mitchell, 1975; and see Barnes, 1972:62). Hay (1930), indicating a more distant relationship, named a new family, the Desmatophocidae, to contain it. Simpson (1945) suggested that Hay's family might instead best be regarded as a subfamily of the Otariidae, but he did not use such a rank in his classification. Mitchell (1966) and Barnes

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(1972) both used the subfamily rank, but they included within the subfamily Desmatophocinae the even more aberrant and highly derived species of *Allodesmus* Kellogg, 1922. Repenning and Tedford (1977:74; see also Repenning, 1976; King, 1983:129–130) recognized a separate family Desmatophocidae within the superfamily Otarioidea, but they retained *Allodesmus* within it. Mitchell (1968, 1975) and Barnes (1979, and in press) classified Desmatophocinae and Allo-desmiae as equal units, along with several other subfamilies (both extant and extinct), within a single, broadly defined pinniped carnivore family, the Otariidae (see Barnes, Domning, and Ray, 1985:table 1). It is in the latter taxonomic context that I treat the subfamily Desmatophocinae in the present study. The Recent sea lions, fur seals, and walruses were also classified by Hall (1981) within one family, the Otariidae, but he used the subfamily name Rosmarinae rather than Odobeninae for the walruses, and included phocids and otariids in the order Pinnipedia instead of the Carnivora.

Most of the various other fossil species, both named and unnamed, that have been classified in the Desmatophocinae by Mitchell (1966) and Barnes (1972), have subsequently been reassigned to other subfamilies (Mitchell, 1975; Repenning and Tedford, 1977; Barnes, 1979, and in press). The concept and content of the Desmatophocinae has thus become much reduced to include only one named species, *Desmatophoca oregonensis*.

A new fossil species belonging to the genus *Desmatophoca* Condon, 1906, has recently been discovered in Washington, and it is the purpose of this paper to describe and diagnose it. The new specimen is from the Astoria Formation, which is part of a sequence of rocks on the north side of the Columbia River that has been prospected extensively by J.L. Goedert and G.H. Goedert. The type locality of the new species of *Desmatophoca* has produced a diverse assemblage of vertebrates, including other mammals and fishes. Among these are at least two additional species of otariid pinnipeds, but they are not yet known by enough material to be more precisely identified. The invertebrates from the Lincoln Creek Formation, which directly underlies the Astoria Formation near Knappton, have been recently described by Zullo (1982—barnacles), Rigby and Jenkins (1983—sponges), and Moore (1984—mollusks). The latter author reviewed the history of collecting and research in the Knappton area and described the geographic and geologic setting (Moore, 1984:figs. 1, 2).

METHODS AND MATERIALS

The holotype of *Desmatophoca brachycephala*, new species, was originally discovered in at least three separate sections of a broken concretion, and some of its parts are still missing. The different sections were joined with plastic resin, and the same material was also used to fill some vacuities. At the rostral extremity, remnants of the canines and incisors were only tenuously attached by rock matrix to the rest of the cranium. They now retain their original positions relative to the mostly missing extremity of the snout only because of this resin, which was poured in prior to removal of the surrounding rock. For economy and to avoid jeopardizing the

integrity of the specimen, the rock was left within the right orbit. Because of the crushing of the bullae and the hardness of the matrix, it was decided not to attempt to open either tympanic cavity of the holotype at this time.

In the restorations of the skulls (Figs. 3, 4b, 5, 7, 9), only those parts that are preserved on at least one side of a skull are shown in solid lines. All other missing parts are represented by dashed lines. The anatomical terminology used here is adapted from that used by Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). Those skull measurements in Table 1 which are the same as those that were defined by Sivertsen (1954:18–20) are identified by the same numbers, in brackets, that were given them by Sivertsen. Other measurements are as defined by Barnes (1972:fig. 1; 1979:4–5).

A complete synonymy and an emended diagnosis of the subfamily Desmatophocinae are given here. The latter is partly based on characters listed by Mitchell (1968:1893–1894) and by Repenning and Tedford (1977:10–11, 74), with appropriate modifications. Geochronologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979) following the revised radiometric scale of Dalrymple (1979), and the correlations proposed by Addicott (1976), Ray (1976), Armen-trout (1981), and Moore and Addicott (1987).

The acronym, LACM, is for the Natural History Museum of Los Angeles County, Los Angeles, California. An author and date in parentheses following a taxonomic name indicates my use of that name at a different rank than originally proposed. Millions of years ago (mega-annum) is abbreviated ma. Anatomical abbreviations used in the illustrations are explained as follows:

- ac—alisphenoid canal
- at—auditory tube (= musculotubular canal, including eustachian tube)
- Bo—basioccipital
- Bs—basisphenoid
- cc—carotid canal (posterior aperture)
- eam—external acoustic meatus
- fh—hypoglossal foramen
- fi—incisive foramen (= palatine fissure)
- fio—infraorbital foramen
- fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
- flp—posterior lacerate foramen
- fo—foramen ovale
- fop—optic foramen
- fpal—palatine foramen
- fpp—posterior aperture of palatine foramina
- Fr—frontal
- fsm—stylomastoid foramen
- gf—glenoid fossa
- hf—tympanohyal pit (= hyoid fossa)
- Ju—jugal
- mp—mastoid process
- Mx—maxilla

Na—nasal
 Oc—occipital
 occ—occipital condyle
 Pa—parietal
 Pal—palatine
 Pmx—premaxilla
 Ps—presphenoid
 Pt—pterygoid
 pp—paroccipital (= jugular) process
 Sq—squamosal
 tb—tympanic bulla

SYSTEMATICS

Class Mammalia Linnaeus, 1758
 Order Carnivora Bowdich, 1821
 Infraorder Arctoidea Flower, 1869
 Parvorder Ursida Tedford, 1976
 Family Otariidae Gill, 1866

INCLUDED SUBFAMILIES. Enaliarctinae Mitchell and Tedford, 1973; Otariinae (Gill, 1866); Desmatophocinae (Hay, 1930); Allodesminae (Kellogg, 1931); Imagotariinae Mitchell, 1968; Dusignathinae Mitchell, 1968; Odobeninae (Allen, 1880).

Subfamily Desmatophocinae (Hay, 1930) Mitchell, 1966

Desmatophocidae Hay, 1930:557, as a family of the suborder Pinnipedia, order Carnivora, to include *Desmatophoca*.

Desmatophocinae (part). Mitchell, 1966:4, 39, 40; Barnes, 1972:5, as a subfamily of the family Otariidae, to include *Desmatophoca*, *Allodesmus*, and less precisely identified species, and, according to Mitchell (1966:39, 40), *Dusignathus* Kellogg, 1927, as well.

Desmatophocinae (Hay, 1930). Mitchell, 1968:1839; Barnes, 1979:38, as a subfamily of Otariidae, exclusive of Allodesminae.

Desmatophocidae (part). Repenning and Tedford, 1977:10, 74–76, as a family of the superfamily Otarioidea, to include *Desmatophoca*, *Allodesmus*, and less precisely identified species.

EMENDED DIAGNOSIS OF SUBFAMILY. A subfamily of the family Otariidae differing from Enaliarctinae by having crania without an embayment in the lateral edge of the basioccipital for a loop of the median branch of the internal carotid artery and by lacking carnassial teeth; differing from all other subfamilies except Allodesminae by having tympanic crest not projecting into tympanic cavity, and by having nasal bones elongate and tapering posteriorly and inserted between frontals (character not yet determined for Imagotariinae and Dusignathinae); differing from Otariinae, Dusignathinae, Imagotariinae, and Odobeninae by having large, elongate posterolaterally directed paroccipital

Table 1. Measurements of holotype skull, LACM 120199, of *Desmatophoca brachycephala*, new species, in mm. Parentheses indicate estimated measurements. Brackets indicate measurements explained by Sivertsen (1954:18–20), and the method of taking the other measurements follows Barnes (1972, 1979, in press).

| | |
|---|--------|
| Total length | (283) |
| Anterior border of orbit to tip of snout | (80) |
| External acoustic meatus to anterior border of orbit | 135.0 |
| Anterior border of orbit to tip of nasals | (28) |
| Post-palatal length (palatal notch to basion) | 121.3 |
| Basion to anterior edge of zygomatic root [18] | 188.0 |
| Length of tooth row, C to M ¹ | (88) |
| Length of tooth row, P ¹ –M ¹ | 62.5 |
| Width of rostrum across canines [12] | (80) |
| Width of palate across base of I ³ alveoli | (34) |
| Width of palate across alveoli of P ² | (64) |
| Width of palate across anterior alveoli of P ⁴ | (80) |
| Width between infraorbital foramina | 65.0 |
| Width across greatest interorbital constriction [6] | 40.0 |
| Width across supraorbital processes [7] | 37.5 |
| Width across greatest intertemporal constriction | (30.0) |
| Width of braincase at anterior edge of glenoid fossa [8] | (73) |
| Zygomatic width [17] | 184.0 |
| Auditory width [19] | 142.0 |
| Mastoid width [20] | 168.0 |
| Paroccipital width | (126) |
| Greatest width across occipital condyles | 69.8 |
| Greatest width of anterior nares | (35) |
| Greatest height of anterior nares | (31) |
| Width of zygomatic root of maxilla [14] | 22.0 |
| Greatest width of foramen magnum | 32.1 |
| Greatest height of foramen magnum | 22.5 |
| Least depth of jugal | 12.0 |
| Transverse diameter of infraorbital foramen | 15.0 |
| Anteroposterior diameter left C alveolus | (26.5) |
| Anteroposterior diameter right P ¹ alveolus | (12.8) |
| Anteroposterior diameter right P ⁴ alveoli | 12.2 |
| Anteroposterior diameter right M ¹ alveolus | 7.2 |

process which is separate from mastoid process and not joined by a crest; differing from most Enaliarctinae, all Otariinae, Imagotariinae, and Odobeninae by having pterygoid process of maxilla enlarged so palate expands ventral to orbit (character not determinable for Dusignathinae); differing from Allodesminae and Odobeninae by having vertical posterior and medial crista on canine crowns; differing from Imagotariinae and Odobeninae by having hyoid fossa separated from stylomastoid foramen by only a thin bridge of bone, not joined by an elongate, narrow sulcus; differing from Otariinae by having posterior lacerate foramen not greatly elongate anteroposteriorly; differing from Allodesminae by having more inflated tympanic bulla, posterior lacerate foramen not expanded transversely, smaller orbit with anterior margin

flared anterodorsally instead of being retracted posteriorly, unreduced incisive foramina, and squamosal-jugal contact not greatly expanded dorsoventrally; and differing further from Odobeninae by having canines which are not modified as tusks.

TYPE AND ONLY INCLUDED GENUS. *Desmatophoca* Condon, 1906.

Desmatophoca Condon, 1906

Desmatophoca Condon, 1906:3.

EMENDED DIAGNOSIS OF GENUS. Identical with that for the subfamily as given above until additional genera are described.

TYPE SPECIES. *Desmatophoca oregonensis* Condon, 1906; type by original monotypy.

INCLUDED SPECIES. *Desmatophoca oregonensis* Condon, 1906, late Early Miocene and/or early Middle Miocene, Oregon; and *Desmatophoca brachycephala*, new species, Early Miocene, Washington.

Desmatophoca oregonensis Condon, 1906

Figures 1, 9a

Desmatophoca oregonensis Condon, 1906:3, 11, figs. 1–3 on p. 9, unnumbered figures on pp. 3, 10.

HOLOTYPE. University of Oregon (Eugene), Museum of Natural History (UOMNH) F735, cranium, partial dentary, and postcranial bones.

TYPE LOCALITY. UOMNH locality 1153, coast near Astoria, Lincoln County, Oregon. The precise collecting locality of the holotype is not known, except that it apparently was west of Newport in the sea cliff where the Astoria formation is exposed (Packard and Kellogg, 1934:20, fig. 1).

REFERRED SPECIMEN. LACM 123285, the anterior part of a cranium with right canine, P^{2–3}, and left I³, canine, and P^{1–3}; collected by D.J. Martel, 18 April 1983.

LOCALITY OF REFERRED SPECIMEN. LACM 4851, among boulders on beach midway between the mouths of Schooner and Moloch creeks, approximately 6.5 km north of Newport, Lincoln County, Oregon, as shown on Yaquina, Oregon, United States Geological Survey topographic map, 1:62,500 scale, 1957 edition. Approximately 44°41'45" north latitude and 124°03'55" west longitude. This locality is approximately 0.75 km north of Schooner Point, which was the collecting locality of a referred specimen of the fossil mysticete, *Cephocetus oregonensis* Packard and Kellogg, 1934 (see Packard and Kellogg, 1934:21, fig. 1, item 6).

FORMATION AND AGE. Astoria Formation, late Early Miocene and/or early Middle Miocene. The rocks that have been referred to the Astoria Formation which crop out on the Oregon coast in Lincoln County, near Newport (Packard and Kellogg, 1934:20, fig. 1; Ray, 1976:fig. 2), produced the mollusks that were used to characterize the Newportian Stage (Addicott, 1976:102, 104, fig. 4). The holotype of *D. oregonensis* was found at an unspecified horizon within the Astoria Formation, and the referred rostrum (LACM 123285)

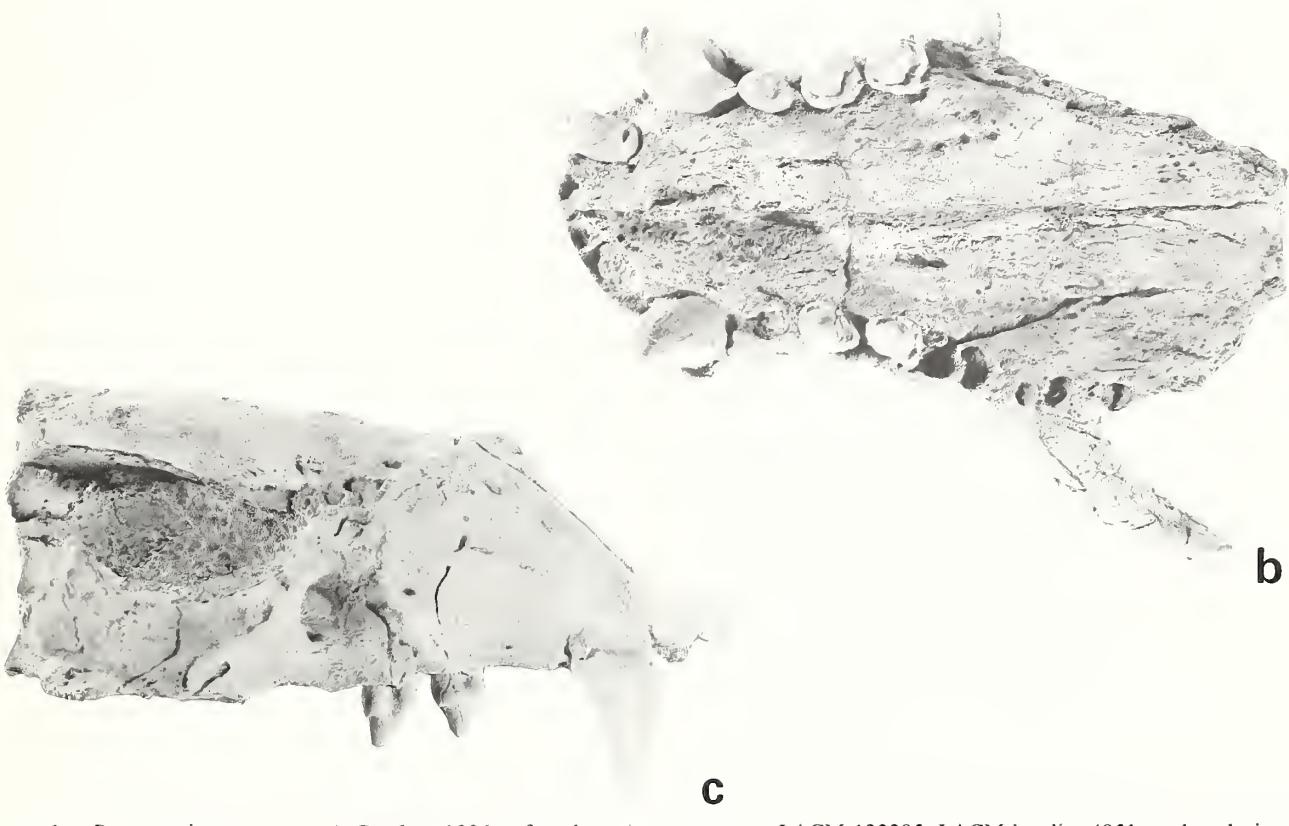
was found at a location near the sea cliff outcrop of the "Iron Mountain bed," a distinctive horizon within the Astoria Formation which produced the dome-skulled chalicotheres fossil that was described by Munthe and Coombs (1979). The land mammals and other lines of evidence derived from this same coastal Oregon part of the Astoria Formation provide a correlation with the Hemingfordian or the early part of the Barstovian North American land mammal ages (Ray, 1976: fig. 2; Munthe and Coombs, 1979:78–80). The concordance between these mammal ages and the Newportian Stage represents an interval of time spanning from approximately 19 ma to 15 ma and from the late part of the Early Miocene through the early part of the Middle Miocene (Armentrout, 1981). This then is also the best current estimate of the geologic age of *Desmatophoca oregonensis*.

DISCUSSION. Condon's (1906) original publication (see also Condon, 1910) on *Desmatophoca oregonensis* includes a brief description, photographs of the dorsal and right lateral surfaces of the partially prepared holotype cranium, and drawings of the P⁴. These have been greatly supplemented by additional observations by Wortman (1906), Downs (1956: 124–125), Mitchell (1966:36–37; 1968:1883, 1893–1894, table V; 1975:12–14), Barnes (1972:63; 1979:35), and Repenning and Tedford (1977:74). E. Mitchell is supervising further preparation of the holotype. He intends to publish a detailed reassessment of the species (Mitchell, 1975:12), and has already presented illustrations that show the major cranial characters of the holotype (Mitchell, 1966:pl. 29; 1975:fig. 2). The U.S. National Museum of Natural History has provided casts of the holotype of *D. oregonensis*.

The recently collected referred specimen of *Desmatophoca oregonensis* (Fig. 1) closely matches the size and morphology of the holotype, and yields additional information on the structure of the P¹, the P³, and of the posterior part of the palate. Both of the presently available specimens appear to represent male individuals because of the relative sizes of their canines and the development of bony rugosities and tubercles. All of the sutures between the bones of the referred snout remain unfused, but the individual had attained the same size as the holotype specimen at the time of its death. Therefore, the referred specimen must represent a young adult individual. This new specimen helps to confirm as diagnostic for the taxon certain characters of the holotype as: rostrum parallel-sided; cranium high between orbits and sloping anteriorly toward nasal bones; nasals elongate and slightly depressed medially, with closely appressed and tapering posterior ends extending posteriorly to a point dorsal to the middle of the orbit; narial opening sloping gently and narrower ventrally than at the dorsal part; presence of a slight fossa on the anterior surface of the rostrum on the maxilla-premaxilla suture dorsal to the diastem between the I³ and the canine; zygomatic portion of the jugal short and thick, mortised by relatively elongate splints of bone dorsolaterally and ventromedially with corresponding dorsomedial and ventrolateral splints from the maxilla; palate flat posteriorly but slightly excavated anteriorly, bearing scattered palatine foramina, of which the anterior one on each side is the largest; canine crown slightly recurved, covered by slightly irregular



a



b

c

Figure 1. *Desmatophoca oregonensis* Condon, 1906, referred specimen, rostrum, LACM 123285, LACM locality 4851; a, dorsal view; b, left lateral view; c, ventral view.

enamel surface, and bearing a vertical crista posteriorly and a less prominent one medially; and cheek teeth with prominent central cusps and lingual cingulae with small cuspules.

The P¹ has a single, cylindrical root, and on LACM 123285,

its crown has both anterior and posterior cristae. The cingulum is most prominent on the posteromedial side of the crown and extends slightly around the posterolateral side of the crown. The root of P² is clearly bifid on the holotype,

but on LACM 123285 it is bilobed with a deep vertical sulcus on the lateral side. On both specimens, the P^3 has two distinctly separate roots, of which the posterior one is bilobed. The tooth is present on both sides of LACM 123285, and its central cusp is high, broad, triangular, and slightly recurved posteromedially. The cingulum is prominent, extends around the medial and posterior sides of the crown, and bears, variably, eight to nine cuspules, of which the most prominent is at the posterior side of the tooth in line with the posterior crista on the crown. On both specimens, the P^4 has two separate roots, of which the posterior one is larger and transversely bilobed as on the P^3 . The roots of M^1 on both specimens have patterns similar to those of P^{3-4} , except that they are smaller and the bilobed posterior root is oriented obliquely.

The referred specimen shows that the species has an M^2 with a single root, round in cross section, and that the pterygoid process of the maxilla, at the posterolateral corner of the palate, is extensive and thin beneath the orbit. These features of the referred specimen have been incorporated into a modified restoration of the ventral view of the skull of the species (Fig. 9a). The lateral borders of the external narial opening (comprised of the premaxillae) are more rounded on the referred specimen than on the holotype. The zygomatic arch of the referred specimen is not complete enough to provide any additional information on the structure of the squamosal-jugal articulation, which, as shown by a plaster impression on the holotype, was slightly expanded dorsoventrally.

Desmatophoca brachycephala, new species

Figures 2–8, 9b

DIAGNOSIS OF SPECIES. A species of *Desmatophoca* differing from *D. oregonensis* by having cranium with shorter and wider rostrum, which is more expanded laterally around larger canines; ventral part of external narial opening wider; interorbital region wider, especially in anterior part; zygomatic arch more slender; optic foramina located more posteroventrally within orbits; palate wider, especially in posterior part and having larger pterygoid process beneath orbit; M^1 with only one small, bilobed root rather than two separate roots; M^2 absent; external acoustic meatus wider and directed more laterally; mastoid process larger and extended more posterodorsally; paroccipital process directed more laterally, instead of posteriorly; posterior lacerate foramen larger and more circular in outline.

HOLOTYPE. LACM 120199, incomplete cranium with crowns of left I^{1-3} , parts of both canines, lacking other teeth and parts of the rostrum, and the right dorsolateral part of the braincase, collected by J.L. Goedert and G.H. Goedert in 1979.

TYPE LOCALITY. LACM 4584 (= LACM Invertebrate Paleontology [LACMIP] locality 5864), east of Knappton, Pacific County, Washington.

FORMATION AND AGE. The type locality of *Desmatophoca brachycephala* near Knappton is in the lower part of a marine rock unit which has been referred to the Astoria

Formation and is Early Miocene, but not earliest Miocene, in age, is correlative with the Pillarian Molluscan Stage, the *Vertipecten fucanus* Molluscan Zone, indirectly correlated with the Saucesian Foraminiferal Stage, and with either the late part of the Arikareean or the early part of the Hemingfordian North American land mammal ages, and therefore is probably between approximately 20 and 23 million years old. This horizon is stratigraphically above the Eocene to earliest Miocene age, marine, Lincoln Creek Formation which crops out downdip and to the west along the Columbia River shoreline. The bases for these determinations are as follows.

The type section of the Astoria Formation is at Astoria, Oregon, directly across the Columbia River south of Knappton, Washington. In her study of the mollusks from the upper part of the Lincoln Creek Formation near Knappton, Moore (1984:1) commented on the age of the Astoria Formation, which directly overlies the Lincoln Creek in this sequence of strata (see also Wells, 1979). Moore also explained that as fossils weather out of exposures of these two formations in the bluffs along the Columbia River, they retain their approximate stratigraphic positions on the beach. This phenomenon is clearly demonstrated by the fact that, over a period of several months, and from a fairly small area, J. and G. Goedert were able to assemble the holotype skull of *D. brachycephala*, as well as other fossils, from broken and extremely weathered parts of concretions.

The type locality of *D. brachycephala* (= LACMIP locality 5864) is approximately one-half km southeast along the north shore of the Columbia River from LACMIP locality 5863, which is shown on the map in Moore's publication (1984:fig. 2). Owing to the dip of the rocks here, the two localities are nearly along strike from one another, and if there is any difference in their stratigraphic positions, the type locality of *D. brachycephala* is possibly only slightly higher in the section than LACMIP locality 5863. These localities are low in the Astoria Formation, have produced fossil mollusks and, based primarily on the occurrence of the bivalve *Acila (Acila) gettysburgensis*, are assigned to the Pillarian Molluscan Stage (Moore, 1984:1, figs. 2, 3; written communication, 13 August 1986). The mollusk, *Vertipecten fucanus*, which characterizes the Pillarian Stage (Addicott, 1976), has not yet been found at the type locality of *D. brachycephala*, however. The boundary between the Pillarian Stage and the younger Newportian Stage in the Astoria Formation near Knappton, although not yet located biostratigraphically, is presumably north of these localities, and higher stratigraphically within the formation. Much of the type section of the Astoria Formation on the south side of the Columbia River is also referable to the Pillarian Stage (Addicott, 1976:101).

There are some minor conflicts regarding the epochal age designation of these rocks. Following Addicott (1976) and Moore (1984), the Pillarian Stage and the localities in the base of the Astoria Formation near Knappton would fall in the later part of the Early Miocene, but following Armentrout (1981) and Moore and Addicott (1987) they would represent the early part of the Early Miocene.

Regardless of this, the entirety of the Pillarian Stage is older

than the Newportian Stage by definition (Addicott, 1976: 102, 104, fig. 4). Therefore, the section of the Astoria Formation near Knappton that yielded *D. brachycephala* is older than the rocks that are referred to the Astoria Formation near Newport on the Oregon coast, and which produced *D. oregonensis* and the mollusks that were used to characterize the Newportian Stage (see also Addicott, 1976: 104). The outcrops of the Astoria Formation near Knappton in Washington that yielded *D. brachycephala* and which contain mollusks of the earlier Pillarian Molluscan Stage may, therefore, represent the early part of the Early Miocene, but are younger than the underlying earliest Miocene part of the Lincoln Creek Formation, are indirectly correlated with the Arikareean North American Land Mammal Age, and may, therefore, be between 20 and 23 million years old. This age determination is most in accordance with the correlations that were proposed by Armentrout (1981).

ETYMOLOGY. The species name, *brachycephala*, is derived from Greek; *brachys*, short, and *kephale*, head; and is in reference to the short snout of this species as compared with *Desmatophoca oregonensis*.

DESCRIPTION AND COMPARISONS. The holotype of *Desmatophoca brachycephala* consists of a nearly complete cranium that was assembled from several pieces of broken fossiliferous rock. These pieces were found within a localized area. From the effects of predepositional erosion and post-depositional breakage, the specimen is lacking all of the cheek teeth, parts of the right and left sides of the palate, parts of the premaxillae, parts of the incisors and canines, the right paroccipital process, and the central and right side of the upper surface of the braincase. It appears to have lain on the seafloor for some time prior to final burial and fossilization, during which time organic and/or inorganic factors caused the erosion of much of the bone surface, principally on the dorsal surface, and the loss of the medial, bony walls of both orbits, the distal ends of the nasal bones, and parts of the nuchal crest. Subsequent tectonic distortion compressed the braincase, the interorbital region, and the tympanic bullae. The holotype of *D. brachycephala* includes structures of the pterygoid hamuli and the zygomatic arches that are not known for *D. oregonensis*. All other parts of the cranium of *D. brachycephala* are directly comparable with corresponding parts on the holotype and the referred specimen (LACM 123285) of *D. oregonensis*.

The holotype of *D. brachycephala* represents an individual in the adult or Group I age class extrapolating from the cranial suture closure method adopted by Sivertsen (1954: 10–13) to determine ages of Recent specimens. Of the nine sutures that he found useful for age evaluation, at least seven are closed or mostly closed on the fossil. Because most of the roof of the braincase is missing, only a short section of the interparietal suture is preserved, but it appears to be completely closed. The original degree of closure of the squamosal–parietal suture is difficult to determine. Its course is partly visible on the left side, but distortion has caused the braincase to break along much of that suture. The interfrontal suture is closed, although it appears to be open in the photograph (Fig. 2) because, between the orbits, it is flanked on each side

by an elongate ridge of bone (Fig. 3). The exact suture age of the holotype following Sivertsen's method is therefore not determinable, but it was at least 28. Recent otariids with suture ages of between 19 and 36 are adults (Group I) according to Sivertsen's method.

In addition to the shared diagnostic characters listed for the subfamily (and for the genus), *D. brachycephala* and *D. oregonensis* are demonstrably congeneric because they share the following cranial characters: narrow interorbital region lacking supraorbital processes; interfrontal suture between the orbits flanked by low, elongate ridges; low-vaulted braincase; wide squamosal fossa between the braincase and the zygomatic arch; laterally flaring mastoid process; anterior aperture of the infraorbital foramen slightly overhung by the anterior edge of the orbit; rostrum wider at the canines than at P³; palate relatively flat and expanded posterolaterally ventral to the orbit; more than one posterior palatine foramen on each side, rather than only a single one connected to an elongate and well-developed palatine sulcus; glenoid fossa with a large anteroventrally projecting postglenoid process and small, ventrally directed preglenoid process at the lateral edge only; tympanic bulla relatively flat, with tuberosities limited to the anteromedial part; broad concavity between the middle part of the tympanic bulla and the postglenoid process bearing small postglenoid foramen near the postglenoid process; thin but wide shelf of squamosal bone projecting laterally from the braincase dorsal to the external acoustic meatus; external acoustic meatus entering the bulla in a posteromedial direction; mastoid process approximately cubic in shape, but excavated posteriorly and with a rugose surface facing ventrolaterally; paroccipital process projecting posterolaterally but slightly deflected medially at its termination, excavated ventrally and with a thin anterolateral edge; basioccipital expanded posteriorly, with raised muscular tubercles adjacent to the tympanic bullae, and with a narrow median pharyngeal tubercle which is flanked by relatively deep, hemispherical fossae; hypoglossal foramen small and close to the posteromedial side of the posterior lacerate foramen and with its aperture facing antero-ventrolaterally; occipital condyles projecting prominently from occipital shield with very convex articular surfaces and separated ventrally by a deep intercondylar notch; and foramen magnum wide and low with a thick dorsal margin.

Most of the cranial morphology of *D. oregonensis* has now been documented but, because the descriptions are varied and widely scattered in the literature, a relatively detailed account of the cranial morphology of *D. brachycephala* is warranted here. As in *D. oregonensis*, the rostrum expands gradually anteriorly from its narrowest point in the cheek region around P³, immediately anterior to the infraorbital foramina. The rostrum of *D. brachycephala* is relatively shorter than that of *D. oregonensis*, considering that the crania of the two species have approximately the same zygomatic widths. The external narial opening is widest ventrally and narrower at its apex, the reverse of the condition in *D. oregonensis*. That part of the premaxilla forming the lower lateral border of the narial opening is wide and rounded, as on the referred specimen of *D. oregonensis* (LACM 123285,

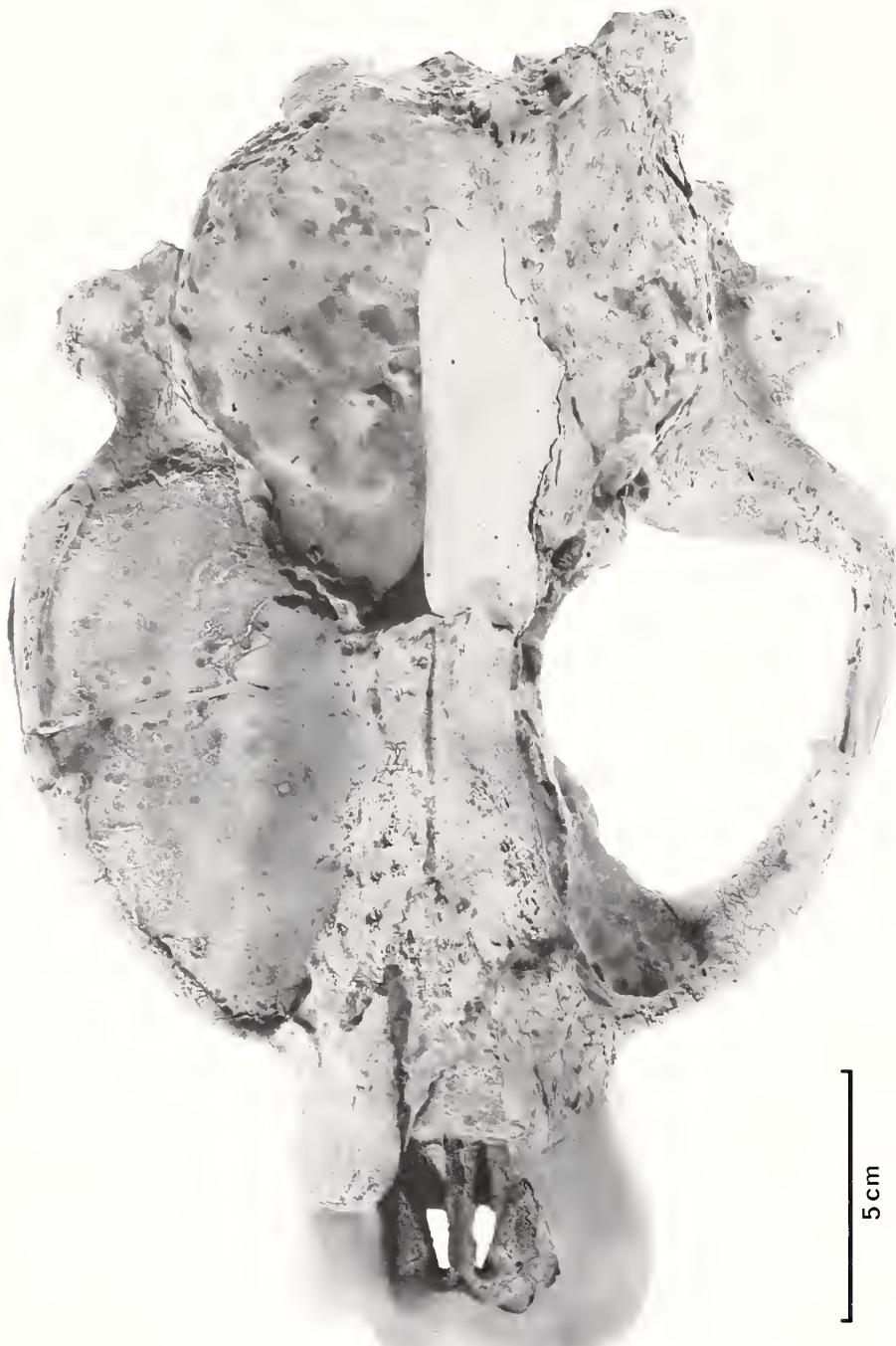


Figure 2. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, dorsal view.

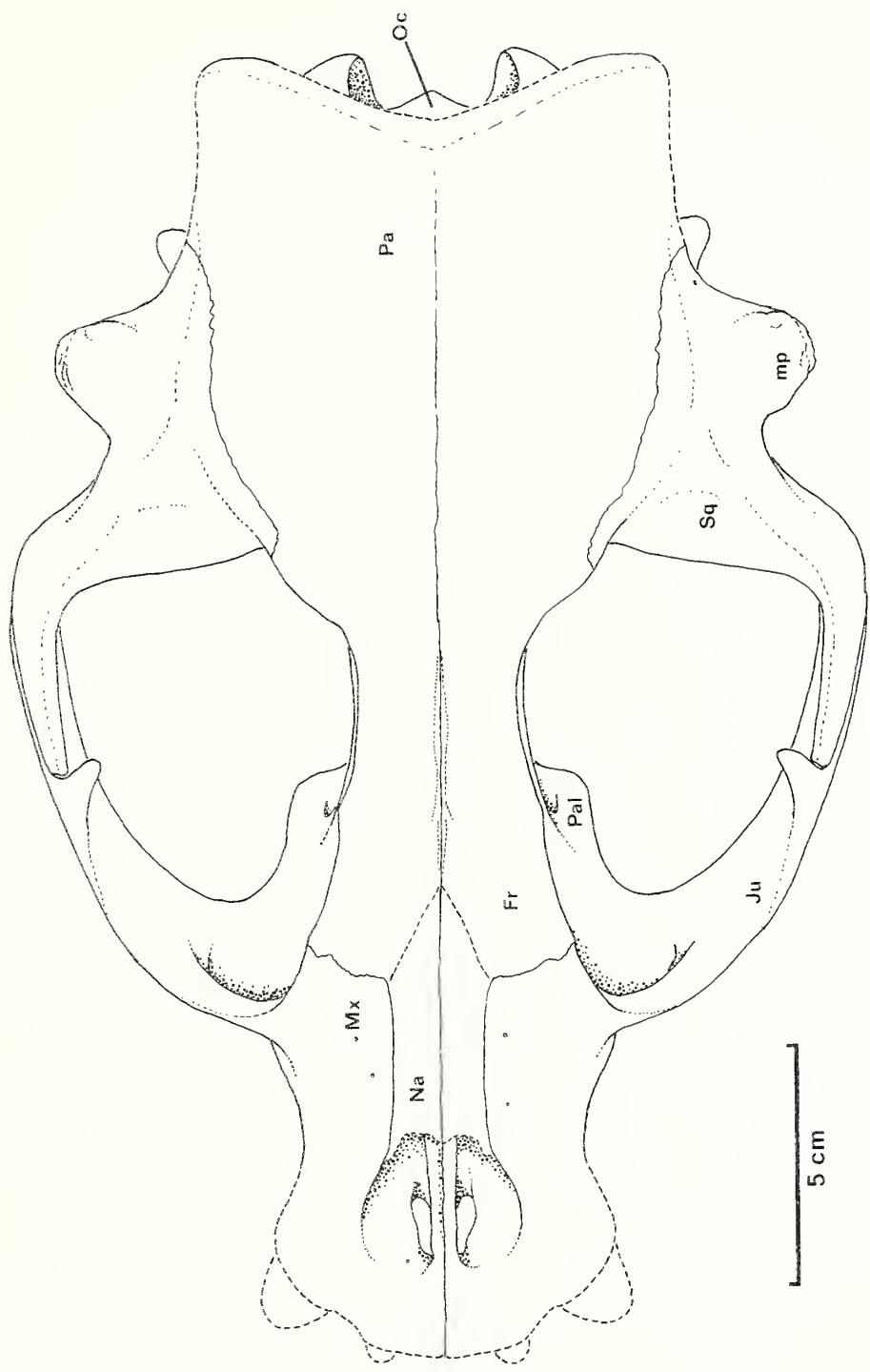


Figure 3. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, dorsal view. Abbreviations used in this and following illustrations are explained in the Methods and Materials section.

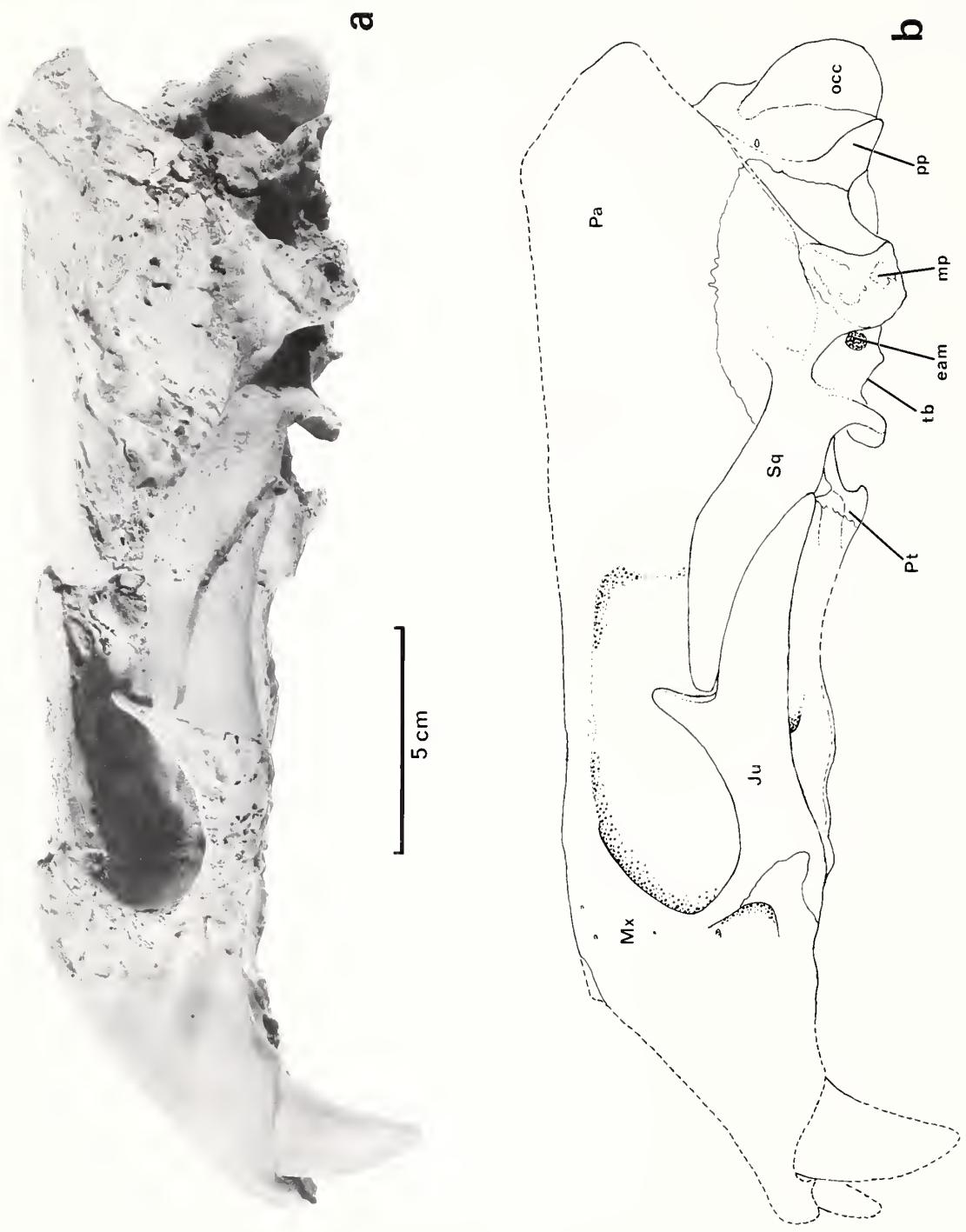


Figure 4. *Desmatophoca brachycephala*, new species, skull, holotype, LACM locality 4584, left lateral view; a, photograph of original specimen; b, restoration.

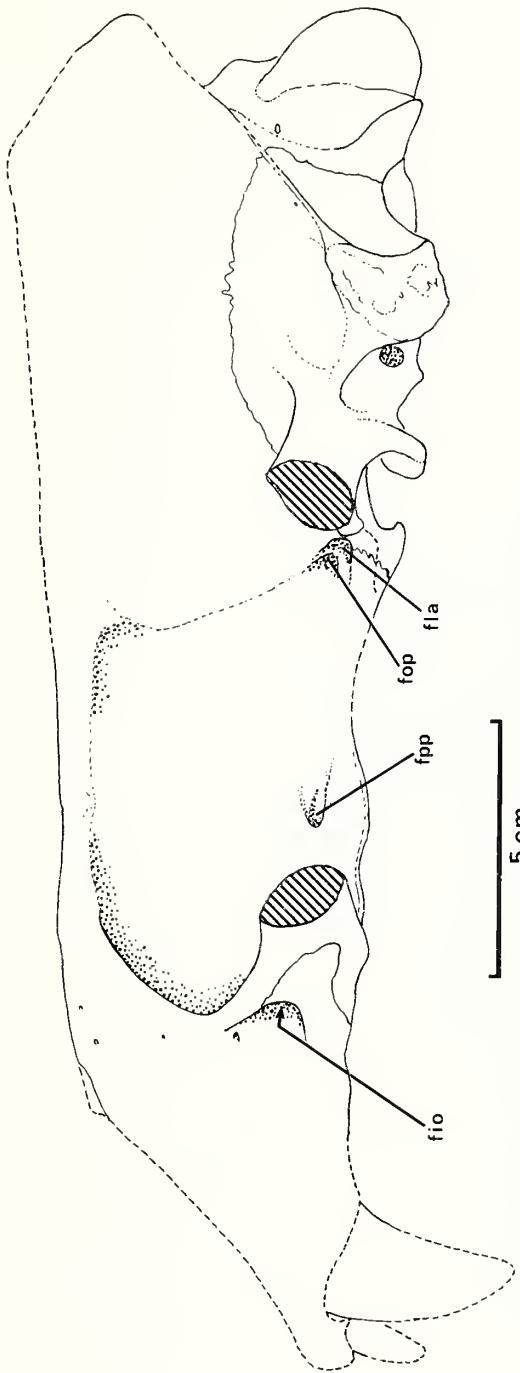


Figure 5. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, left lateral view with zygomatic arch omitted to show structures within the orbit.

Fig. 1a), not formed into a narrow crest as on the holotype of *D. oregonensis*. This feature may be variable, therefore, rather than of taxonomic significance. The narial apertures of the incisive foramina are elongate anteroposteriorly and closely appressed, but shorter and more divergent posteriorly than in *D. oregonensis*.

The nasals of *D. brachycephala* are narrower anteriorly than those of *D. oregonensis*. Their combined form is of a tapered wedge extending posteriorly between the frontals, but the sutures at that location are indistinct, and the posterior margins of the nasals cannot be exactly determined. On either side of the nasal bones, the premaxilla-maxilla sutures are obliterated by fusion.

At the anterior margin of the orbit, the dorsal margin of the zygomatic arch flares anteriorly over the anterior opening of the infraorbital foramen and forms a "cup" for the eyeball, much as in the enaliarctines and otariines. This structure is very different from the posteriorly receding dorsal margin of the zygomatic arch in species of *Allodesmus*. The dorsal margin of the zygomatic arch in *D. brachycephala* is narrower and projects farther anteriorly than in *D. oregonensis*.

The interorbital region of *D. brachycephala* is wider and shorter (measuring approximately 20 mm less, anteroposteriorly, between the braincase and the anterior border of the orbit) than in *D. oregonensis*. The sulci on either side of the braincase, which mark the locations of the pseudosylvian sulcus on the brain of *D. oregonensis* (a character also present in *Enaliarctos mealsi* Mitchell and Tedford, 1973), are much shallower and less distinct in *D. brachycephala*. There are also small fossae on either side of the midline on the anterior dorsal part of the braincase in *D. oregonensis*. These are probably homologues of the parasagittal fossae (Mitchell and Tedford, 1973:225) of *Enaliarctos mealsi*, and their presence or absence cannot be determined in *D. brachycephala* due to breakage. The nuchal crest is broken off in the holotype of *D. oregonensis* and, therefore, not known for that species. That part of the crest which is preserved on the holotype of *D. brachycephala* is thick and projects posteriorly over the occipital shield nearly as far as the posterior surfaces of the occipital condyles (Figs. 2, 4a).

The squamosal fossa is the broad recess in the squamosal between the braincase and the zygomatic arch, dorsal to the glenoid fossa, and which floors the temporal fossa. It appears to be characteristically wide in species of Desmatophocinae compared with most other otariids, and is relatively wider in *D. brachycephala* than it is in *D. oregonensis*. Its anterior part, between the anterolateral corner of the braincase and the zygomatic arch, is nearly flat and creates a bony shelf over the anterior part of the glenoid fossa (Fig. 3). The lateral expansion which affected this part of the cranium of *D. brachycephala* also involved the mastoid process, which therefore has a much more extensive, flat dorsal surface than in *D. oregonensis*.

The complete zygomatic arch has not been previously known for the genus, because the structure is missing on the holotype of *D. oregonensis*. This has been the source of some speculation, particularly because the zygomatic arches of the species in the subfamily Allodesminae are greatly modified.



Figure 6. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, ventral view.

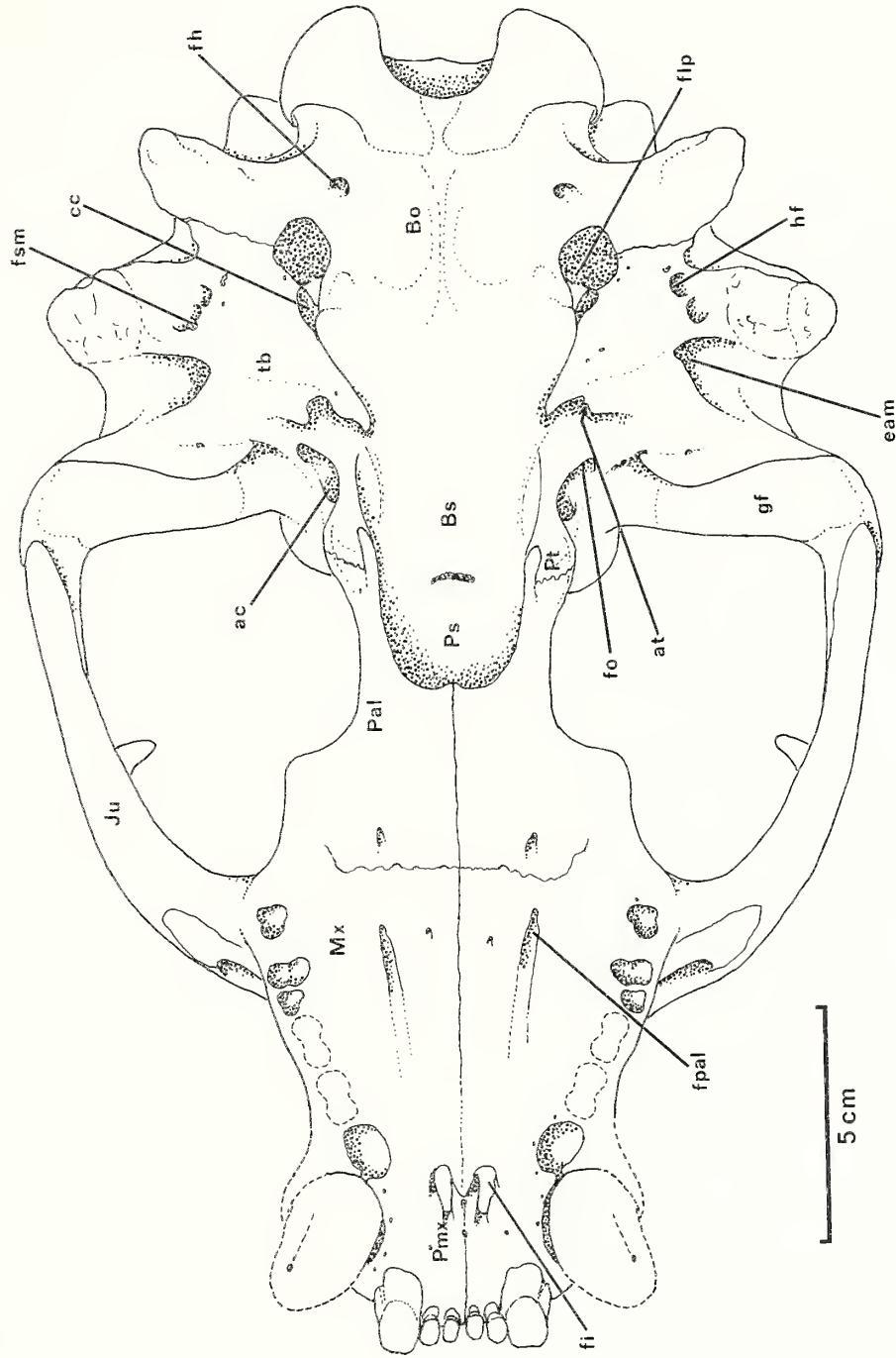


Figure 7. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, ventral view.

A matrix impression (see Condon, 1906:3) of the missing part of the right zygomatic arch of the holotype of *D. oregonensis* shows the zygomatic process of the squamosal to be slightly expanded dorsoventrally, but it appears to be basically of the primitive type (Mitchell, 1966:pl. 29d; 1968: 1893; 1975:fig. 2). The right jugal-squamosal junction is completely preserved on the holotype of *D. brachycephala*, and is close to the generalized, primitive carnivore type. The zygomatic process of the squamosal tapers anteriorly to a blunt point which abuts the posterior side of a tapered, dorsally projecting postorbital process of the jugal (Fig. 4b). In the primitive carnivore condition (as in enaliartines and otariines), the squamosal does not abut the postorbital process of the jugal. Overall, the zygomatic arch of *D. brachycephala* is relatively thick, although not quite as thick as in the preserved comparable parts of the holotype of *D. oregonensis*. The condition in *D. brachycephala* is more primitive than that in *D. oregonensis*, and neither species has the exaggerated vertical expansion of the squamosal and jugal at their junction which is so characteristic of the species of Allodesminae.

The palate of *D. brachycephala* is flatter and broader posteriorly, but narrower and more arched anteriorly than that of *D. oregonensis* (Fig. 9). The incisive foramina of *D. brachycephala* are also more divergent posteriorly and recessed more deeply into the palate. The largest posterior palatine foramen on each side opens into an irregularly shaped, elongate palatine sulcus. This pair of sulci differs from those which are characteristic of the species of *Enaliarctos*, which owe their prominence to being sharply defined, parallel, nearly symmetrical, and to not being flanked by other, smaller foramina on the palate. In *D. brachycephala*, as in *D. oregonensis*, each of the large posterior palatine foramina is associated with two or more smaller ones. The expansive pterygoid process of the maxilla beneath the orbit of *D. brachycephala* is even larger than in *D. oregonensis*. It forms a thin infraorbital shelf with a prominent corner. This structure is not as prominent as in the Early Miocene enaliartine, *Pinnarctidion bishopi* Barnes, 1979, but it is more prominent than in *D. oregonensis* and in the Middle Miocene allodesmine, *Allodesmus packardi* Barnes, 1972.

The crowns of the incisors of *D. brachycephala* are aligned transversely at the front of the palate (Figs. 6, 7). Some distortion may have occurred during fossilization, however, because much of the crown of I¹ is actually farther posterior than the two lateral ones, but the root of this tooth is not present to confirm its exact original alignment. Both I¹ and I² have crowns with their apices worn down to flat surfaces. The crown of I¹ is one-half the diameter of I². More of I³ is preserved than of the two previous teeth. The tooth is very procumbent and its root is oval in cross section. The root is not entirely preserved, but it measures at least 11 mm transversely and 15 mm anteroposteriorly in cross section at the alveolar rim. The crown shows neither cingulae nor cusps as preserved because it has an extensive posterolabial wear facet and its apex is broken off.

Neither canine is complete. All that remains of the right one is the lingual half of the root within the alveolus and,

projecting from the alveolus, is the lingual part of the root at the base of the enamel. The left one is more complete. The lingual side of each canine root has a shallow longitudinal sulcus. The canine of *D. brachycephala* must have been otherwise essentially circular in cross section, and at least 25 mm in diameter at the alveolar rim. I estimate from the remnant of the left canine and the curvature of its alveolar margin that its diameter there was approximately 20 percent greater than in *D. oregonensis*.

There are no cheek teeth preserved on the holotype of *D. brachycephala*. The alveolus for P¹ is located posterolingual to the canine, and is closely appressed to it, so much so that the alveoli of these two teeth are partly contiguous and extremely procumbent (derived conditions). In *D. oregonensis*, this alveolus is more separate from the canine and posterior to it. The lingual side of the alveolus of P¹ has a faint crest, indicating that the root of this tooth had a slight longitudinal, lingual sulcus. The root was otherwise nearly circular in cross section and approximately 10 mm in diameter.

The areas that were occupied by the alveoli for P² and P³ have been broken away on both sides of the skull (Fig. 6), and there is no way to determine the morphologies of these teeth. The space that they occupied on the right side, between the alveoli for P¹ and P⁴, spans only 25 mm anteroposteriorly. This is nearly 15 mm less than the corresponding space on the holotype of *D. oregonensis*, so these two teeth in *D. brachycephala* must have been more crowded together (Fig. 9). Judging from its alveoli, the root morphology of P⁴ in *D. brachycephala* is nearly the same as in *D. oregonensis*. A separate anterior root on this tooth occupied a roughly four-sided alveolus. The primitively separate two posterior roots were fused into a single, transversely bilobed structure (Fig. 7), of which the medial lobe is the homologue of the separate root that is above the protocone in fissipeds and primitive enaliartine otariids (see Mitchell and Tedford, 1973; Barnes, 1979). In *D. brachycephala*, the P⁴ is located more anteriorly relative to the zygomatic arch than in *D. oregonensis*. The anterior and posterior alveoli of this tooth in *D. brachycephala* are closely appressed, indicating that the P⁴ roots were approaching the stage of fusion (derived character). A diastem of approximately 6 mm, such as is also present in *D. oregonensis*, separates the alveoli of P⁴ and M¹.

The single M¹ alveolus of *D. brachycephala* measures 8 mm anteroposteriorly by 6 mm transversely. It is bilobed, clearly reflecting the root structure of the M¹. The posterior lobe of the root of this tooth was larger than the anterior one. In contrast, as noted previously, the more primitively constructed M¹ alveolus of *D. oregonensis* is double, clearly indicating that the same tooth in that species had two separate roots (Fig. 9). Of these, the anterior root was small and round, and the posterior one was larger and expanded (bilobed) transversely.

An M² was never present in *D. brachycephala*, in contrast to *D. oregonensis*, in which its presence is indicated by an essentially circular alveolus, approximately 7 mm in diameter, on the referred snout (LACM 123285). This loss of M² in *D. brachycephala* is possibly an individually variable character, of course, but if a larger population sample in the future

should confirm that it is diagnostic, then it is a derived feature of *D. brachycephala*. Some individuals of living species of Otariinae experience pathologic or fortuitous loss of the M², but for species in other subfamilies, for example *Allodesmus packardi* and Recent walruses, *Odobenus rosmarus* (Linnaeus, 1758), similar tooth loss is an example of convergence.

The width of the pterygoid of *D. brachycephala* at the level of the pterygoid hamulae is enhanced by a lateral protuberance, which is also present in most otariids except the otariines and *Enaliarctos mealsi*. The pterygoid hamulus is relatively thick, short, and bends ventrolaterally. There is a broad concavity between it and the above-mentioned lateral protuberance.

Most parts of the medial walls of both orbits of the holotype of *D. brachycephala* were broken away and/or decomposed prior to fossilization, and much anatomical information has therefore been lost. No lacrimal foramen is detectable on either the holotype or the referred specimen (LACM 123285) of *D. oregonensis*. Enough of the bone forming the anterior margin of the orbit remains on the holotype skull of *D. brachycephala* to demonstrate the absence of the same foramen in that species as well. In both species there is a small nutrient foramen in the orbit just ventromedial to the orbital aperture of the infraorbital foramen, and, located more posteriorly, is the posterior aperture of the canal leading to the posterior palatine foramina (Fig. 5). Posterior to the latter, on the referred specimen of *D. oregonensis* is a round sphenopalatine foramen, but the holotype of *D. brachycephala* is too damaged in this area to ascertain the location of such a structure.

The area of the orbital aperture of the optic foramen is likewise damaged in *D. brachycephala*, but judging by the curvature of the surrounding bone (Fig. 5), it appears to have been located more posteroventrally (derived character) than it is in *D. oregonensis*. Compared with *D. oregonensis*, the anterolateral corner of the braincase of *D. brachycephala* protrudes farther laterally, as does the pterygoid ventrolateral to the alisphenoid canal, resulting in the creation of a broader, more recessed orbital fissure, which contains the anterior lacerate foramen, the foramen rotundum, and anterior end of the alisphenoid canal. In the posteroventrally recessed position of the orbital fissure as well, *D. brachycephala* is again the more derived of the two species.

Desmatophoca oregonensis and *D. brachycephala* both have the aperture of the foramen ovale recessed in an elongate fossa that is confluent with the posterior end of the alisphenoid canal. This fossa is separated from the medial part of the glenoid fossa by an oblique strut of bone extending to the pterygoid. In both species, the posterior end of the alisphenoid canal is located at a point adjacent to the middle of the glenoid fossa. This is a relatively posterior location (derived) when compared with the anatomy of primitive carnivores, and with that of enaliartine and otariine pinnipeds, but is not as far posterior as in species of *Allodesmus* (see Barnes, 1972), which have the most derived condition among the otariids.

The glenoid fossa of the squamosal is approximately 45 mm wide and is bordered posteriorly by a prominent, but

relatively thin postglenoid process which projects anteroventrally and is widest medially. In the lateral part of the glenoid fossa, the anterior border is deflected ventrally to create a small preglenoid process. The medial edge of the glenoid fossa, as in *Allodesmus* spp., is marked by a sulcus that curves posteriorly into a small pit, which is probably the anterior end of the canal for the chorda tympani nerve. The lateral ends of the glenoid fossae are canted anterolaterally on the holotype skulls of both species of *Desmatophoca*, but with the present sample, it is not possible to assess whether this is a diagnostic character for the genus or whether it is individually variable as in *Allodesmus kernensis* (see Barnes, 1972). The glenoid fossae on the skulls of both species of *Desmatophoca* are not as rectangular in shape as in species of *Allodesmus*. They enclose nearly 180 degrees of rotational movement of the mandibular condyle by virtue of the prominent postglenoid process and the smaller preglenoid process laterally. The position of the glenoid fossa on the cranium of *D. brachycephala* is farther lateral relative to the tympanic bulla than in *D. oregonensis* (Fig. 9).

The bulla is fused to the postglenoid process over a broad, concave area, at the anterior edge of which is a very small, vestigial postglenoid foramen. Both bullae are damaged on the holotype of *D. brachycephala*, but the right one is the most complete. It is prolonged anteromedially in the form of irregular styliform processes that extend ventral to the auditory tube (which in life contained, in part, the eustachian tube), the median lacerate foramen, and the anterior end of the carotid canal. A transverse crest on the surface of the bulla extends from this anteromedial part of the bulla to a point ventral to the external acoustic meatus. Anterior to this crest, the bulla surface slopes anterodorsally, but posteriorly it is nearly flat. As in species of *Allodesmus*, and as in *Enaliarctos mealsi* and *D. oregonensis*, the posteromedial corner of the bulla is retracted ventral to the posterior end of the carotid canal, but unlike those species, the bulla is also retracted dorsal to the end of the same canal as well. The effect of this is an enlarged anteromedial part of the posterior lacerate foramen (Fig. 7).

The posterior lacerate foramen is approximately 50 percent larger than in *D. oregonensis* (Fig. 9), and in both species the foramen has an ovoid shape, although it is not as elongate as in *Enaliarctos mealsi* or in species of Otariinae. As is apparently characteristic of the genus *Desmatophoca*, the pit (hyoid fossa) for attachment of the tympanohyoid is not very close to the posterior lacerate foramen (as it is in *Allodesmus* spp.), but instead is positioned on the posterolateral side of the bulla, close to the stylomastoid foramen, and between the bulla and the mastoid process. The tympanohyal pit is separated from the small stylomastoid foramen by only a small crest of bone, but it is separated from the posterior lacerate foramen by a broad, convex surface.

The external acoustic meatus of *D. brachycephala* is wider and directed more laterally than it is in *D. oregonensis*. This is a more primitive morphological state in *D. brachycephala*. The mastoid process is relatively and absolutely larger (derived character), than in *D. oregonensis* and is more rounded in shape (Fig. 9). In contrast to *D. oregonensis*, the process

descends ventrally well below the ventral surface of the tympanic bulla, and projects farther dorsolaterally and is continuous with a prominent but narrow extension of the nuchal crest (Fig. 4). The rugose ventrolateral face of the mastoid process is larger than in *D. oregonensis*.

The paroccipital process differs in both its orientation and shape from that of *D. oregonensis*. This process on both species of *Desmatophoca* resembles those of *Allodesmus* spp. only insofar as this process is large and is separated from the mastoid process by a wide notch. Otherwise, the paroccipital process of *D. brachycephala* (and of *D. oregonensis*) differs from those of species of *Allodesmus* by projecting more posteriorly, not posteroventrally, by being much more flattened dorsoventrally, and by bending slightly medially at the posterior extremity. There is no fossa present on the ventral surface of the skull between the paroccipital process and the tympanic bulla as in species of Enaliarctinae and Otariinae, but the bone surface is instead virtually flat and, in *D. brachycephala*, it is even slightly convex when compared with *D. oregonensis*.

The basioccipital and basisphenoid expand posteriorly in both species of *Desmatophoca*, and the widest part of the basioccipital is between the tympanic bullae (Fig. 9). The holotype skulls of both species are virtually the same width between the bullae. The basioccipital is proportionally wider at this point in *D. brachycephala* than in *D. oregonensis*, however, and the appearance of this is enhanced by the basioccipital being medially constricted posteriorly between the larger posterior lacerate foramina and being more tapered anteriorly toward the basisphenoid. Both species have very prominent fossae for insertion of the rectus capitus longus muscles anterior to the condyles, but in *D. brachycephala* these fossae are wider and shallower and the median pharyngeal tubercle between them is more prominent. Species of allodesmines, enaliartines, and otariines have less prominent fossae and tubercles, and their extensive development in species of *Desmatophoca* is a derived character.

In both species of *Desmatophoca*, the occipital condyles do not tilt strongly laterally (Fig. 8). They project prominently from the occipital shield and extend ventrally below the ventral surface of the basioccipital. The intercondylar notch is relatively narrow and deep in both species of *Desmatophoca*, especially so in *D. brachycephala*, and somewhat as in *Enaliarctos mealsi*. The articular surfaces of the condyles are not bilaterally symmetrical on the holotype of *D. brachycephala*. The one on the left side is abnormal because it does not extend ventromedially as near to the midline as does the one on the right side, nor as do the surfaces on both sides of the holotype of *D. oregonensis*. The foramen magnum of *D. brachycephala* is compressed dorsoventrally (Fig. 8), even more than it is in *D. oregonensis*. There are prominent fossae dorsal to each occipital condyle, and another fossa is centered just below the apex of the occipital shield. Between these, a prominent tubercle extends obliquely dorsolaterally toward the nuchal crest from above each side of the foramen magnum.

RELATIONSHIPS

The subfamily Desmatophocinae can be accommodated within the expanded concept of the family Otariidae that was

used by Mitchell (1968, 1975), Barnes (1972:62; 1979), Mitchell and Tedford (1973), and Hall (1981). There is nothing in the known morphology of either species of *Desmatophoca* that would seem to negate the previously postulated origin of the subfamily from or near a taxon in the Enaliarctinae. Prior characterizations of the desmatophocines as being large, moderately derived, early sea lion-like animals with some retained primitive characters also seem to be correct (Mitchell, 1968, 1975; Barnes, 1972; Repenning and Tedford, 1977; King, 1983:129–130, fig. 3.1). Multiple-rooted posterior cheek teeth, widely separated mastoid and paroccipital processes, relatively primitive and non-mortised (e.g., fissiped-like) zygomatic arches, and small supraorbital processes of the frontal are all primitive characters that the desmatophocines share with the enaliartines. The relatively elevated position of the optic foramina within the interorbital region of *D. oregonensis*, the loss of M^2 in *D. brachycephala*, the presence of the anteriorly flared dorsal margin of the zygomatic arch at the front of the orbit, the different shape of the paroccipital process, and other derived characters of both species are some of the ways in which desmatophocines differ from any of the known species in the subfamily Allobesminae. This situation, plus the fact that the unique combination of derived characters of the allobesmines (e.g., exceptionally bulbous-crowned and nearly homodont cheek teeth, lack of vertical carinae on the canines, dorsoventrally expanded (mortised) squamosal-jugal contact, large orbit with its anterior border retracted posteriorly above infraorbital foramen, flatter tympanic bulla, transversely expanded posterior lacerate foramen, and posteroventrally positioned optic foramina within the interorbital region) is not shared with, nor uniquely derivable from the characters of the Desmatophocinae, are part of the argument against either synonymizing the two subfamilies or uniting them in a higher category exclusive of the family Otariidae. In fact, there has been no evidence presented that any members of the other later otariid subfamilies (Otariinae, Imagotariinae, Dusignathinae, Odobeninae) evolved from the Desmatophocinae, and this subfamily appears to have become extinct without leaving any descendants (see Mitchell, 1975; Repenning and Tedford, 1977; Barnes, 1979).

Within the genus *Desmatophoca*, *D. oregonensis* is, in most of its cranial characters, the more primitive of the two known species. Among its most obvious primitive characters are the elongate skull, a smaller posterior lacerate foramen, smaller canine, two separate roots on the M^1 , and the retained M^2 . *Desmatophoca brachycephala*, the geochronologically earlier taxon, has only a few characters in which it is more primitive than *D. oregonensis*: a broader interorbital region, a more slender jugal, and a less dorsoventrally expanded squamosal-jugal articulation, for example. It is interesting, though, that in the majority of its cranial characters, *D. brachycephala* is clearly the more derived species of the two because, for example, it has lost the M^2 , has a larger and more cylindrical canine, a single (albeit multilobed) root on the M^1 formed by fusion of previously separate roots, a P^1 which is crowded adjacent to the posteromedial side of the canine, a shorter rostrum, a more anterodorsally flaring anterior margin of the orbit, a larger mastoid process, a smaller and more laterally

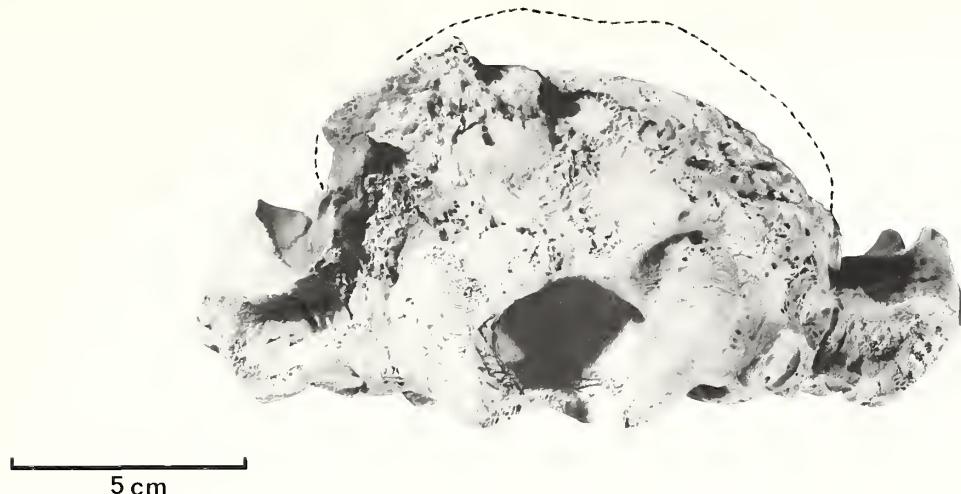


Figure 8. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, posterior view.

directed paroccipital process, the hyoid fossa closer to the stylomastoid foramen and separated from it by only a thin ridge of bone, a broader squamosal fossa, a broader braincase, the mastoid process projecting farther laterally and more deeply excavated posteriorly, and a larger posterior lacerate foramen. The various differences between the two species of *Desmatophoca*, both in geochronological occurrence and in suites of primitive and derived characters, rule out any sort of ancestral-descendant relationship between them. These differences do not preclude the possibility of their sharing a common ancestor, however.

I interpret the above-cited differences as being clearly diagnostic at the species level, and not attributable to individual variation or sexual dimorphism. The holotypes of both species have the kinds of cranial rugosities, crests, and processes that appear as male secondary sex characters in individuals of Recent otariid species, and both holotypes represent adult individuals. Both skulls are nearly the same size, although the holotype of *D. brachycephala*, which is broader and has larger canines, is slightly shorter than that of *D. oregonensis*.

Not only does the discovery of *D. brachycephala* expand the contents and diagnoses of both the genus *Desmatophoca* and the subfamily Desmatophocinae, but it also adds another taxon to the list of examples of cranial convergence between species in the families Otariidae and Phocidae (true seals). Various examples of phocid–otariid convergence have been pointed out by Mitchell (1968:1887–1888, 1892; 1975) and Barnes (1972:63, 64, 66; 1979:30). *Desmatophoca brachycephala* has general cranial proportions similar to those of some phocids, especially the Recent monk seals of the genus *Monachus* Fleming, 1822. The skull of *D. brachycephala* is also broad and dorsoventrally flattened, somewhat as in the al洛desmine, *Allodesmus packardi* Barnes, 1972, but differs notably by having more widely flared zygomatic arches and a broader snout.

It is tempting to speculate on the possible life habits of

Desmatophoca brachycephala, but additional specimens would first be necessary. Obvious pinniped characters of the species (e.g., enlarged nares, orbit, braincase, cranial foramina and posterior part of the palate, relatively uninflated bulla, reduced or lost lacrimal bone and lacrimal foramen, near homodonty) indicate that it must have been relatively well adapted to an aquatic existence, but in the absence of information on its middle ear, dentition, mandible, and postcranial skeleton, comments on its diving ability, prey items, mode of feeding, and locomotion would be mostly speculation.

CONCLUSIONS

The extinct subfamily Desmatophocinae is a useful taxonomic grouping within the marine carnivore family Otariidae because it contains morphologically distinctive animals that had a considerable evolutionary history separate from other recognized subfamilies in the family. The Desmatophocinae are apparently not so closely related to the subfamily Al洛desminae that the two should be synonymized, an idea that has been supported by some previous authors, including myself. The subfamily Desmatophocinae, now represented by two named species from rocks bordering the eastern North Pacific Ocean, has a known geochronologic range from the Early Miocene to the early Middle Miocene. These are relatively large pinnipeds, apparently relatively rare, which, for their time, and in comparison with contemporaneous and slightly older and smaller species in the primitive subfamily Enaliarctinae, are relatively highly derived. The desmatophocines apparently represent the earliest lineage within the Otariidae to have evolved large size and some derived characters that are convergent with some of those present in the other, later otariid subfamilies. The Desmatophocinae apparently died out without evolving into any later group.

Desmatophoca Condon, 1906, is the type genus of the subfamily. Its type species is *Desmatophoca oregonensis* Con-

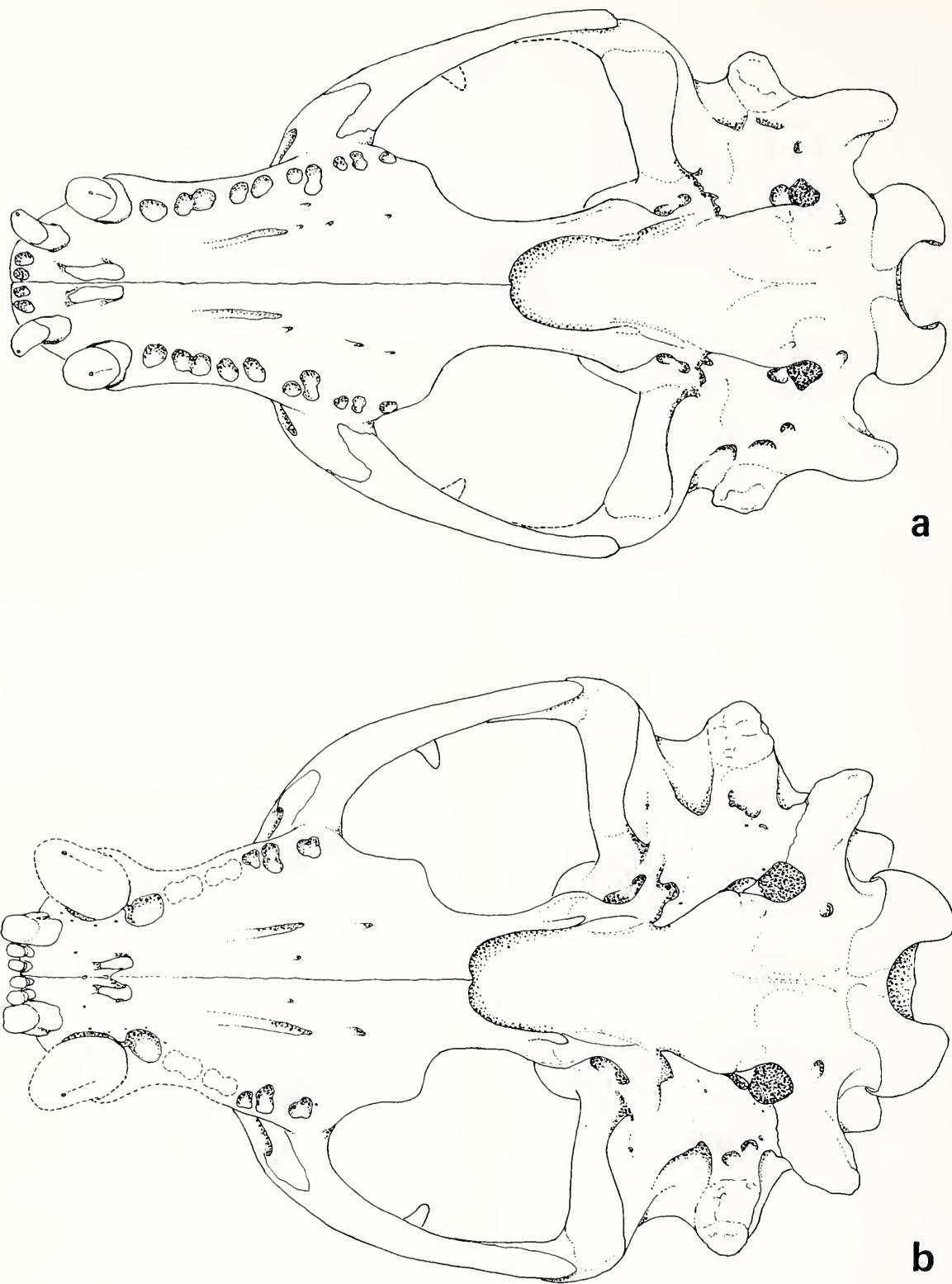


Figure 9. Comparative ventral views of holotype skulls of species of *Desmatophoca*; **a**, *D. oregonensis* Condon, 1906 (modified from Mitchell, 1975:fig. 2, with additional information from referred specimen, LACM 123285); **b**, *D. brachycephala*, new species; reduced to the same cranium length.

don, 1906, known only by specimens from late Early Miocene and/or early Middle Miocene age rocks (circa 15–19 ma) that are referred to the Astoria Formation, and which are exposed near Newport on the Pacific coast of Oregon.

A second species, *Desmatophoca brachycephala*, new species, has been found in slightly older, Early Miocene strata (circa 20–23 ma), that are exposed near Knappton in Washington. The rocks that yielded the holotype and only known specimen of this species have also been referred to the Astoria Formation, but they were deposited in a different sedimentary realm from those on the coast of Oregon, and are correlative with the type section of the formation directly across the Columbia River from Knappton at Astoria, Oregon. Although *D. brachycephala* is the earlier of the two species, judging by most of its characters (broader cranium, shorter rostrum, and other derived dental and cranial features), it is more highly derived than *D. oregonensis*. Neither species is suitable as a morphological or chronological ancestor of the other, but they could share a common ancestor. Like some previously described fossil otariids, some general features of the skull of *D. brachycephala* are convergent with those of true seals in the family Phocidae. It is unfortunate, but probable, that studies of the more numerous specimens of *D. oregonensis*, already in museum collections, will, by inference, provide more information about *D. brachycephala* before additional specimens of this rare pinniped become available.

The discovery of *D. brachycephala* extends the geochronologic range of the genus and of the subfamily farther back in the Early Miocene and indicates that there must have been a considerable, but as yet undocumented, evolutionary history of desmatophocines prior to that time.

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MIDDLE MIocene MARINE BIRDS FROM THE
FOOTHILLS OF THE SANTA ANA MOUNTAINS,
ORANGE COUNTY, CALIFORNIA



Hildegarde Howard and Lawrence G. Barnes



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MIDDLE MIocene MARINE BIRDS FROM THE FOOTHILLS OF THE SANTA ANA MOUNTAINS, ORANGE COUNTY, CALIFORNIA

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ABSTRACT. A mixed marine and non-marine fossil vertebrate assemblage of Middle Miocene age has been recovered from several localities on both sides of Oso Creek in the foothills of the Santa Ana Mountains in Orange County, California, U.S.A. The fossils were found during grading operations for construction of Upper Oso Dam, and were derived from a coarse clastic marine rock unit. This rock unit, which crops out near the southeast margin of the Los Angeles Basin (both a topographic and depositional feature), has been mapped as the Topanga Formation. It overlies rocks assigned to the Early Miocene Vaqueros Formation and is in turn overlain by rocks mapped as the Late Miocene Monterey Formation.

Among the available sample of 54 avian bones in the assemblage from Upper Oso Dam are fossils representing *Diomedea ?milleri* Howard (albatross), *Puffinus priscus* Miller, *Puffinus* ?new species, *Puffinus* spp. (shearwaters), *Sulidae* (boobies and gannets, two species), *Anatidae* (undescribed large diving duck), and *Alcodes*, aff. *A. ulnulus* Howard (flightless auk). This is the oldest fossil avifauna yet described from Cenozoic marine strata in the Orange County area, and the only marine avifauna in California of Middle Miocene age that has yet been reported from south of the outcrops of the Sharktooth Hill Bonebed in Kern County. The birds in the assemblage from Upper Oso Dam have their closest affinities with the species from the Sharktooth Hill Bonebed. No species of alcids are known from that bonebed, however, and the primitive flightless auk genus, *Alcodes*, had been previously recorded only in slightly younger, Late Miocene fossil assemblages from the Monterey Formation in Orange County.

INTRODUCTION

From 1978 to 1983, field parties organized by the Natural History Museum of Los Angeles County (LACM) collected fossils from Middle Miocene marine sediments in the Oso Creek area (Fig. 1) in the foothills of the Santa Ana Mountains near Mission Viejo, Orange County, California (Raschke, 1984). The fossil-bearing sediments were exposed during the mechanized grading of hills on both sides of Oso Creek during construction of an earth-fill dam, named Upper Oso Dam (33°39'30" north latitude, 117°37'35" west longitude). The subjects of the present study are the 54 bird bones thus obtained which represent probably 34 individuals.

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The bones were found in a gray and yellowish-red colored, pebble-bearing, coarse sand deposit that is several meters thick and has been identified on geologic maps (e.g., Morton et al., 1973:pl. 1) as belonging to the Topanga Formation. These sediments at Upper Oso Dam directly underlie shales and siltstones that have been mapped as the Monterey Formation, which is Late Miocene in age. The Monterey Formation has elsewhere yielded the birds that were previously reported by Howard (1966, 1968, 1976, 1978) from localities in Laguna Hills (Leisure World) and Laguna Niguel, approximately 10 km to the southwest in Orange County (Fig. 1).

It may no longer be correct to refer to the coarse sands at Upper Oso Dam as the Topanga Formation because the type section of that formation is in the Santa Monica Mountains, approximately 100 km to the north within the Los Angeles Basin, where the name has been elevated to the status of a group (Yerkes and Campbell, 1979). Because the Topanga Formation is no longer used in the Santa Monica Mountains, and because of lithologic differences and the lack of lateral continuity between the two areas, the formation name is probably no longer applicable to rocks anywhere in Orange County.

Raschke (1984) provided a preliminary notice of the occurrence of vertebrate fossils at Upper Oso Dam, and future reports will be published on the geology in the vicinity and on the other fossils. The fossil assemblage from the Middle Miocene sediments at Upper Oso Dam is correlated with the Barstovian North American Land Mammal Age and the Sharktooth Hill Local Fauna from the Round Mountain Silt in Kern County, farther north in California (Raschke, 1984: 64). Some evidence for these age determinations derives from

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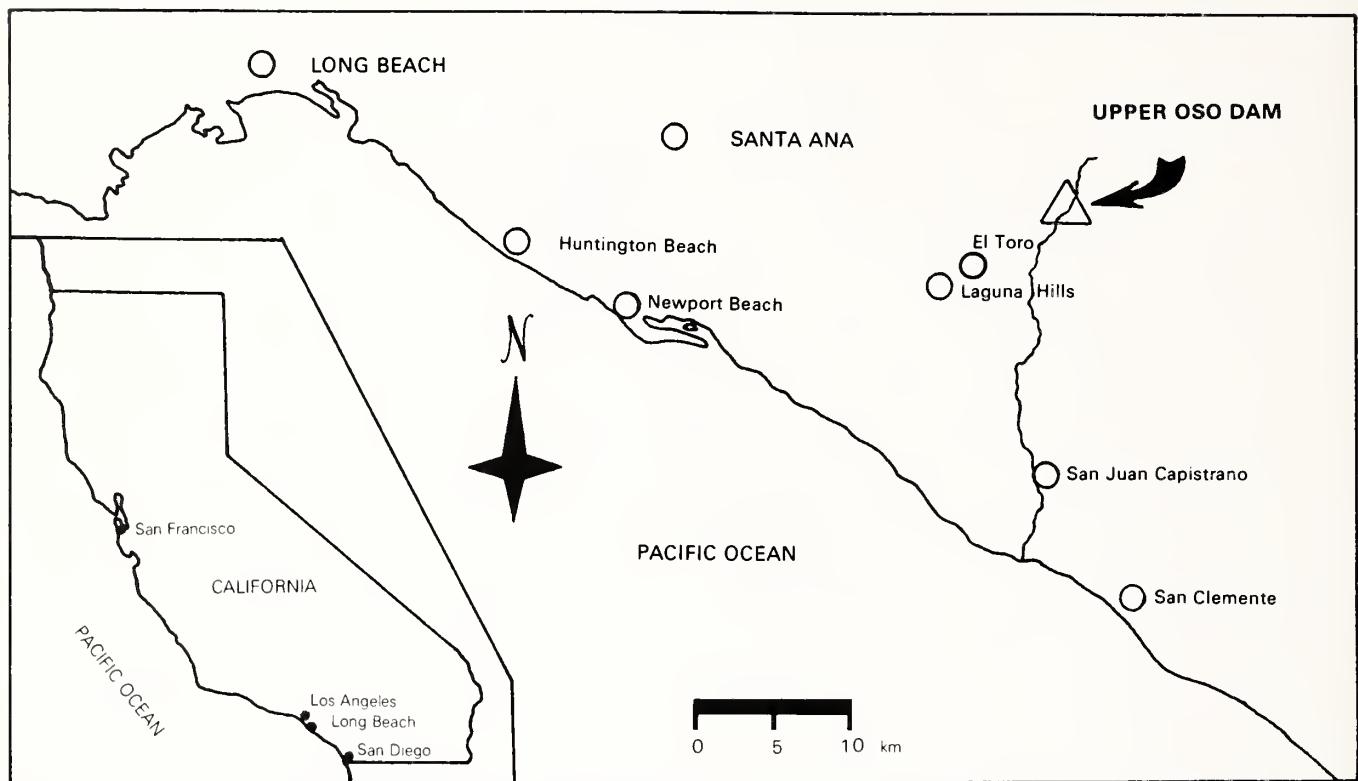


Figure 1. Location of the sites that produced the fossil birds described in this study, at Upper Oso Dam, Oso Creek, Orange County, California.

unpublished data from other fossil specimens in the LACM from Upper Oso Dam, including those of sharks, bony fishes, turtles, and mammals. Among these other taxa, the sharks and mammals are probably the most useful age indicators, considering the state of our knowledge of Pacific coast marine and terrestrial vertebrates. The shark assemblage is typically Middle Miocene in aspect and includes *Isurus hastalis* (Agassiz, 1843); *I. planus* (Agassiz, 1856); *Isurus* spp.; *Procarcarodon megalodon* (Agassiz, in Charlesworth, 1837); *Carcharhinus* sp. and/or *Negaprion* sp.; *Galeocerdo aduncus* Agassiz, 1843; *Hemipristis serra* Agassiz, 1843; *Squalus sericulus* Jordan and Hannibal, 1923; *Squatina lerichei* Jordan and Beal, 1913; and *Myliobatis* sp. These have similar morphologies and occur in approximately similar relative abundances as do the same taxa from the Sharktooth Hill Bonebed. Terrestrial mammalian taxa from Upper Oso Dam, not strictly limited to, but characteristic of the Barstovian Land Mammal Age, include a horse, *Merychippus* sp.; a stilt-legged camel, *Aepycamelus* sp.; and a large paleomerycid (Raschke, 1984:64). The mammals also include at least three species of otariid pinnipeds: *Allodesmus* sp., *Neotherium* sp., and an undescribed genus and species. The same or similar species of all three of these pinniped genera occur in the Sharktooth

Hill Bonebed. Among the odontocete cetaceans from Upper Oso Dam are *Kentriodon* sp., cf. "Squalodon" *errabundus* Kellogg, 1931, and a large, unnamed species; again, all similar to, or the same as, taxa from the Sharktooth Hill Bonebed. The age of that bonebed, as determined on the basis of several lines of evidence (see Barnes, 1976; Barnes and Mitchell, 1984), is late Middle Miocene, correlated with the Barstovian North American Land Mammal Age (Wood et al., 1941, the "Tebmor" provisional provincial mega-invertebrate stage of Addicott (1972), and the Relizian or Luisian foraminiferal stage, and is between approximately 13 and 15 million years old. Additional, indirect evidence for the Barstovian age of the vertebrate-bearing sands at Upper Oso Dam is the fact that they overlie strata referred to the Vaqueros Formation (Morton et al., 1973:pl. 1), which have produced land mammals that are characteristic of the Hemingfordian North American Land Mammal Age (Raschke, 1984:62, fig. 1; D.P. Whistler, personal communication).

Unfortunately, many of the bird bones from Upper Oso Dam that we describe here are fragmented, crushed, and distorted. Some of this is the result of geologic phenomena, but some resulted from the fossils' being scraped and run over by machinery. Specific identifications have, therefore,

been difficult. Five families are represented, the most abundant of these being the shearwaters (family Procellariidae, 26 bones, 16 individuals), and the booby-gannet family (Sulidae, 22 bones, 10 individuals). Other fossils belong to members of the albatross family (Diomedidae, two bones of one individual), waterfowl family (Anatidae, one bone), and auk family (Alcidae, three bones of three individuals). At least eight species are represented. (We did not calculate minimum numbers of individuals, but made our determinations on the basis of the stratigraphic and geographic separation of the specimens.)

The families Procellariidae and Sulidae are well represented in the fossil record, with seven species of the Sulidae and eight species of the Procellariidae (including two fulmars) having been previously described from California Miocene deposits (Howard, 1983). A thorough study of each of these families is needed and, therefore, identifications herein of the shearwater and sulid specimens should be considered tentative. The Sulidae are now in the process of being reviewed by K.I. Warheit of the Department of Paleontology at the University of California, Berkeley. Fossil avian species have been described from the Sharktooth Hill Bonebed by Wetmore (1930), Miller (1961, 1962), Howard (1966, 1984), and Warter (1976). Howard (1983) summarized these and other published records of fossil birds from California.

MATERIALS AND METHODS

Acronyms used for institutions are:

CAS: California Academy of Sciences, San Francisco, California.

LACM: Natural History Museum of Los Angeles County, Los Angeles, California.

UCLA: University of California at Los Angeles, California.

UCMP: University of California Museum of Paleontology, Berkeley, California.

UCMVZ: University of California Museum of Vertebrate Zoology, Berkeley, California.

USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In addition to the fossil material in the LACM collections, referred specimens and casts of holotypes from CAS, UCMP, UCLA, and USNM have been available for this study. An accurate cast of the holotype of *Puffinus inceptor* Wetmore, 1930, was used for comparisons instead of the original specimen (CAS 5223). Modern skeletal material is from the LACM collections, with the exception of specimens of *Aethia pusilla* (Pallas, 1811), which are from UCMVZ. The fossils described from Upper Oso Dam are from LACM localities 4545, 4546, and 4547 which, in that order, are progressively older and stratigraphically lower within the deposit. The locality number LACM 4464 is assigned to fossils that were found weathered out and loose at LACM localities 4545, 4546, or 4547, and therefore lacking more precise stratigraphic data. The classification herein follows that of the Sixth Edition of the

American Ornithologists' Union Checklist of North American Birds (1983).

SYSTEMATICS

Order Procellariiformes

Family Diomedidae (albatrosses)

Diomedea Linnaeus, 1758

Diomedea ?milleri Howard, 1966

Figure 2C

REFERRED SPECIMENS. Associated proximal half of right ulna and distal end and shaft fragments of right radius from one individual, LACM 120439, from LACM locality 4547.

DISCUSSION. Albatross bones have been previously reported from several Miocene age sites in California, but only two species, both first recognized on the basis of fossils from the Sharktooth Hill Bonebed, have been named: *Diomedea californica* Miller, 1962, and *D. milleri* Howard, 1966. *Diomedea californica* has also been found in the Late Miocene Monterey Formation in the Laguna Hills in Orange County (see Howard, 1978). The holotype of the species is a tarso-metatarsus, slightly larger than that of the living Short-tailed Albatross, *D. albatrus* Pallas, 1769, but not as large as that of the extant Wandering Albatross, *D. exulans* Linnaeus, 1758. *Diomedea milleri* is a considerably smaller species, and is still known only from the Sharktooth Hill Bonebed. Its holotype is the proximal end of an ulna having a proximal breadth of 14.4 mm, as compared to 17.6 mm for the same bone of the living Black-footed Albatross, *D. nigripes* Audubon, 1839 (see Howard, 1966:4).

The albatross ulna, LACM 120439, from Upper Oso Dam (Fig. 2C), is 15.8 mm for the same measurement. The radius associated with this ulna is also narrower of shaft than is the same bone of a Recent *D. nigripes*. The area immediately distal to the ulnar cotylae, which contains the diagnostic characters of the species *D. milleri*, is crushed on LACM 120439. However, a clearly defined ridge on the palmar side of the shaft below this area suggests that there was a distinct angle between the palmar and internal surfaces of the shaft immediately below the internal cotyla, as was described for *D. milleri*. Although the present specimen, LACM 120439, appears to have a more prominent acromion and external cotyla than does the holotype of *D. milleri*, these areas are slightly eroded in the latter, possibly altering its morphology.

Family Procellariidae (shearwaters)

Puffinus Brisson, 1760

Puffinus priscus Miller, 1961

Figures 2A, B, F, G

REFERRED SPECIMENS. Left humerus, LACM 120415; associated right and left humeri and incomplete right

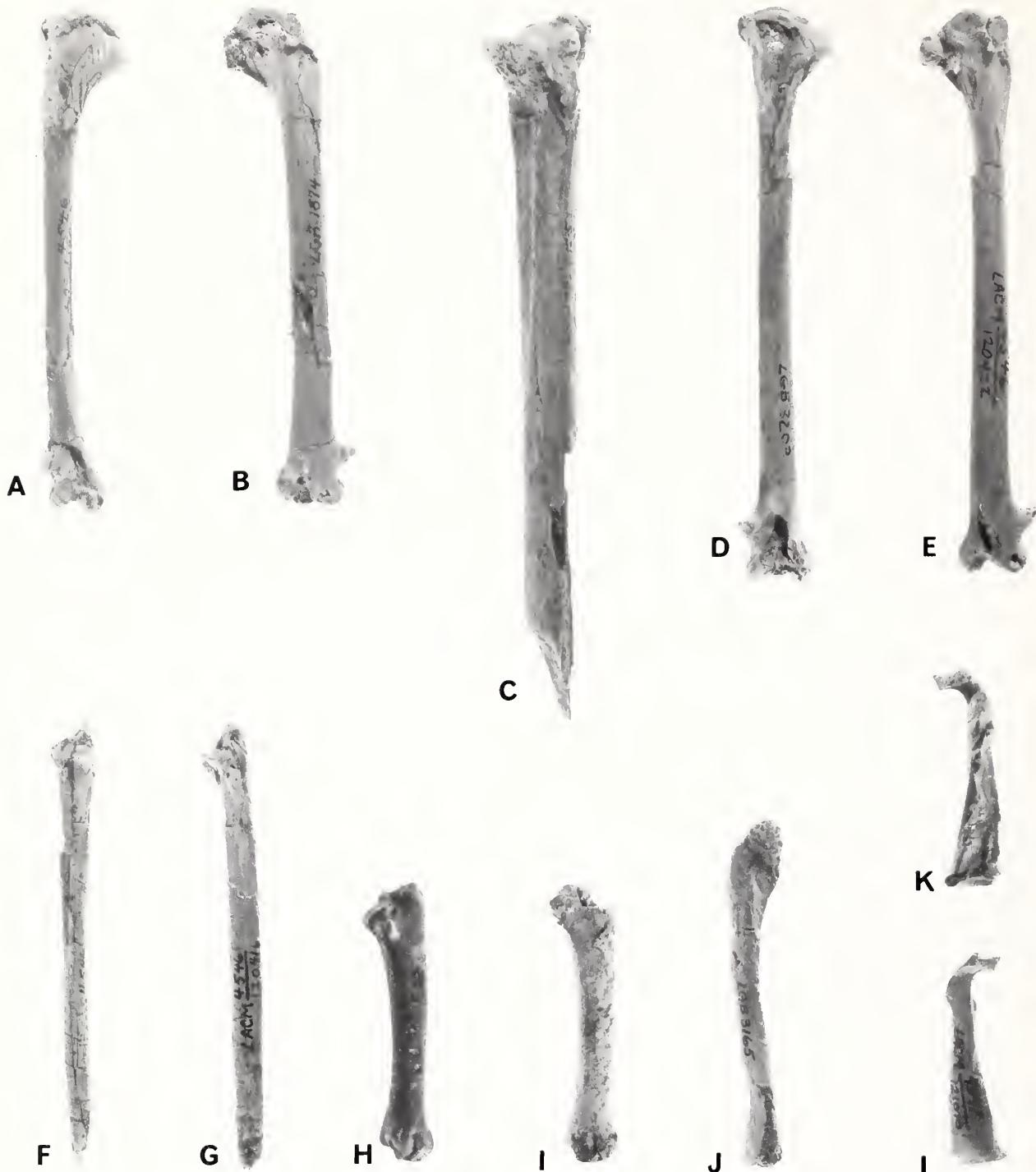


Figure 2. A, B, *Puffinus priscus* Miller, 1961, right humerus, LACM 120416, palmar and anconal views; C, *Diomedea ?milleri* Howard, 1966, right ulna, LACM 120439, internal view; D, E, *Puffinus* ?new species, right humerus, LACM 120422, palmar and anconal views; F, G, *Puffinus priscus* Miller, 1961, right ulna, LACM 120416, palmar and internal views; H, I, external views of left ulnae of *Alcodes* Howard, 1968; *H*, *A. ulnulus* Howard, 1968, holotype, LACM 18277, from Monterey Formation in Laguna Hills, LACM locality 1945; I, *Alcodes*, aff. *A. ulnulus* Howard, 1968, LACM 120434, from Upper Oso Dam, LACM locality 4546; J–L, *Alcodes*, aff. *A. ulnulus* Howard, 1968; J, left humerus, LACM 120414, anconal view; K, L, right coracoid, LACM 121010, posterior and anterior views. All views natural size, except H and I, which are $\times 1.5$.

ulna from one individual, LACM 120416; distal end of right humerus, LACM 120417; proximal fragment of left ulna, LACM 120424; all from locality LACM 4546. Proximal three-fourths of right humerus, LACM 126159, from locality 4464.

TENTATIVELY REFERRED SPECIMENS. Right and left distal ends of tibiotarsi, LACM 120425 (right) and 120426 (left); right tarsometatarsus lacking proximal end, LACM 120419; all from locality 4546.

DISCUSSION. The referred humeri from Upper Oso Dam agree in their general conformation, in their size, and in the flatness of their shafts (Figs. 2A, B) with the holotypic distal end of this element (UCMP 58185) from the Sharktooth Hill Bonebed and/or with additional unpublished specimens (three of which—LACM 18140, LACM 44556, and LACM 126219—are complete) from the same stratum, that are now referable to *Puffinus priscus* Miller, 1961. Howard (1968:7–8) questionably referred a partial humerus from the Late Miocene age Monterey Formation in Orange County to the same species. The ranges of measurements of the humeri from Upper Oso Dam are: length—79.3 to 81.2 mm, breadth of distal condyles—7.4 to 7.8 mm, distance from distal surface of condyles to proximal surface of ectepicondylar prominence—9.5 to 9.9 mm. The same measurements of humeri from the Sharktooth Hill Bonebed which are assigned to *P. priscus* are: length—80.3 to 82.5 mm ($n = 3$), breadth of distal condyles—7.1 to 7.7 mm ($n = 6$, holotype—7.5 mm), and distance from distal condyles to proximal surface of ectepicondylar prominence—8.9 to 10.0 mm ($n = 5$, holotype—9.5 mm).

Each of the two ulnae, one of which (Figs. 2F, G) is associated with humeri (LACM 120416), has a high, pointed olecranon (possibly exaggerated by crushing) and a long, pointed, and upturned external cotyla. These characters are suggestive of those of the extant Black-vented Shearwater, *P. opisthomelas* Coues, 1864, although to an exaggerated degree.

The tarsometatarsus, which measures 6.1 mm in distal breadth, is tentatively assigned to *P. priscus* on the basis of favorable comparisons between it and tarsometatarsi of the species from the Sharktooth Hill Bonebed. Of the three tarsometatarsi of *Puffinus* now available from the latter locality, one specimen (LACM 104058) is incomplete, comprising only the distal half. It agrees in size with LACM 120419 from Orange County, is slightly smaller than the other two, and, we believe, is assignable to *P. priscus*.

The tibiotarsi resemble the only distal end of this element assignable to *Puffinus* that has been found in the Sharktooth Hill Bonebed, LACM 122994. That specimen is tentatively referred to *P. priscus* on the basis of its size relative to the tarsometatarsi noted above.

Puffinus ?new species

Figures 2D, E

REFERRED SPECIMENS. Associated, complete, but poorly preserved right humerus, crushed proximal end of ulna, and proximal and distal fragments of radius from one

individual, LACM 120422, from locality LACM 4546; collected 23 April 1980 by L.G. Barnes.

DESCRIPTION. Although in general characters the humerus (Figs. 2D, E) resembles those of species in the subgenus *Puffinus*, the shaft is more rounded and less flattened throughout. It is, therefore, clearly distinguishable from the holotype of *P. priscus* Miller, 1961 (UCMP 58185), but slightly less so from the holotype of *P. mitchelli* Miller, 1961 (UCMP 58184) (casts of both holotypes are at hand). In length (90.4 mm), LACM 120422 is intermediate between three Sharktooth Hill specimens of *P. priscus* (80.2 to 82.5 mm) and the one measurable specimen (LACM 17500) of *P. mitchelli* (98.1 mm). Although the ulna from Upper Oso Dam is severely crushed, the breadth across the cotyloae could not have exceeded 7.5 mm.

Poor preservation of this humerus from Upper Oso Dam makes difficult any detailed comparison with the holotype (CAS 5223) of *P. inceptor* Wetmore, 1930, which is the distal end of a humerus. The specimen from Orange County (LACM 120422) is broken through the internal condyle, but appears to lack the notable internal thrust of the distal end that is characteristic of *P. inceptor*, and is reflected in the measurements given by Wetmore (1930:87): breadth of shaft—5.9 mm, greatest distal breadth—12.2 mm. In the humerus from Upper Oso Dam, the shaft breadth is 6.3 mm, the greatest distal breadth 11.2 mm.

DISCUSSION. Many other Miocene species of the genus *Puffinus* have been previously recorded from California (see Howard, 1983). Among these, *P. diatomicus* Miller, 1925, from the Late Miocene age Sisquoc Formation in Santa Barbara County has the humerus represented in both the holotype and referred skeletal impressions. Miller (1925) measured the lengths of these humeri as 80 to 84 mm (considerably less than for LACM 120422). The humerus is also the holotype for each of the two previously named Late Miocene species from Orange County; *P. calhouani* Howard, 1968, and *P. barnesi* Howard, 1978. Each of these is smaller and has a more compressed shaft than does LACM 120422 from Upper Oso Dam. Compared with the holotypic distal end of a humerus of the Early Miocene species, *P. micraulax* Brodkorb, 1963, from Florida, LACM 120422 is broader. The holotypic distal end of the humerus of *P. conradi* Marsh, 1970, from the Middle Miocene Calvert Formation of Maryland, is broader and has a thicker shaft.

Although the humerus of LACM 120422 appears to be distinct from all of the above, the poor condition of the available material precludes naming a new species. Should more specimens assignable to this shearwater be discovered, comparisons should also be made with the French Middle Miocene species, *P. aquitanicus* (Milne-Edwards, 1874) and *P. antiquus* (Milne-Edwards, 1874). In fact, Olson (1985:211) has noted the need for a worldwide revision of fossils assigned to the genus *Puffinus*.

Puffinus, spp. undetermined

REFERRED SPECIMENS. Complete right ulna, LACM 120420; distal three-fourths of left ulna, LACM 124360;

proximal and distal ends of right ulna, LACM 120421; fragment of proximal end of left ulna, LACM 126155; associated fragments of distal end of ulna and proximal end of radius and carpometacarpus of one individual, LACM 126156; complete radius, LACM 120423; right carpometacarpus, LACM 120419; associated fragments of distal end of left ulna and tarsometatarsal shaft of one individual, LACM 126157; all from locality LACM 4546. Distal fragment of radius, LACM 120412; incomplete right humerus, LACM 126160; both from locality LACM 4464.

DISCUSSION. The size range alone among these specimens suggests that at least two species are represented. Most are of small size and in this respect are suggestive of *P. priscus*. One poorly preserved humerus (LACM 126160) and one ulna (LACM 120420) are, however, notably larger. This humerus has been partly restored, but appears to have a more flattened shaft toward the distal half of the bone than do humeri of *P. mitchelli* from the Sharktooth Hill Bonebed. The length of this poorly preserved humerus, from the proximal edge of the brachial impression to the head is 83.2 mm. The same measurement of a Sharktooth Hill humerus, LACM 17500, referred to *P. mitchelli*, is 86.6 mm. The ulna from Upper Oso Dam, LACM 120420, has a length of 95.7 mm. In contrast, the largest ulna known from the Sharktooth Hill Bonebed (LACM 124359) measures only 88.2 mm long. Both are markedly larger than the incomplete ulna (LACM 120416) from Upper Oso Dam that is associated with the humerus that we assigned above to *P. priscus*.

Order Pelecaniformes

Family Sulidae (boobies and gannets)

Sulidae, spp. undetermined

REFERRED SPECIMENS. Associated right and left humeri, right and left ulnae, and a badly crushed radius of one individual, LACM 120433; associated left coracoid and proximal fragment of shaft of left humerus of one individual, LACM 120428; right tarsometatarsus lacking part of proximal end, LACM 120432; proximal end of radius, LACM 120429; proximal end of humerus, LACM 120430; distal end of humerus, LACM 120431; skull fragment, LACM 120427; all from locality 4546. Associated incomplete radius and ulna of one individual, LACM 120438; humerus, LACM 123910; seven associated incomplete and poorly preserved bones of one individual lying together in matrix with the following elements represented: incomplete mandible, proximal end of right humerus, three fragments of left humerus, fragment of left ulna, distal end of right radius, proximal end of left radius overlying left carpometacarpus, LACM 126161; all from locality LACM 4547.

DISCUSSION. These specimens will be included in Warheit's study of the family Sulidae. A brief examination of the

material from Upper Oso Dam reveals two humeri (LACM 120433, 120431) whose measurements exceed those of specimens of *Morus vagabundus* Wetmore, 1930, the only species of sulid that has been described from the Sharktooth Hill Bonebed. The distal breadth of the holotypic humerus of *M. vagabundus* is 18.3 mm, whereas the same measurement of LACM 120431 is 21.0 mm. The length of a referred humerus of *M. vagabundus* is 170 mm (Howard, 1966:6), and the length of LACM 120433 from Upper Oso Dam is 183 mm.

A second species of sulid from the deposits at Upper Oso Dam is indicated by specimens LACM 120428, 120432, and 120438. Although difficult to measure exactly, they suggest a smaller species. That more than one species of sulid is also represented in the Sharktooth Hill Bonebed was noted by Miller (1961:401), who reported a proximal fragment of an ulna that is larger in size than the one referred to *M. vagabundus* by Wetmore (1930). Howard (1966:7) also reported from the same bonebed two tarsometatarsi that differ from each other in qualitative characters as well as in size.

Order Anseriformes

Family Anatidae (ducks, geese, and swans)

Subfamily Anatinae (ducks)

Tribe Mergini (divers)

Mergini, genus and species undetermined

REFERRED SPECIMEN. Distal end of left femur, LACM 125994, from locality LACM 4546.

DESCRIPTION. The fibular condyle of this femur is thrust laterally, and the popliteal area is deeply depressed and angular, as is the case in diving ducks such as those of the genera *Somateria* Leach, 1819; *Mergus* Linnaeus, 1758; and *Melanitta* Boie, 1822. The fossil specimen is significantly larger than the femora of extant species of these genera, however, and the breadth of its distal end is 20.7 mm.

DISCUSSION. This femur represents a large diving anatid that was the size of a goose. In its general conformation it is suggestive of femora from the Sharktooth Hill Bonebed, which represent a large anatid species. Compared with them, however, the femur from Upper Oso Dam is more slender and the muscle scar on the internal side of the posterior face is more proximally located. Anteriorly, the intercotylar area appears to be more deeply excavated, but allowance must be made for the poor preservation of the Orange County specimen.

The femora and other bones of the anatid from the Sharktooth Hill Bonebed, which are now under study by Howard, appear to represent a new species, and probably a new genus. The single femur from Upper Oso Dam indicates the presence of a large diving anatid in the Orange County area.

contemporaneous with a probably eongeneric, but specifically distinct bird in the Kern County area.

Order Charadriiformes
 Family Alcidae (auks et al.)
Alcodes Howard, 1968
Alcodes, aff. *A. ulnulus* Howard, 1968
 Figures 2I-L

REFERRED SPECIMENS. Left ulna, LACM 120434 from locality LACM 4546; left humerus, LACM 120414, from locality LACM 4545; right coracoid, LACM 121010, from locality LACM 4547.

DESCRIPTION. The holotype of *Alcodes ulnulus* Howard, 1968, is a complete left ulna (LACM 18277, Fig. 2H). The distal end of a right ulna (LACM 18279) and the proximal end of a right carpometearpus (LACM 18278) were also referred to the same species by Howard (1968). An incomplete proximal portion of a right ulna (LACM 18280), 10 percent larger than the holotype, was tentatively referred to the species in the same publication.

The ulna (LACM 120434, Fig. 2I) from Upper Oso Dam is not as well preserved as the holotype, but resembles it by having a relatively thick shaft for its length. It is, however, slightly longer, and relatively narrower than the holotype of *A. ulnulus*. In contrast to LACM 120434 from Upper Oso Dam, the ulna of a Recent specimen of the Least Auklet, *Aethia pusilla* (UCMVZ 60629), is longer and narrower, and that of the Pliocene, flightless, auk-like swimmer, *Mancalla milleri* Howard, 1970, is shorter and broader (see Table 1). Although *Alcodes ulnulus* clearly had evolved in the direction of flightlessness, it was not as derived as any species in the genus *Mancalla* Lucas, 1901.

The humerus, LACM 120414, although incomplete (Fig. 2J), resembles the paratypic specimen (LACM 2813) of the Pliocene species, *Mancalla milleri*, in the compression of its distal end and in the height of its ectepicondylar prominence. The deltoid crest, however, is not as extensive as that of *M. milleri*, and the shaft is narrower throughout. Other distinctive characters, peculiar to the Upper Oso Dam specimen, are: proximally the pectoral attachment and external tuberosity are distinctly external to the capital shaft ridge and separated from the ridge by a depression, and the ridge is more angular; the depression below the head, internal to the capital shaft ridge extends distally to the line of the distal edge of the incomplete bicipital crest. Unfortunately, the bone is too poorly preserved to make meaningful measurements.

The coracoid from Upper Oso Dam, LACM 121010, resembles that of *M. milleri* in its straight shaft and narrow sternal facet (Figs. 2K, L). It is shorter, however, than the

Table 1. Measurements of alcid ulnae (in mm).

| | <i>Alcodes,</i> aff. <i>A. ul-</i> | | <i>Aethia</i> | |
|------------------|---------------------------------------|------------------------------|-------------------------------------|--|
| | <i>Alcodes</i> | <i>ulnulus</i> (holotype) | <i>pusilla</i> (UCMVZ 120434) | <i>Mancalla</i> <i>milleri</i> (minimum) |
| Internal length | 27.4 | 29.4 | 32.5 | 23.6 |
| Breadth of shaft | 2.9 | 2.9 | 1.6 | 3.2 |
| Depth of shaft | 4.9 | 3.9 | 2.7 | 5.3 |

smallest known coracoid of *M. milleri*, from which it further differs as follows: triosseal canal angular at the anterior edge, with the tip of the furcular facet projecting farther anteriorly; anterior surface of the shaft evenly rounded throughout its length, lacking the flattening and internal projection distally that is characteristic of *M. milleri*. Its greatest length is 34.3 mm; whereas the minimum length of any specimen of *M. milleri* is 38.5 mm (Howard, 1970:8).

DISCUSSION. These three bones are the only alcid specimens collected at Upper Oso Dam. Indeed, they are the first reported from any Middle Miocene deposit in California, including the Sharktooth Hill Bonebed. Alcids were much more abundant and diverse by Late Miocene time in southern California, however, as evidenced by the presence of at least five genera among the 27 alcid bones that have been recorded (Howard, 1968) from the lower part of the Late Miocene age Monterey Formation at a Laguna Hills site in Orange County (LACM locality 1945, the type locality of *Alcodes ulnulus*).

The genus *Alcodes* had not been previously recorded elsewhere, until the present study. When originally described, because of its apparent flightlessness, it was placed, somewhat questionably, by Howard in the subfamily Mancallinae. This subfamily had been used traditionally for flightless species in the genera *Mancalla* and *Praemancalla* Howard, 1976. Recently, his studies of the flightless alcids have led Olson (1985), however, to question the need to recognize the subfamily.

SUMMARY AND CONCLUSIONS

Fossil birds comprise part of a vertebrate assemblage discovered in marine Middle Miocene rocks at Upper Oso Dam, near Mission Viejo, Orange County, California. The fossils were collected from coarse clastic rocks that underlie shales and siltstones mapped as the Monterey Formation. The Monterey Formation has been the source of most of the previously described Late Miocene birds from localities elsewhere in Orange County. The fossil bird bones from Upper Oso Dam described in this report are from a sandstone unit that has been mapped as the Topanga Formation. Recent changes in the nomenclature of the rocks in the type area of

the Topanga Formation, to the north in Los Angeles County, resulted in discontinuance of its use as a formation name. Because of this, and for other reasons, its use is probably no longer correct for rocks in Orange County, and at the present time, there is not an appropriate formational name for the source rock of these fossils.

The age of the sandstone deposit bearing these fossils at Upper Oso Dam was determined on the basis of relationships with overlying and underlying rock units, and identifications of marine and terrestrial vertebrates. The deposit is Middle Miocene in age, correlative with the Barstovian North American Land Mammal Age, and approximately correlative with the Sharktooth Hill Bonebed, which is in the upper part of the Round Mountain Silt in Kern County, California. Special attention was given, therefore, to comparisons between the avian material from these two faunal assemblages.

The poor preservation of the avian material from Upper Oso Dam has made difficult the specific assignment of the 54 avian bones represented. They are, however, identifiable as follows (numbers of individuals are given in parentheses):

Family Diomedidae (albatrosses)

Diomedea milleri Howard, 1966 (1)

Family Procellariidae (shearwaters)

Puffinus priscus Miller, 1961 (5)

Puffinus ?new species (1)

Puffinus, spp. undetermined (10)

Family Sulidae (boobies and gannets)

Sulidae, two spp. undetermined (10)

Family Anatidae (waterfowl)

Tribe Mergini, genus and species undetermined (1)

Family Alcidae (auks et al.)

Alcodes, aff. *A. ulnulus* Howard, 1968 (3)

The fossil bird assemblage from Upper Oso Dam is more like that from the Sharktooth Hill Bonebed than any other yet documented from the eastern North Pacific margin. However, only four of the nine avian families now represented by species in the Sharktooth Hill Local Fauna (Howard, 1984) are represented in the collection from the Upper Oso Dam site. The albatross from Upper Oso Dam is questionably assigned to *Diomedea milleri*, a species that is known only from Sharktooth Hill. A shearwater, *Puffinus priscus*, definitely occurs at both localities. Possibly one or both of the other species of *Puffinus* that have been described from Sharktooth Hill are also represented by the other material that we assign to this genus from Upper Oso Dam. The sulid bones (although not yet identified to the species level) suggest the presence of two species at the Orange County locality, as is also the case for the Sharktooth Hill Bonebed.

A single anseriform femur documents the occurrence of a large diving anatid in the deposits at Upper Oso Dam. The only previously named marine anatid from California is *Presbychen abavus* Wetmore, 1930, first described from the Sharktooth Hill Bonebed, then later found in the Late Miocene Monterey Formation in Orange County (Howard, 1968). The species from Upper Oso Dam is not *P. abavus*, but is instead probably congeneric with another, undescribed species

that has been recently discovered in the Sharktooth Hill Bonebed (Howard, manuscript in preparation).

Of particular interest are the three bones from Upper Oso Dam belonging to a species of the family Alcidae. We have assigned these to the primitive flightless auk genus, *Alcodes*, and they are similar to, but not demonstrably conspecific with specimens of *A. ulnulus*. Significantly, no alcid specimens have ever been found in the Sharktooth Hill Bonebed. This contrasts with relatively abundant and diverse Late Miocene alcids, including *A. ulnulus*, in the geologically younger Monterey Formation in Laguna Hills, not far from Upper Oso Dam in Orange County.

The fossil bird assemblage from Upper Oso Dam is the oldest one yet known in Orange County. It is the southernmost documented occurrence of Middle Miocene marine birds from the Pacific border of the United States, and indeed, is the only Middle Miocene avifauna yet described from California aside from that of the Sharktooth Hill Bonebed, which is located approximately 322 km to the north.

We have noted taxonomic differences as well as similarities between the bird assemblages from these two sites. Unfortunately, poor preservation of some of the bones from Upper Oso Dam has caused us to qualify several identifications. The apparently real absence of alcids in the Sharktooth Hill Local Fauna, however, is a striking difference between that assemblage and those of Middle and Late Miocene age from Orange County. The site of deposition of the Upper Oso Dam avifauna in Orange County is on the opposite (west) side of the San Andreas Fault from the Sharktooth Hill Bonebed and, accounting for estimates of prior lateral (northward) displacement (see Hill and Dibblee, 1953; Crowell, 1975), might have originally been as much as 300 km farther south in the Middle Miocene than at the present time. This means that the two sites of deposition may have been over 600 km apart in Middle Miocene time, and this latitudinal difference must be one of the factors accounting for the faunal differences. The flightless alcids may not have had such wide distributions as the flying pelagic species. They may have been restricted to a southerly distribution, and the significant latitudinal differences between the two areas may explain why members of the group have never been found in the Kern County fossil record but are relatively common in Orange County sediments.

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CONTRIBUTIONS TOWARD A REVISION OF THE NEW WORLD
NOMADINE BEES. 2. THE GENUS *MELANOMADA*
(HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling and Jerome G. Rozen, Jr.



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CONTRIBUTIONS TOWARD A REVISION OF THE NEW WORLD NOMADINE BEES. 2. THE GENUS *MELANOMADA* (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling¹ and Jerome G. Rozen, Jr.²

ABSTRACT. The cleptoparasitic bee genus *Hesperonomada* is synonymized with *Melanomada*. *Melanomada*, together with *Triopasites* and *Paranomada* in North America and *Brachynomada* and perhaps *Kelita* in South America, is a closely knit group (the *Melanomada* complex) that is morphologically distinctive, both as adults and larvae, within the tribe Nomadini as it presently is constituted. A key to the North American genera of this complex is given, as is a key to the six known species of *Melanomada*. Three new species of *Melanomada* are described and illustrated: *M. annectens* (California, U.S.A.), *M. chica* (Baja California Sur, Mexico), and *M. nimia* (Kansas, U.S.A.).

The mature larvae of *M. annectens* is described and illustrated and the relationships of the genus to other members of the complex, and to the Nomadini as a whole, are discussed in terms of larval characteristics.

As far as known, all North American members of the *Melanomada* complex are eleptoparasites of the anthophorid genus *Exomalopsis*. Known host relationships are discussed, suspected relations are mentioned, and the relationships of both the South American *Brachynomada* and *Kelita* to the Panurginae are outlined.

INTRODUCTION

Recently, we undertook a study of the nesting biology of *Exomalopsis nitens* Cockerell, near Corona, Riverside County, California, in hope of recovering information about, and immature stages of, its reported cleptoparasite *Hesperonomada melanantha* (Rozen, 1984; Rozen and Snelling, 1986). Upon examining the cleptoparasite from the nesting area, we determined that the species was not *H. melanantha*, and, although the two species were obviously similar, this new species shared a number of features with the genus *Melanomada*. These characteristics immediately placed into question the distinctiveness of the genera *Hesperonomada* and *Melanomada*. This present contribution, in which *Hesperonomada* is synonymized with *Melanomada*, results from our attempt to resolve the relationships of these two genera, and makes known a number of distinctive new species belonging to *Melanomada*. We not only describe the new species but also present information about the host relationships and immature stages of one of these.

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Snelling has been primarily responsible for preparing the Systematics section of this manuscript, whereas Rozen has drafted the sections on Immature Stages and Host Associations and Bionomics.

SPECIMENS EXAMINED

Adult specimens examined during the course of this study were from the following collections: Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), University of Kansas (UKAN), United States National Museum of Natural History (USNM), and Utah State University (UTSU). Larval specimens are in the American Museum of Natural History.

SYSTEMATICS

The Nearctic genera *Melanomada* Cockerell, 1903b (including *Hesperonomada* Linsley, 1939, synonymized herein), *Triopasites* Linsley, 1939, and *Paranomada* Linsley and Michener, 1937, together with the South American *Brachynomada* Holmberg, 1886, form a close-knit and distinctive group within the Nomadini. An additional South American genus, *Kelita* Sandhouse, 1943, may be a part of this same complex, but possesses some unique features that are greatly at variance with this group and it is, therefore, not included in the following discussion.

The following apomorphies (many cited by Ehrenfeld and Rozen, 1977, and Rozen, 1977) define this group within the tribe Nomadini; plesiomorphic states are indicated in brackets. (1) Anterior and posterior basal angles of mandible about equally distant from eye [anterior angle more distant than

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basal angle in other Nomadini]. (2) Maxillary palpus with three to six segments and less than one-half as long as galea (except in *Melanomada chica*) [other Nomadini with six-segmented maxillary palpus more than one-half as long as galea]. (3) Metacoxa with inner, dorsal carina or lamella [absent in other Nomadini (small but present in *Hexepeolus*)]. (4) Metasomal sternum 6 of female produced posteriorly as a short, acute or rounded, hairy process (Fig. 4) [truncate or bilobed in other Nomadini]. (5) Metasomal sternum 7 of female with a pair of slender, apical lobes with a few coarse setae arising from their inner apical margins (Fig. 5) [sternum 7 subtruncate or with a pair of broad, well-separated lobes with coarse, spine-like setae at apex or along outer margins]. (6) Metasomal sternum 7 of male without basal apodeme (Figs. 8, 10, 12, 14) [basal apodeme present in other Nomadini]. (7) Gonostylus of male genitalia long and narrow (Figs. 16–18) [short and broad in most other Nomadini, but with some exceptions in *Hypochrotaenia* and *Nomada*]. (8) Integument smooth and shiny; punctures, when present, not confluent or contiguous [integument dull to shiny; punctures of head and thorax commonly confluent, at least in some areas]. (9) Mesepisternum of female, and often male as well, with dense, prostrate highly plumose pubescence on upper one-half or more, lower one-half or less with pubescence sparse and simple, or nearly so [in other Nomadini, mesepisternal pubescence usually uniform, and usually weakly plumose, but sometimes densely pubescent above and becoming less dense ventrad]. (10) Prepygidial brush of female metasomal tergum 5 suberect, the hairs acute or subacute [prepygidial brush of female suberect to prostrate, hairs, except anteriorly, spatulate or apically broadened and reflective]. (11) Mature larva³ with well-developed, paired dorsal tubercles (Fig. 19) [no dorsal tubercles in other Nomadini]. (12) Mature larva with well-developed hypostomal ridge [ridge weak in other Nomadini]. (13) Vertex of mature larva with protrusions [vertex recessed in other Nomadini]. (14) Mandibles of larva long (Figs. 22–24) [short in other Nomadini].

Although the *Melanomada* complex appears highly distinctive, we do not believe it should be accorded tribal status because of the limited number of synapomorphies defining it, because of the unclear relationship of *Kelita* to it, and because of our limited knowledge of *Brachynomada*. Nonetheless, these genera are very different from what we know of the other members of the Nomadini.

Within the complex, *Paranomada* is the most distinctive, easily recognized by the greatly flattened body and the smooth and shiny, virtually impunctate integument. The remaining genera are more similar one to another, although *Triopasites*, with its characteristic marginal cell and the patch of plumose hairs on the second metasomal sternum, is difficult to confuse with the others. *Brachynomada*, in South America, seems to be very close to *Melanomada*, but is too poorly known for an adequate assessment of its characters.

As mentioned above, *Kelita* shares some characters with the members of this complex. Of the features cited above,

3. Larval features are known only for representatives of *Melanomada*, *Triopasites*, *Nomada*, and *Hypochrotaenia*.

Kelita differs from the *Paranomada–Melanomada–Triopasites–Brachynomada* complex in characters 2 (maxillary palpus more than one-half as long as galea), 3 (metacoxa without inner, dorsal carina), 7 (gonostylus short and broad), 8 (integument of head and mesosoma pebbled), 9 (entire mesepisternum covered with prostrate, plumose pubescence), and 10 (prepygidial hairs short and broad). Sternum 5 of the female has a transverse ridge across the base and the ridge is produced distally along the midline as a narrow, variably acute process. Sternum 6 of the female is similar to that of the genera of the *Melanomada* complex, but bears at its apex a few very short, broad, blunt setae. Additional unusual features of *Kelita* are cited by Ehrenfeld and Rozen (1977).

As a group, the members of the *Melanomada* complex may be recognized by the following abbreviated suite of characters: anterior and posterior basal angles of mandibles almost equidistant from eye; maxillary palpus not more than one-half as long as galea (except in *M. chica*), three- to six-segmented; male gonostylus long and slender; metasomal sternum 6 of female produced posteriorly as an acute or rounded, hairy process and sternum 7 with a pair of slender apical lobes with a few coarse setae along their margins; integument smooth and shiny between fine, well-separated punctures.

KEY TO ADULTS OF THE NEARCTIC GENERA, *MELANOMADA* COMPLEX

- 1a. Mesosoma about as deep as wide; integument conspicuously punctate (exceptionally, vertex and thoracic dorsum very sparsely and minutely punctate), mesepisternum always sharply punctate; mesocoxa as long as, or a little longer than, distance from its base to base of hind wing 2
- b. Mesosoma greatly flattened, width distinctly greater than depth; integument smooth and shiny, all areas virtually without punctures; mesocoxa much longer than distance from its base to base of hind wing *Paranomada*
- 2a. Forewing with two or three submarginal cells and apex of marginal cell acute, ending on wing margin; margin of metasomal sternum 2 not abruptly depressed and without broad, dense patch of plumose hairs *Melanomada*
- b. Forewing with three submarginal cells and apex of marginal cell narrowly rounded and bent away from wing margin; margin of metasomal sternum 2 abruptly depressed and, across middle one-third, with a conspicuous, dense patch of pale, profusely plumose hairs *Triopasites*

Melanomada Cockerell

Nomada subg. *Melanomada* Cockerell, 1903b:587. Type-species: *Nomada grindeliae* Cockerell, 1903a. Monotypic and original designation. Cockerell, 1911a:649. Cockerell, 1911b:226. Swenk, 1913:8, 15. Linsley and Michener, 1937: 285.

Hesperonomada Linsley, 1939:5. Type-species: *Hesperonomada melanantha* Linsley, 1939. Monotypic and original designation. Linsley and Michener, 1937:291–292. Michener, 1944:274–275. Snelling, 1986:6. NEW SYNONYMY.

Melanomada: Michener, 1944:275. Rodeck, 1945:202–203. Snelling, 1986:6.

Both Michener (1944) and Snelling (1986) separated *Hesperonomada* from *Melanomada* by its five-segmented (rather than six) maxillary palpus and the presence of two (rather than three) submarginal cells in the forewing. Michener further noted that in *Melanomada* the mesocoxa is about as long as the distance from its summit to the base of the hind wing; the mesocoxa was said to be shorter in *Hesperonomada*. Two of the new species described below exhibit intermediate states and effectively eliminate the distinctions that formerly separated these two genera.

Both of these new species described below (*M. annectens*, *M. chica*) possess two submarginal cells in the forewing, as in *Hesperonomada melanantha*, but they have a six-segmented maxillary palpus, as in *Melanomada*. In both, also, the mesocoxa is about as long as the distance from its summit to the base of the hind wing. One of the new species (*M. annectens*) (Fig. 6) in particular, is annectant between *Melanomada* and *Hesperonomada*. It has a small vein stub present on vein M that is evidently the remnant of crossvein 1st r-m (especially well developed in males), for it is in the correct position.

Rodeck (1945) united the two genera, though it is not clear whether he intended to treat *Hesperonomada* as a synonym or subgenus of *Melanomada*. However, he later treated the two genera as separate (Rodeck, 1951). In our view, *Hesperonomada* can no longer be considered separate and distinct, either as a genus or as a subgenus of *Melanomada*.

KEY TO SPECIES OF MELANOMADA

- 1a. Forewing with two submarginal cells 2
- b. Forewing with three submarginal cells 4
- 2a. Maxillary palpus six-segmented; large, triangular mesobasal area of clypeus smooth, shiny, and impunctate 3
- b. Maxillary palpus five-segmented, with segments 4 and 5 fused (Fig. 2); clypeus uniformly densely punctate, sometimes with narrow median impunctate line on basal one-half *melanantha* (Linsley)
- 3a. Maxillary palpus about one-half as long as galea, apical segment distinctly shorter than preceding segment and uniformly cylindrical (Fig. 1); mesoscutal punctures about 0.01 mm diameter or more and separated by much less than a puncture diameter in center of disc *annectens*, new species
- b. Maxillary palpus slightly longer than galea, apical segment distinctly longer than preceding segment and abruptly wider over apical one-half (Fig. 3); mesoscutal punctures minute, hardly greater in diameter (about 0.006 mm) than hairs arising from them and separated by two

or more puncture diameters across middle of disc *chica*, new species

- 4a. Clypeal disc weakly convex or flattened, but if flattened, then disc of mesoscutum is uniformly and densely punctate; sides of declivitous face of propodeum partially concealed by dense, prostrate, highly plumose hairs 5
- b. Clypeal disc weakly concave and disc of mesoscutum polished, punctures variable in size and variably spaced, with extensive impunctate areas; side of declivitous face of propodeum thinly covered by subappressed, short-plumose hairs that do not conceal integument *grindeliae* (Cockerell)
- 5a. Clypeal disc weakly convex; punctures in center of mesoscutum variably spaced, with some interspaces exceeding three puncture diameters; surface of mesosternum, especially near coxae, partially concealed by dense, prostrate, highly plumose pubescence; middle of propodeal triangle granulose and without evident longitudinal rugulae *sidaefloris* (Cockerell)
- b. Clypeal disc flattened; mesoscutal punctures uniform in size, evenly spaced in center with interspaces 1.5 puncture diameters or less; mesosternum not concealed by dense pubescence; middle of propodeal triangle with several fine, longitudinal rugulae *ninia*, new species

Melanomada annectens, new species

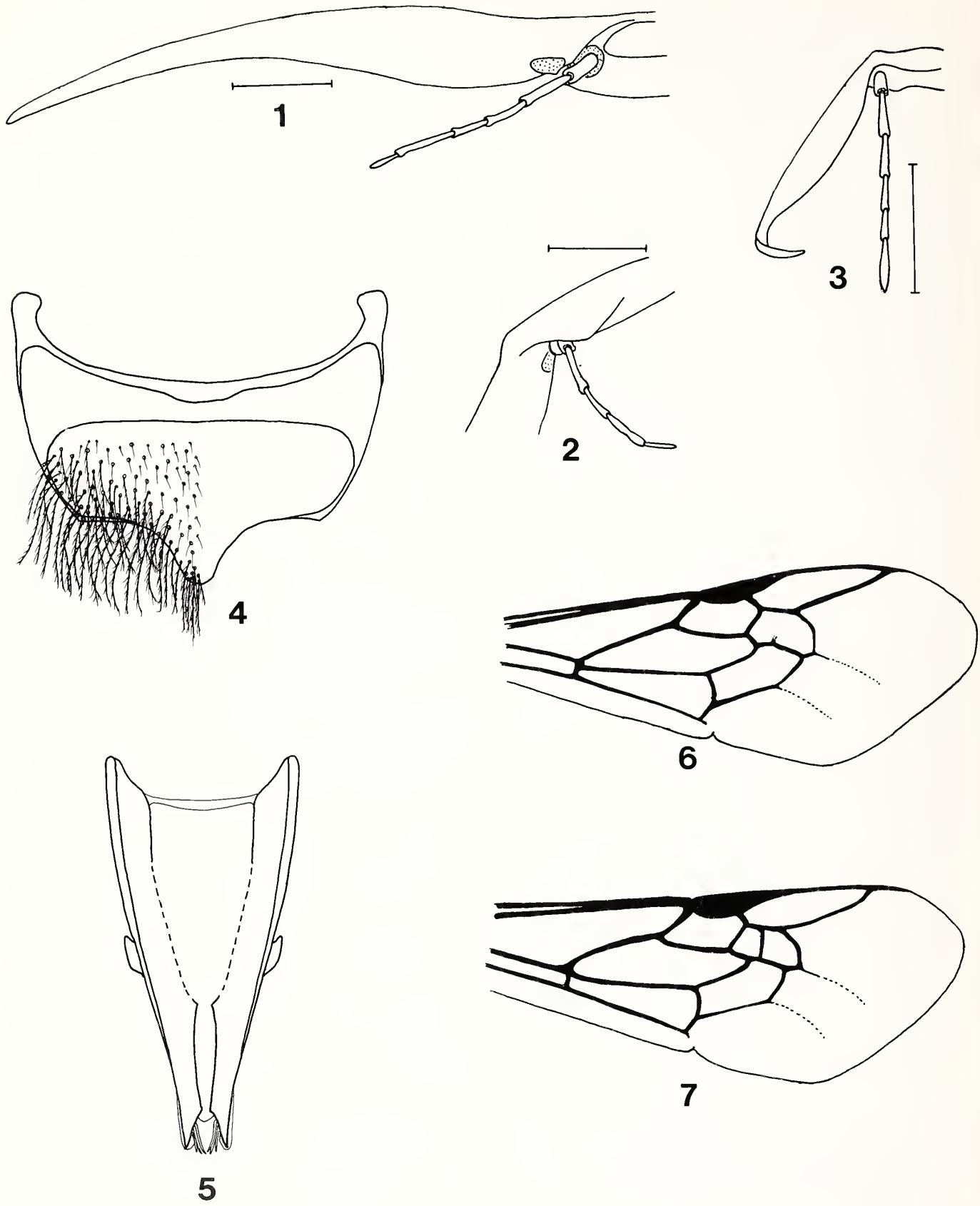
Figures 1, 6, 10, 11, 17, 25

DIAGNOSIS. This species is separable from *M. grindeliae* and *M. sidaefloris* by the presence of two, rather than three, submarginal cells in the forewing and from *M. melanantha* by the six-segmented, rather than five-segmented, maxillary palpus. It is further distinguished from all three by the presence of a distinct, median impunctate area on the clypeus. From *M. chica* it is separated by its coarser punctuation, maxillary galea being about twice as long as the maxillary palpus, densely punctate mesoscutum, and larger size.

DESCRIPTION. Female. Measurements. Head width 1.86–2.05; head length 1.35–1.67; wing length 4.7–4.8; total length 6.0–6.6 mm.

Head 1.2–1.4 times broader than long; vertex strongly arched above tops of eyes; inner eye margins strongly convergent below; lower interocular distance 0.85–0.87 times upper interocular distance. Posterior ocelli separated from preoccipital margin by much less than their diameter; ocellular distance 2.6–3.8 times anterior ocellus diameter; intercellular distance 1.8–2.0 times anterior ocellus diameter. Scape about 2.7 times longer than distance between antennal sockets and, in full frontal view, its apex on level of anterior margin of anterior ocellus; first flagellar segment slightly longer than broad; second flagellar segment 1.15–1.31 times longer than first; middle flagellar segments about one-third longer than first and about one-third longer than broad.

Glossa normal, i.e., much longer than combined lengths of first two labial palpal segments; labial palpus flattened, first segment about 11.5 times longer than wide and about 2.3 times longer than second; maxillary palpus six-segmented, less than one-half as long as galea, second segment about



1.6 times longer than sixth, sixth segment normal in shape, i.e., approximately parallel-sided and narrowed at apex.

Integument smooth and shiny; clypeus with broad, impunctate median line, disc otherwise conspicuously punctate, with most punctures about 0.02–0.03 mm diameter, separated by 1–2 puncture diameters, and with smaller punctures (about 0.01 mm diameter) irregularly scattered between; frons, vertex, and preocciput similarly punctate, but much of face obscured by densely plumose, appressed pubescence. Mesoscutum and scutellum subcontiguously punctate, but with irregular interspaces up to a puncture diameter; punctures 0.02–0.03 mm diameter. Upper, densely pubescent portion of mesepisternum with punctures contiguous to subcontiguous, mostly about 0.03 mm diameter; lower, sparsely pubescent area with punctures similar but subcontiguous to dense. Metasomal tergal discs slightly roughened between punctures; those of second tergum distinct, slightly transverse, about 0.015 mm diameter; punctures becoming slightly coarser and closer on succeeding segments.

Foreswing (Fig. 7) with two submarginal cells, second with 1st r-m stub arising from M.

Head and mesosoma blackish, metasoma ferruginous; mandible, labrum, apical margin of clypeus, underside of first flagellar segment, pronotal lobe, and most of legs (except irregular darker areas on femora and protibia), dusky ferruginous. Tegula ferruginous. Wings transparent brownish, marginal cell and broad apical area darker; veins and stigma dark brown.

Male. Measurements. Head width 1.84–2.13; head length 1.48–1.74; wing length 4.7–5.3; total length 5.5–6.3 mm.

Head about 1.2 times broader than long; vertex strongly convex above tops of eyes; lower interocular distance 0.85–0.88 times upper interocular distance. Posterior ocelli separated from preoccipital margin by less than their diameter; ocellocular distance 2.4–2.5 times anterior ocellus diameter; interocellar distance 2.1–2.3 times anterior ocellus diameter. Scape as described for female; first flagellar segment slightly longer than broad; second flagellar segment 1.0–1.1 times longer than first.

Otherwise about as described for female, but impunctate area of clypeus inverted-deltoid in shape, apex almost reaching apical margin. Abdomen blackish, with segment margins reddened, and legs dark reddish brown.

TYPE MATERIAL. Holotype female, allotype, and 3 female paratypes: Indian Truck Trail, 12 mi. S Corona, Riverside Co., California, 24 May 1985 (J.G. Rozen and R.R. Snelling), at nest site of *Exomalopsis nitens* Coekerell. Paratypes (all from same locality): 4 ♀♀, 19 June 1984 (R.R. Snelling); 2 ♀♀, 4 ♂♂, 20 June 1984 (R.R. Snelling and E. Williams); 1 ♀, 2 May 1985 (R.R. Snelling); 1 ♀, 4 ♂♂, 19 May 1985 (R.R. Snelling); 2 ♀♀, 1 ♂, 22 May 1985 (J.G. Rozen); 1 ♀, 1 ♂, 25

May 1985 (J.G. Rozen and R.R. Snelling); 3 ♀♀, 3 ♂♂, 26 May 1985 (J.G. Rozen and R.R. Snelling). Holotype and allotype in LACM; paratypes in AMNH, LACM, UKAN, USNM.

ADDITIONAL MATERIAL (not paratypes). *Los Angeles Co.*: 1 ♂, Hollywood, 12 Aug. 1956 (D.L. Dahlsten; LACM); 1 ♂, Westwood Hills, 27 July 1935 (paratype of *H. melanantha*; UCB). *Orange Co.*: 1 ♀, Irvine Park, 3 Sept. 1962 (M.E. Irwin; UTSU). *San Diego Co.*: 1 ♀, Laguna Beach, no date (Baker; paratype of *H. melanantha*; UCB?); 1 ♂, La Jolla, 14 Aug. 1911 (J.C. Bridwell; USNM); 1 ♀, near La Mesa, 28 June 1954 (F.X. Williams; USNM).

ETYMOLOGY. The specific name is a Latin adjective, meaning joining or linking and refers to the intermediate position of this species in revealing the relationship of *Melanomada* and *Hesperonomada*.

DISCUSSION. Both sexes of *M. annectens* closely resemble those of *M. melanantha*. The most conspicuous difference lies in the number of maxillary palpal segments, five in *M. melanantha* and six in *M. annectens*. In *M. melanantha* the fifth segment may be seen to result from the fusion of segments five and six; this combined segment is longer than the second segment (Fig. 2).

The clypeus is uniformly densely punctate in both females and males of *M. melanantha*, although there may be a very narrow median line that is free of punctures. Females of *M. annectens* have approximately the middle one-fourth to one-third of the clypeal disc impunctate or nearly so. In the males, the impunctate area is an inverted delta, with the base extending between the subantennal sutures and the apex reaching almost to the apical margin of the clypeus.

Other differences between the two species include the slightly longer first flagellar segment of *M. annectens* that is little, if any, shorter than the second; in *M. melanantha* the first segment is distinctly shorter than the second. Males of both species have the outer, dorsal margins of the pro- and mesocoxae more or less carinate, but the carinae are sharper and higher in *M. annectens* than in *M. melanantha*. Similarly, the inner dorsal carina of the metacoxa is better developed in *M. annectens*.

The second submarginal cell of the forewing is consistently different between the two species. In *M. annectens* there is a small remnant of crossvein 1st r-m (Fig. 6). This remnant is consistently lacking in the forewing of *M. melanantha*.

Genitalic structures of the males of the two species are very similar. Sternum 7 of *M. annectens* (Fig. 10) is about twice as long as broad, with its apex more broadly rounded; in *M. melanantha* (Fig. 8) sternum 7 is about as broad as long, its apex more acute. Similarly, the apical process of sternum 8 is broader and more rounded in *M. annectens* (Fig. 11) than in *M. melanantha* (Fig. 9). *Melanomada annectens* has a slight distal broadening of the gonostylus (Fig. 13), whereas

←
Figures 1–7. *Melanomada* species. 1, maxillary palpus and galea of *M. annectens*; 2, maxillary palpus of *M. melanantha*; 3, maxillary palpus and galea of *M. chica*; 4, 5, metasomal sterna 6 and 7, *M. grindeliae*, female; 6, 7, forewing of *M. annectens* and *M. grindeliae*, respectively. Scale line (Figs. 1–3) = 0.25 mm.

in *M. melanantha* it is uniformly slender (Fig. 16). The apex of the penis valve is narrower in *M. melanantha* (Fig. 16) than in *M. annectens*.

Melanomada chica, new species

Figures 3, 25

DIAGNOSIS. This species may be separated from *M. grindeliae* and *M. sidaefloris* by its small size, exceptionally fine and sparse punctures, two (rather than three) submarginal cells in the forewing, and six-segmented (rather than five-segmented) maxillary palpus. From *M. annectens* and *M. melanantha*, *M. chica* may also be distinguished by its small size and minute, sparse punctures. It is further distinguished from *M. melanantha* by the six-segmented maxillary palpus. From all species it is identifiable by the maxillary palpi being as long as the galea.

DESCRIPTION. Female. Measurements. Head width 1.16; head length 0.93; forewing length 2.9; total length 3.5 mm.

Head about 1.3 times wider than long; vertex strongly convex above summits of eyes; inner eye margins strongly convergent below; lower interocular distance 0.78 times upper interocular distance. Posterior ocelli separated from preoccipital margin by less than their diameters; interocellar distance 1.7 times anterior ocellus diameter; ocellocular distance 2.4 times anterior ocellus diameter. Scape about 1.7 times longer than distance between antennal sockets and, in frontal view, short of anterior ocellus by about its apical width; first flagellar segment broader than long; second flagellar segment about 1.4 times longer than first; middle flagellar segments about as long as broad.

Glossa shorter than combined lengths of first two segments of labial palpus; labial palpus flattened, first segment about five times longer than wide and about three times longer than second; maxillary palpus six-segmented, slightly longer than galea (Fig. 3), second and sixth segments longest and subequal, sixth segment narrow and parallel-sided for about one-half its length and abruptly broader in apical one-half.

Punctures everywhere minute; clypeal punctures separated by a puncture diameter or more, a few relatively coarser punctures (up to about 0.02 mm diameter), but most much finer (about 0.006 mm diameter), punctures densest near apical margin. Lower part of face smooth and shiny, with only sparse minute punctures, most hardly greater in diameter than hairs arising from them; upper frons, vertex, and preocciput largely bare and with scattered barely perceptible punctures. Mesoscutal and scutellar punctures variably spaced across discs, but most interspaces more than two puncture diameters, most punctures about 0.006 mm diameter, a few up to 0.01 mm. Upper mesepisternum smooth and shiny between close punctures up to about 0.02 mm diameter, lower portion smooth, shiny, and sparsely pubescent, punctures sparse, most less than 0.01 mm diameter. Metasomal terga shiny, but not polished, between sparse, obscure, transverse, piligerous punctures that are best defined, densest, and coarsest (up to 0.02 mm diameter) on fourth and fifth terga.

Forewing with two submarginal cells.

Upper half of head and entire thorax blackish; lower half of head, antennae, and legs dusky ferruginous, tibiae and following segments lighter; metasoma ferruginous. Tegula clear yellowish red. Wings transparent brownish, darker along apical margins; veins and stigma dark brown.

Male. Unknown.

TYPE MATERIAL. Holotype female: vicinity of Estacion Microondas "Ligui," 425 m elev., 48 km S Loreto, Baja California Sur, MEXICO, 7 Sept. 1977 (R.R. Snelling), in LACM.

ETYMOLOGY. The specific name is a Spanish adjective meaning small, and is appropriate for this diminutive species.

DISCUSSION. The diminutive size and shortened mouthparts, except the maxillary palpus, will immediately separate *M. chica* from all other species of *Melanomada*. The short mouthparts are a common characteristic of bees associated with prostrate species of the plant genus *Euphorbia*.

Presumably the bee host of *M. chica* will prove to be one of the smaller species of *Exomalopsis*, such as *E. rufiventris*, which occurs in the vicinity of the type locality.

Melanomada grindeliae (Cockerell)

Figures 4, 5, 7, 12, 13, 18, 25

Nomada grindeliae Cockerell, 1903a:210; ♂.

Nomada (Melanomada) grindeliae: Cockerell, 1903b:587.

Nomada (Melanomada) heleniella Cockerell, 1911a:648; ♀.
♂. NEW SYNONYMY.

Melanomada grindeliae: Michener, 1944:275.

Melanomada heleniella: Rodeck, 1951:1207.

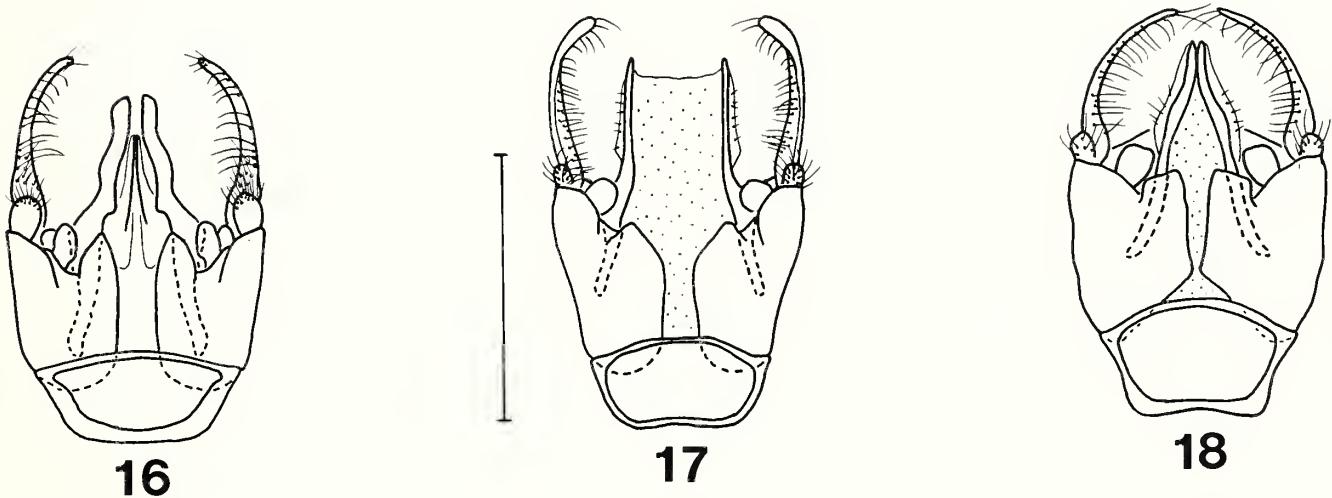
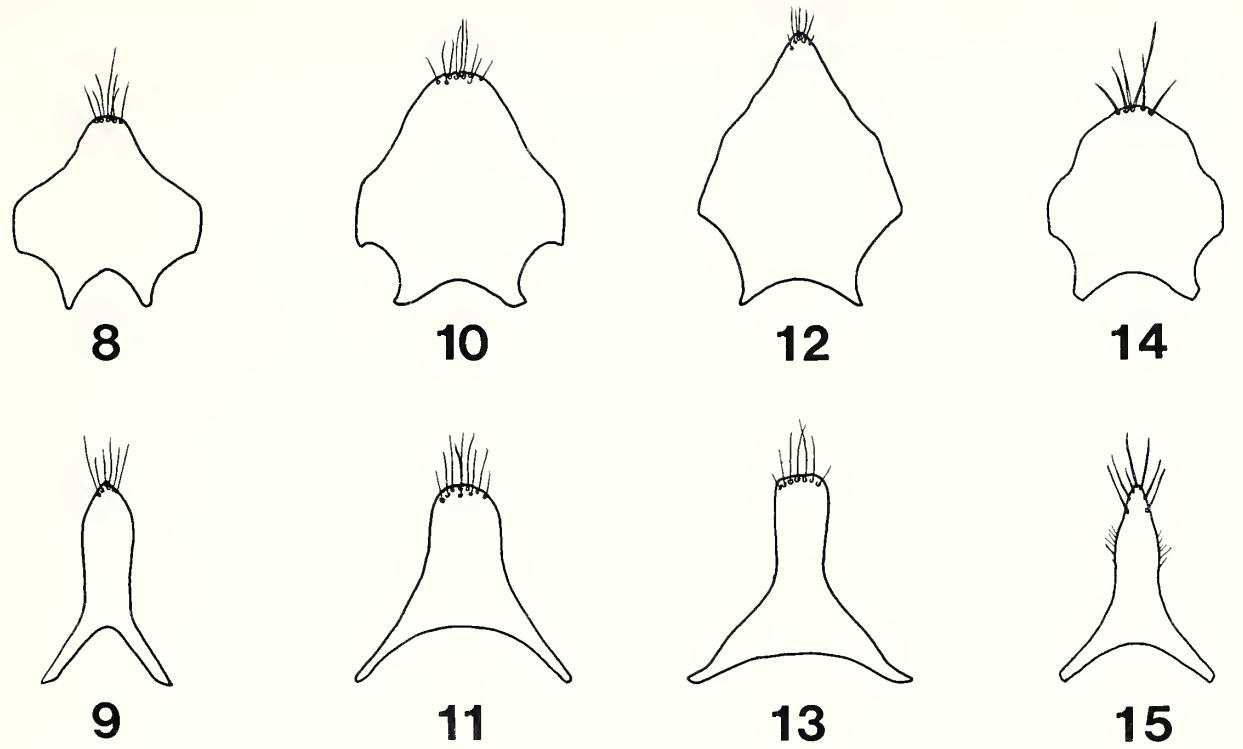
DIAGNOSIS. *Melanomada grindeliae* is separable from *M. annectens*, *M. chica*, and *M. melanantha* by the presence of three, rather than two, submarginal cells in the forewing; it is further separable from *M. chica* by the short maxillary palpus, only about one-half as long as the galea, and notably larger size (head width more than 1.25 mm); it differs from *M. sidaefloris* and *M. nimia* by the sparsely pubescent propodeal declivity and other characters noted in the key.

The types of *N. grindeliae* (ANSP) and *N. heleniella* (USNM) have been examined and compared directly with one another. Aside from the slightly smaller size of the *N. heleniella* types, there are no notable differences between the two.

In addition to the types, we have seen several specimens of both sexes from Lincoln, Nebraska, the type locality of *N. grindeliae*. Other material that we examined includes the following.

COLORADO, Pueblo Co.: 1 ♂, Pueblo, 5000 ft. elev., 19 Aug. 1960 (R.H. Dreisbach; UTSU). KANSAS, Chase Co.: 1 ♀, 2 mi. W Elmdale, 30 Sept. 1975 (Michener and Chabot; UKAN). Douglas Co.: 1 ♀, Lawrence, 5 Sept. 1954 (C.W. Rettenmeyer; UKAN), on *Solidago* sp.; 1 ♀, same locality, 7 Sept. 1954 (E.A. Cross; UKAN), on *Bidens* sp. OKLAHOMA, Alfalfa Co.: 2 ♂♂, 6 mi. S Driftwood, 27 Sept. 1969 (K.L. Johnson; UKAN), on *Aster subulatus*.

Two females collected at Lincoln, Nebraska, by J.C. Crawford (USNM) bear the notation "at *Nomia* place." We assume that this is a casual association. The true host of *M.*



Figures 8–18. Males, *Melanomada* species. Metasomal sterna 7 and 8, respectively, of: 8, 9, *M. melanantha*; 10, 11, *M. annectens*; 12, 13, *M. grindeliae*; 14, 15, *M. nimia*. Genitalia, ventral view: 16, *M. melanantha*; 17, *M. annectens*; 18, *M. grindeliae*. Scale line = 0.50 mm.

grindeliae will probably be a species of *Exomalopsis*, such as *E. pygmaea* (Cresson), which occurs throughout the known range of *M. grindeliae*.

Melanomada melanantha (Linsley), new combination

Figures 2, 8, 9, 16, 25

Hesperonomada melanantha Linsley, 1939:6–7; ♀ ♂.

DIAGNOSIS. This species is distinguished from all other *Melanomada*, except *M. annectens* and *M. chica*, by the presence of two, rather than three, submarginal cells in the forewing; from *M. annectens* and *M. chica* it may be distinguished by the five-segmented, rather than six-segmented, maxillary palpus.

The type locality of *M. melanantha* is in Monterey County, California. Paratypes were from Contra Costa, Los Angeles, and San Diego counties. The specimens from the latter two counties are not *M. melanantha*, but rather *M. annectens*. In addition to the types, we have seen the following specimens of *M. melanantha*, all from California.

Alameda Co.: 1 ♀, Pleasanton, 20 Sept. 1957 (O.A. Stevens; USNM), on *Centaurea* sp. Contra Costa Co.: 1 ♀, Antioch, 25 Aug. 1955 (C.D. MacNeill; UCB); 1 ♀, 1 ♂, same locality, 22 Sept. 1954 (J.G. Rozen; AMNH), on *Grindelia* sp.; 1 ♂, same locality, 5 Sept. 1936 (M.A. Embury; UCB); 2 ♀♀, same locality, 22 Sept. 1954 (P.D. Hurd, C.D. MacNeill; UCB, USNM), on *Grindelia* sp.; 4 ♀♀, 1 ♂, same locality, 14 Oct. 1954 (P.D. Hurd, M.S. Wasbauer; UCB, USNM), on *Grindelia* sp.; 3 ♀♀, 2 mi. W Pittsburgh, 19 Sept. 1957 (J.A. Powell; UCB), 2 on *Grindelia camporum*, 1 on *Baccharis glutinosa*. San Joaquin Co.: 1 ♂, Stockton, 12 June 1916 (R. Stinchfield; UCB), on *Grindelia* (*camporum*?). Santa Clara Co.: 1 ♂, no locality or date (Harkins; UCB).

The differences between this species and the superficially similar *M. annectens* are discussed under the latter. The host of *M. melanantha* is unknown.

Melanomada nimia, new species

Figures 14, 15, 25

DIAGNOSIS. This species can be readily distinguished from others with three submarginal cells in the forewing (*M. grindeliae* and *M. sidaefloris*) by the uniformly densely punctate mesoscutum (sparsely punctate in other species).

DESCRIPTION. Female. Measurements. Head width 1.45–1.65; head length 1.22–1.36; wing length 3.9–4.3; total length 4.5–4.9 mm.

Head 1.2–1.3 times broader than long; vertex moderately arched above tops of eyes; inner eye margins strongly convergent below; lower interocular distance 0.82–0.84 times upper interocular distance. Posterior ocelli separated from preoccipital margins by much less than their diameter; ocellular distance 2.4–2.7 times anterior ocellus diameter; interocular distance 2.0 times diameter of anterior ocellus. Scape about 1.5–1.6 times longer than distance between antennal sockets and, in frontal view, its apex distinctly short

of level of anterior ocellus; first flagellar segment broader than long; second segment 1.5–1.6 times longer than first.

Glossa much longer than combined lengths of first two labial palpal segments; labial palpus flattened, first segment more than 10 times longer than wide and more than twice longer than second; maxillary palpus six-segmented and less than one-half as long as galea.

Integument smooth and shiny; clypeus with sparse, fine punctures and irregularly distributed minute punctures; supraclypeal area mostly impunctate, with scattered fine and minute punctures laterad; frons and vertex with sparse, minute punctures; face, including clypeus, below midlength largely obscured by dense, appressed, copiously plumose pubescence. Mesoscutum and scutellum shiny between fine punctures (about 0.02 mm diameter) that are mostly separated by less than their diameters. Mesepisternal punctures fine and subcontiguous, integument largely obscured by copiously plumose, appressed hairs. Sides of propodeal disc largely obscured by copiously plumose appressed hairs; median, apubescent area of basal triangle dull, with a few fine longitudinal rugulae. Basal abdominal terga shiny between scattered, obscure, minute punctures; succeeding terga with surface increasingly roughened, hence duller.

Forewing with three submarginal cells.

Head and thorax blackish, metasoma and legs beyond coxae ferruginous; mandible (except piceous distal two-thirds), labrum, apical margin of clypeus, pronotal lobe, and tegula, also ferruginous. Underside of flagellum dark reddish brown, basal segment paler. Wings transparent, slightly brownish, marginal cell darker; veins and stigma dark brown.

Male. Measurements. Head width 1.44–1.57; head length 1.17–1.27; wing length 3.7–4.0; total length 4.4–4.8 mm.

Head 1.2 times broader than long, vertex moderately arched above tops of eyes; inner eye margins strongly convergent below, lower interocular distance 0.81–0.83 times upper interocular distance. Ocelli as described for female. Scape as described for female; first flagellar segment slightly longer than broad and about 1.3 times length of second; median flagellar segments about as broad as long.

Otherwise about as described for female, but legs and metasomal segments 3–6 dark brownish to blackish.

TYPE MATERIAL. Holotype female, allotype, and two female paratypes from 2 mi. W Elmdale, Chase Co., KANSAS, 30 Sept. 1975 (Michener and Chabot); 2 ♀♀, 2 ♂♂, Yates Center, Woodson Co., KANSAS, 7 Sept. 1949 (Michener and Beamer). Holotype, allotype, and most paratypes in UKAN; one female paratype in LACM.

ETYMOLOGY. The specific name is a Latin adjective, meaning too much or excessive and is in reference to the densely punctate mesoscutum.

DISCUSSION. This species is most similar to the sympatric *M. grindeliae*, but in the latter species the punctures of the mesoscutum are finer and, at least in the middle of the disc, separated by three times a puncture diameter or more. Other differences include the more convex clypeus, much denser mesepisternal and propodeal pilosity of *M. nimia*, as well as the red-marked metasoma of the *M. nimia* male.

From *M. sidaefloris* both sexes differ in the much sparser mesosternal pubescence. Although some plumose hairs are present anterior to the mesocoxae, they are not appressed to form a dense, surface-concealing patch, as in *M. sidaefloris*. The mesoscutal punctuation of *M. nimia* is much denser than that of *M. sidaefloris*, as noted in the key.

The finely, longitudinally rugulose median area of the propodeal triangle separates *M. nimia* from both *M. grindeliae* and *M. sidaefloris*. From the West Coast species, *M. melanantha*, *M. annectens*, and *M. chica*, *M. nimia* is immediately separable by the presence of three submarginal cells in the forewing.

The genitalic capsule of *M. nimia* (not illustrated) is very similar to that of *M. grindeliae*, but with much sparser setae along the shaft of the gonostyli. The hidden sterna, however, are different. Sternum 7 (Fig. 14) of *M. nimia* is proportionately broader, though similar in shape. Elongate, slender, and apically acute, sternum 8 of *M. nimia* (Fig. 15) is very distinctly different from the short, broad, and truncate to subtruncate segments of most other species of *Melanomada*.

Melanomada sidaefloris (Cockerell)

Figure 25

Nomada pennigera var. *sidaefloris* Cockerell, 1898:59; ♂.
Melanomada sidaefloris: Rodeck, 1945:203. Rozen, 1977:7–9; larva.

DIAGNOSIS. This species is separable from *M. annectens*, *M. chica*, and *M. melanantha* by the presence of three submarginal cells in the forewing. Although very similar to *M. grindeliae*, both sexes are readily separable by the presence of dense patches of profusely plumose, mainly prostrate pubescence on the side and venter of the thorax and on the side of the propodeal disc. The mesoscutum of *M. grindeliae* is uniformly very sparsely punctate, while in *M. sidaefloris* the punctures are moderately dense in most areas, becoming irregularly spaced and sparse posteromedially. This species is also similar to *M. nimia*, but in that species the mesoscutum is very uniformly punctate, the punctures separated by about one-half a puncture diameter, and the propodeal triangle bears several short longitudinal rugulae.

In addition to the type, from Mesilla, New Mexico, we have seen a few specimens all from New Mexico (Hidalgo County) and Arizona (Cochise County), but presumably the range of this species will include western Texas and the northern Mexican States of Chihuahua and Sonora. Rozen (1977) found *M. sidaefloris* to be a cleptoparasite in the nests of *Exomalopsis sidae* Cockerell.

Melanomada species A

Figure 25

Two specimens from Kingsville, Kleberg County, Texas, a female collected 30 May 1977 and a male collected 6 May 1976, both by J.E. Gillaspay (UTSU), do not agree with any of the above species and probably represent an additional species in this genus. We are reluctant to name this form from such inadequate material. In our key above, these will

run to *M. sidaefloris*, which they somewhat resemble. The mesosternum is unlike that of *M. sidaefloris* in that it is thinly pubescent, the smooth shiny integument fully visible and bearing minute, irregularly scattered punctures. In *M. sidaefloris* the highly plumose hairs are dense enough to conceal the surface, which is densely and finely punctate. The hypostomal area is also minutely and sparsely punctate, unlike that of *M. sidaefloris* in which punctures are dense and small.

Melanomada species B

Figure 25

This is known from a single male collected by P.D. Hurd at Villa Guadalupe, Jalisco, Mexico, 26 July 1951 (UCB). It closely resembles the male of *M. sidaefloris*, but the mesoscutal punctures are more uniformly spaced. Its most outstanding feature is the presence of extensive, median, polished and apubescent areas on metasomal sterna 3–5. This characteristic will distinguish this from all other *Melanomada* we have seen. As with the preceding, we refrain from naming the species at this time because of the paucity of available material.

IMMATURE STAGES

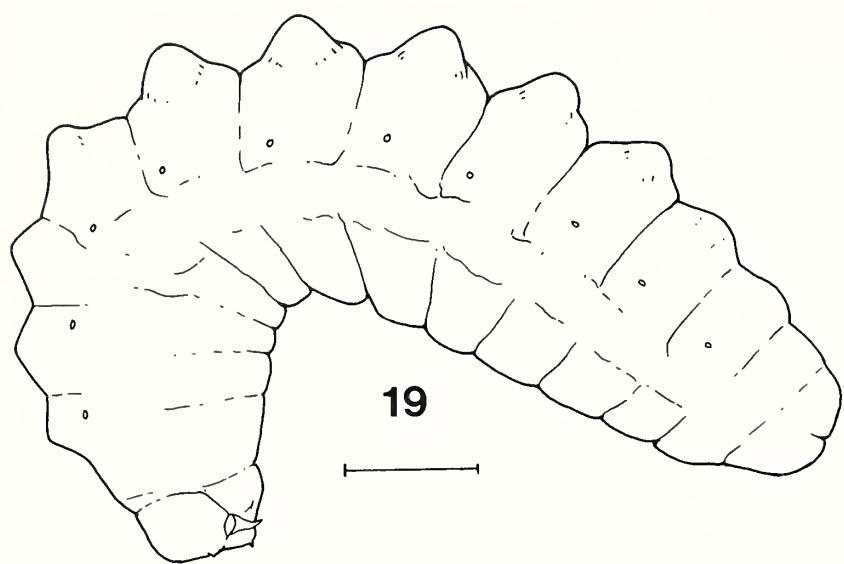
The mature larva of only *Melanomada sidaefloris* was previously described and compared with other nomadine larvae (Rozen, 1977; Rozen et al., 1978). The larva of *M. annectens*, treated below, confirms the similarity of this species to *M. sidaefloris* and to members of the *Melanomada* complex. The larvae of this complex are quite dissimilar to those of *Nomada* and *Hypochrotaenia*. Although pupae of the *Melanomada* complex are poorly known, those of *M. sidaefloris* (Rozen, 1977) and *Paranomada velutina* are quite similar to one another and different from those of *Nomada*.

Mature larva of *Melanomada annectens* Snelling and Rozen

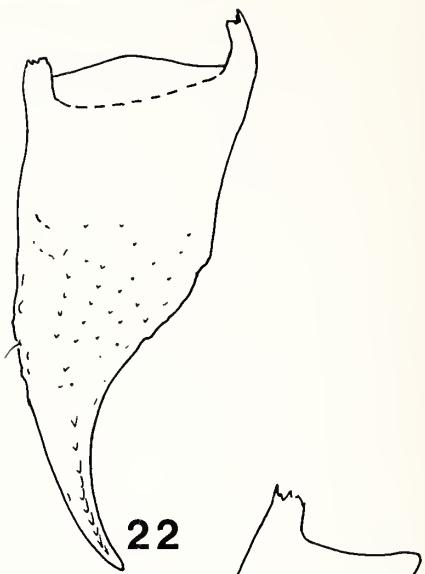
Figures 19–24

DIAGNOSIS. The mature larva of this species is very similar to that of *M. sidaefloris* and can be distinguished from it only with some difficulty. The slightly darker head capsule, somewhat less produced vertex, and somewhat more pronounced dorsal body tubercles of *M. annectens* seem to be reliable differences.

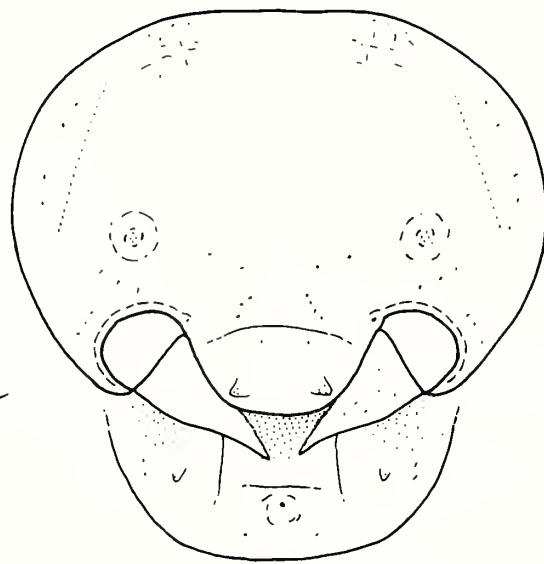
DESCRIPTION. Head (Figs. 20, 21). As described for *M. sidaefloris* (Rozen, 1977) except for following: Integument more darkly pigmented than in *M. sidaefloris* so that sclerotized part of head capsule appears darker than rest of body. Vertex as seen in lateral view only slightly produced on each side above antenna, less so than in *M. sidaefloris*; produced area somewhat wrinkled. Antennal papilla with four sensilla; antennal protuberances less developed than in *M. sidaefloris*. Mandible (Figs. 22–24) with dorsal apical edge finely and evenly serrate; ventral apical edge perhaps somewhat more coarsely serrate, but teeth shorter and more rounded than those on dorsal edge.



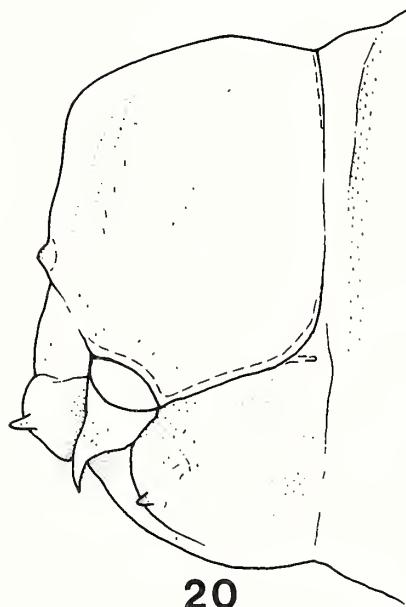
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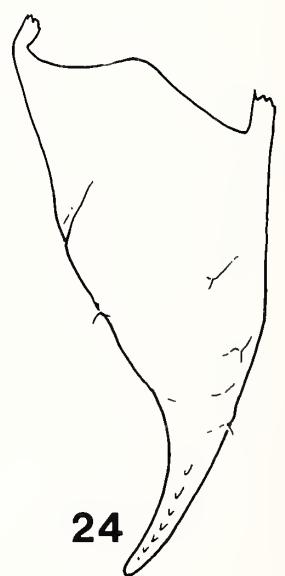
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Figure 25. Distribution of species of *Melanomada*: *M. annectens* (★); *M. chica* (○); *M. grindeliae* (●); *M. melanantha* (◎); *M. nimia* (☆); *M. sidaefloris* (◐); *M. species A* (+); *M. species B* (◐).

Body. Integument spiculate in some areas. Paired dorsal tubercles (Fig. 19) slightly more pronounced than those of *M. sidaefloris*; first four pairs of tubercles somewhat transverse rather than conical (this was particularly evident on

one specimen that had not yet entered diapause). Other features of body as described for *M. sidaefloris*.

Material studied. Four postdefecating larvae, 4 predefecating larvae, 12 mi. S of Corona, Riverside Co., California,



Figures 19–24. *Melanomada annectens*, postdefecating larva. 19, body, side view; 20, head, side view; 21, same, frontal view; 22–24, right mandible, dorsal, adoral, and ventral views. Scale line (1 mm) refers to Figure 19 only.

25 May 1985, J.G. Rozen, Jr. and R.R. Snelling. From nests of *Exomalopsis nitens* Cockerell.

HOST ASSOCIATIONS AND BIONOMICS

All known North American cleptoparasites of the *Melanomada* complex are nest associates of members of the genus *Exomalopsis* (Rozen, 1984). In *Melanomada*, *M. sidaefloris* has been associated with *Exomalopsis consobrina* Timberlake (Rozen, 1977, 1984) by collections made 26 mi. south of Animas, New Mexico in 1976, and to *Exomalopsis sidae* Cockerell at 5 mi. north of Willcox, Arizona in 1983 (Rozen, 1984). Although *M. annectens* (as *Hesperonomada melanantha*) was associated with *Exomalopsis nitens* (Rozen, 1984, table 2), the cleptoparasite had been misidentified and is in reality *M. annectens* (Rozen and Snelling, 1986). Other possible cleptoparasite-host associations are mentioned in the section on Systematics.

The bionomics of *M. sidaefloris* were presented by Rozen (1977, 1984) and of *M. annectens* by Rozen and Snelling (1986).

The South American genera *Kelita* and *Brachynomada* are nest associates of Panurginae (Andrenidae), a further distinction from the *Melanomada* complex. *Brachynomada* near *argentina* Holmberg was associated with *Psaenythia annulata* (Gerstaeker) (Rozen, 1977). *Kelita chilensis* (Friese) is a known parasite of *Lipanthus parvulus* (Friese) (Rozen, 1970), and *Kelita tuberculata* Ehrenfeld and Rozen is possibly associated with *Lipanthus alicahue* Ruz and Toro (Ehrenfeld and Rozen, 1977; Ruz and Toro, 1983).

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For the opportunity to study specimens from the collections in their care, we are indebted to: J.A. Chemsak (UCB), S.I. Frommer (UCR), S.S. Shanks and R.J. McGinley (USNM), C.D. Michener (UKAN), and W.J. Pulawski (CAS). We are particularly indebted to S.S. Shanks and W.J. Pulawski for making available important type material. The type of *M. grindeliae* was made available by D. Azuma (ANSP).

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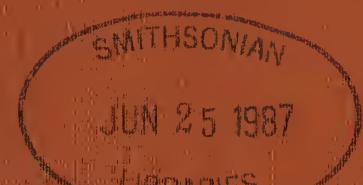
CONTRIBUTIONS IN SCIENCE

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NEW SPECIES FROM THE GULF OF MEXICO

Daniel M. Cohen

NEW BYTHITID FISH, *DINEMATICHTHYS MINYOMMA*,
FROM THE CARIBBEAN SEA.

Allegra N. Sedor and Daniel M. Cohen



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NOTES ON THE BYTHITID FISH GENUS *SACCOGASTER* WITH A NEW SPECIES FROM THE GULF OF MEXICO

Daniel M. Cohen¹

ABSTRACT. A new bythitid fish species, *Saccogaster rhamphidognatha*, is named from the Gulf of Mexico. Diagnostic characters are a hook-like projection on the maxillary, seven branchiostegal rays, and 12 pectoral fin rays. A revised diagnosis for *Saccogaster* is presented, with a key to the eight species in the genus. The third known specimen of *S. staigeri* is recorded from the northwest Gulf of Mexico, a 1600-km range extension. Data are given for two Australian specimens, from New South Wales and Western Australia, which are tentatively identified as *S. tuberculata*.

INTRODUCTION

This paper reports on four specimens of the rarely encountered bythitid genus *Saccogaster*, which recently have come to hand. Two of these small ophidiiform fishes, caught in the Gulf of Mexico nearly two decades ago, were discovered in the Collection of Fishes of Texas A&M University and sent to me for study. Each represents a different species. One of them is the third known specimen of *S. staigeri*, and the other is undescribed and represents the eighth known species of *Saccogaster* and the second to be discovered since the genus was reviewed by Cohen and Nielsen (1972). Two other specimens, both recently caught, one off Sydney and the other off the northwest shelf of Australia, were sent to me from the Australian Museum and are tentatively identified as *S. tuberculata*, known also from the South China Sea and Hawaii. In this paper I rediagnose the genus based on additional material, present a new key to the eight species, describe one new species, and present new information about *S. staigeri* and *S. tuberculata*.

Terminology and methods follow Cohen and Nielsen (1972, 1978). Study material is housed in the Australian Museum, Sydney (AM), the Natural History Museum of Los Angeles County (LACM), and Texas A&M University (TCWC).

Saccogaster Alcock

DIAGNOSIS. Ophidiiform fishes of the family Bythitidae, subfamily Bythitinae as defined by Cohen and Nielsen (1978: 42). Scales absent from head, reduced or absent on body. Tail section of body not attenuate. Anal fin originating on

posterior half of body. Pectoral fin supported by elongate radials (enclosed in a free peduncle in some species, adnate in others). Maxillary vertically expanded posteriorly. Opercular spine present. Palatine teeth present. Developed rakers on first arch 0–6. Ventral fins with 1 ray in each. Pectoral fin rays 12–23. Branchiostegal rays 7, 8, or 9. Precaudal vertebrae 12–20. Males with a stalked intromittent organ.

KEY TO SPECIES OF *SACCOGASTER*

- 1a. Scales absent 4
- b. Scales present on body 2
- 2a. Spine on opercle with three points; pectoral fin rays 22; dorsal fin rays 92 *S. hawaii*
- b. Spine on opercle with a single point; pectoral fin rays 16–18; dorsal fin rays 75–88 3
- 3a. Gill filaments on first arch not notably reduced in size; palatine tooth row several teeth wide; dorsal fin rays 75–83 *S. maculata*
- b. Gill filaments on first arch notably reduced in size; palatine teeth in a single row; dorsal fin rays 87–88 *S. staigeri*
- 4a. An antorse, hook-like projection at posteroventral angle of maxillary; pectoral fin rays 12; branchiostegal rays 7 *S. rhamphidognatha* new species
- b. No hook-like projection at posteroventral angle of maxillary; pectoral fin rays 14–23; branchiostegal rays 8 or 9 5
- 5a. Pectoral fin borne on a free, fleshy peduncle; gill opening extending above level of top pectoral ray 6
- b. Pectoral fin without a free, fleshy peduncle; gill opening restricted, not extending above level of top pectoral ray 7
- 6a. Pectoral fin rays 20–23; anal fin rays 56–61; developed rakers on first gill arch 3 *S. tuberculata*
- b. Pectoral fin rays 14; anal fin rays 64; developed rakers on first arch 6 *S. parva*

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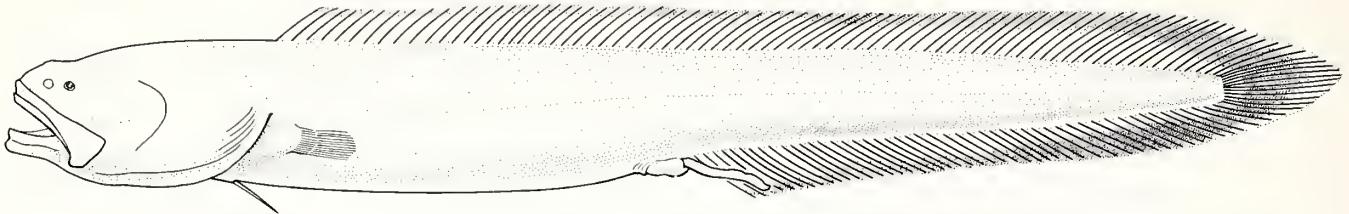


Figure 1. *Saccogaster rhamphidognatha* new species. Holotype, LACM 44189-1. Standard length 59.7 mm. Drawn by Sharon Belkin.

- 7a. Posterior end of maxillary sheathed dorsally; anal fin rays 53–54; nasal chambers not sooty black *S. normae*
- b. Posterior end of maxillary not sheathed; anal fin rays 37; nasal chambers sooty black *S. melanomycter*

Saccogaster rhamphidognatha new species

Figure 1

HOLOTYPE. The only known specimen, LACM 44189-1 (formerly TCWC 3915.4), ♂, Gulf of Mexico, off Mississippi delta, 29°13.5'N, 88°16.5'W, 210 m, RV ALAMINOS, stat. 69A13-43, Oct. 4–16, 1969.

DIAGNOSIS. An antrorse, hook-like projection at the posteroventral angle of the maxillary; branchiostegal rays 7; pectoral fin rays 12.

DESCRIPTION. Counts and measurements are presented in Table 1. Body slender, greatest depth about 8 in SL (standard length). Preanal about 1.8 in SL. Head compressed, about 4.7 in SL. Skin translucent to transparent. Scales absent.

Lateral line obsolete on body. Head pores apparently restricted to 1 in supraorbital series over upper lip medial to anterior nostril, 2 in the infraorbital series on the upper lip, and 2 in the mandibular series near the tip of the lower jaw.

Snout not notably fleshy or inflated. Posterior nostril large, about equal in diameter to clear window over eye; anterior nostril a small, simple pore above upper lip and lateral to supraorbital pore. Lower jaw slightly included. A short, strong, compressed non-emergent spine on the opercle. Upper rear part of maxillary free, not sheathed; a prominent antrorse hook present at the posteroventral angle.

Gill opening extending dorsally to above the level of the relatively narrow pectoral fin base, about even with the dorsal margin of the adnate skin-covered pectoral peduncle.

First gill arch with 2–3 flat spiny plates on the upper arm, a short spiny protuberance at the angle followed by 1 (right arch) or 2 (left arch) similar protuberances on the lower arch, followed by 6 spiny plates. Gill filaments on first arch short. Pseudobranch of 2 filaments present.

Dentition on premaxillary a narrow, exterior band of granular teeth and an inner band of larger, needle-like teeth. Vomer with a broadly U-shaped band of small, pointed teeth, which continues posteriorly onto the palatines. Dentary with a narrow exterior row of small, slightly compressed teeth and a single interior row of larger, pointed teeth.

Dorsal fin originating over centrum 7, anal fin under cen-

trum 24. Pectoral fin rays broken off short. Pectoral radials elongate but pectoral peduncle adnate. The pectoral fin base is narrow and does not occupy the entire distal margin of the peduncle. A single, short ray in each ventral fin, the rays immediately adjacent.

The type is an apparently mature male. The basal part of the intromittent organ is a fleshy, posteriorly directed protuberance, longer than wide, with the vent on the anteroventral surface; a prominent, 6-mm-long penis protrudes from the round, distal aperture.

Coloration pale on the head and body; vertical fins brownish distally.

Vertebrae 20 + 38 = 58; neural spines 5–8 variously depressed and truncate. First parapophyses on centrum 7.

RELATIONSHIPS. *Saccogaster rhamphidognatha* resembles four other *Saccogaster* species: *tuberculata*, *parva*, *normae*, and *melanomycter* (description of the first three in Cohen and Nielsen, 1972, of the last in Cohen, 1981) in a derived character, loss of scales, which is reductive and could have occurred independently in any combination of the five. The new species shares with two of these scaleless species, *S. normae* and *melanomycter*, two additional derived characters that are not reductive, an adnate pectoral fin peduncle and a restricted gill opening. Although all three of these species are well distinguished by autapomorphies, I interpret them as being more closely related to each other than to any other *Saccogaster* species.

ETYMOLOGY. The species name *rhamphidognatha* is coined from the Greek *rhamphidos*, a hook, and *gnathos*, the jaw.

Saccogaster staigeri Cohen and Nielsen, 1972

STUDY MATERIAL. TCWC 6146.1, ♀, northwest Gulf of Mexico, 27°44.9'N, 95°20.1'W, 338–384 m, RV ALAMINOS, stat. 68A13-19, 2-m dredge, Nov. 19, 1968.

This specimen is the third known, and the first taken since the species was described. Counts and measurements are presented in Table 1 and agree well with the type material.

Body scales are sparse and non-imbricate and thus resemble the pattern found in the female paratype rather than in the male holotype. The lateral canal has 1 pore, above the upper angle of the gill opening; supraorbital pore 1, above the upper lip and medial to the tubular anterior nostril; infraorbital pores 2, along the upper lip posterior to the anterior nostril. There are 7, larger teeth at the tip of the premaxillary, another character in which this specimen is more similar to

Table 1. Measurements and counts on *Saccogaster rhamphidognatha*, *S. staigeri*, and *S. tuberculata*.

| | <i>S. rhamphidognatha</i> | | <i>S. staigeri</i> | | <i>S. tuberculata</i> | | | |
|--------------------------|---------------------------|------|--------------------|------|-----------------------|------|----------------|-------|
| | Holotype | | | | | | | |
| | LACM 44189-1 | | TCWC 6146.1 | | AM I 26002-005 | | AM I 22814-029 | |
| | ♂ | ♀ | ♂ | ♀ | ♀ | ♀ | ♂ | ♀ |
| | mm | % SL | mm | % SL | mm | % SL | mm* | % SL* |
| SL | 59.7 | | 65.2 | | 84.5 | | 160 | |
| Snout to dorsal fin | 14.1 | 23.6 | 19.6 | 30.1 | 25.6 | 30.3 | 48.0 | 30.0 |
| Snout to anal fin | 33.1 | 55.4 | 39.4 | 60.4 | 45.5 | 53.8 | 91.0 | 56.9 |
| Snout to ventral fin | 11.1 | 18.6 | 15.6 | 23.9 | 16.4 | 19.4 | 33.7 | 21.1 |
| Body depth at vent | 6.0 | 10.1 | 8.1 | 12.4 | 13.7 | 16.2 | 25.0 | 15.6 |
| Head length | 12.6 | 21.1 | 19.0 | 29.1 | 21.8 | 25.8 | 40.0 | 25.0 |
| Snout length | 2.8 | 4.7 | 4.1 | 6.3 | 4.7 | 5.6 | 8.0 | 5.0 |
| Eye diameter | 0.9 | 1.5 | 1.8 | 2.8 | 2.7 | 3.2 | 4.4 | 2.8 |
| Interorbital width | 2.4 | 4.0 | 3.9 | 6.0 | 5.0 | 5.9 | 8.8 | 5.5 |
| Upper jaw length | 6.0 | 10.1 | 9.3 | 14.3 | 10.9 | 12.9 | 19.4 | 12.1 |
| Depth of maxilla | 2.4 | 4.0 | 3.2 | 4.9 | 3.6 | 4.3 | 6.4 | 4.0 |
| Cleithrum to ventral fin | 1.3 | 2.2 | 2.7 | 4.1 | 2.0 | 2.4 | 7.0 | 4.4 |
| Ventral fin length | 3.7 | 6.2 | 7.5 | 11.5 | 8.7 | 10.3 | 17.6 | 11.0 |
| Pectoral peduncle length | — | — | 4.0 | 6.1 | 4.0 | 4.7 | 7.3 | 4.6 |
| Pectoral fin base width | 1.5 | 2.5 | 3.0 | 4.6 | 4.3 | 5.1 | 9.5 | 5.9 |
| Pectoral fin length | — | — | 9.4 | 14.4 | 11.8 | 14.0 | 21.1 | 13.2 |
| Dorsal fin rays | 77 | | 88 | | 89 | | 85 | |
| Anal fin rays | 49 | | 53 | | 56 | | 61 | |
| Pectoral fin rays | 12 | | 18 | | 22 | | 23 | |
| Caudal fin rays | 12 | | 13 | | 12 | | 12 | |
| Branchiostegal rays | 7 | | 8 | | — | | 9 | |
| Vertebrae | 20 + 38 = 58 | | 14 + 38 = 52 | | 12 + 43 = 55 | | 56 | |

* Specimen is bent at midlength; hence, longer measurements and proportions are imprecise.

the female paratype with 9 teeth rather than to the male holotype with 20. Whether this variation might be related to sex or size cannot yet be determined, as the holotype is 93.1 mm SL and the paratype 61.2 mm SL, similar to 65.2 mm SL for the present specimen.

DISTRIBUTION. The holotype was caught off the east coast of Florida, the paratype in the eastern Gulf of Mexico south of Tortugas Island off the tip of Florida. The present specimen is an extension of known range of about 1600 km to the northwestern Gulf of Mexico.

Saccogaster tuberculata (Chan, 1966)

STUDY MATERIAL. AM I 26002-005, ♀, New South Wales, 33°34'S, 152°02'E, 658 m, FRV KAPALA, stat. no. K 86-01-06, 11 Feb., 1986. AM 22814-029, ♀, Western Australia, 18°29'S, 116°36'E, 696–704 m, mud bottom, RV SOE-LA, 6 April, 1982.

This species has been known previously from four specimens, the holotype from the South China Sea, and three other examples from a single locality in the Hawaiian Islands (Co-

hen and Nielsen, 1972). The two specimens (measurements and counts presented in Table 1) here discussed (recorded from Australia by Paxton et al., in press) are tentatively identified as *S. tuberculata*. Although they agree with the species diagnosis and in most respects with the description given by Cohen and Nielsen (1972), there are some differences between the two Australian specimens and between Australian and other specimens. Some of these differences may be attributed to size as specimen AM I 26002-005 from New South Wales (NSW) is smaller than any others, and AM I 22814-029 from Western Australia (WA) is larger.

The skin in NSW is thin with a moderate degree of fine pigmentation giving the fish a light brownish cast; the skin over the venter is clear and the viscera are visible as there is neither peritoneal pigmentation nor musculature around this area. WA has thick pale skin as described for other specimens and a pigmented peritoneum that conceals the viscera.

The lateral line in NSW has only about a dozen papillae; in WA it is obsolete. There is a pore slightly posterior to the rear margin of the maxillary in WA; no such pore exists in

either NSW or in previous specimens. WA is apparently unique in having a prominent pore, about as large as the eye, on the rear margin of the preopercle.

There are nine branchiostegal rays in WA; an accurate count is not possible in NSW; there are eight branchiostegals in other specimens.

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NEW BYTHITID FISH, *DINEMATICHTHYS MINYOMMA*, FROM THE CARIBBEAN SEA

Allegra N. Sedor^{1,2} and Daniel M. Cohen¹

ABSTRACT. *Dinematichtys minyomma* is described as a new species, based on a single collection of 51 specimens from a coral reef in the Bay Islands, Honduras. It is tentatively assigned to the genus on the basis of a single character, the position of the anterior nostril high on the snout. Unique diagnostic characters include a small eye (10.2–15 in head), few lateral scale rows (79–89), few dorsal fin rays (73–80), and few anal fin rays (55–62).

INTRODUCTION

The specimens here described were collected some 20 years ago, and their lack of a name has been recognized for nearly as long. The chief reason for their anonymity has been uncertainty about appropriate generic placement. Although this uncertainty remains, the problem is now better defined, and we describe this species in order to provide a name for use in forthcoming studies, and to call attention to the species's existence.

METHODS

Counts of vertebrae were taken from radiographs, and exclude the ural centrum. Dorsal and anal fin ray counts were also taken from radiographs, and include the last unsupported ray. Caudal fin ray counts include principal and procurrent rays. Measurements are to the nearest 0.1 millimeter. Eye measurements were taken on the spectacle. Lateral scale row counts were taken along a midlateral pale line originating near the opercular angle. Because the scales are deciduous, it is not possible to obtain exact counts for all specimens, so minima and maxima, including counts of scale pockets where possible, are reported for these individuals. Clearing and staining methods followed Dingerkus and Uhler (1977). Figure 2 was drawn with a camera lucida.

The term "sclerified" is used here in its most general sense (Wake, 1979) to refer to the hardening that occurs in the tissues of the copulatory apparatus of these fishes ("ossified" of Cohen and Nielsen, 1978). Staining failed to indicate the presence of cartilage or bone in any of these tissues except

the penis (see below). Because only one specimen was cleared and stained, the possibility cannot be ruled out that the failure of these tissues to stain is an artifact of preservation, though this is not indicated by the quality of the staining of the other tissues in the specimen. In any case, a more precise characterization of these tissues cannot be made without clearing and staining of additional specimens or, possibly, histological studies of fresh specimens.

All other methods follow Cohen and Nielsen (1978).

Abbreviations: USNM: National Museum of Natural History; LACM: Natural History Museum of Los Angeles County; TABL: U.S. National Marine Fisheries Service Tropical Atlantic Biological Laboratory, Miami; SL: standard length.

GENERIC PLACEMENT

The tribe *Dinematichtyini* of the bythitid subfamily *Bromophycinae* as defined by Cohen and Nielsen (1978) contains nine nominal genera, including *Dinematichtys*. The problematical status of *Dinematichtys* is discussed in detail by Cohen and Nielsen (1978), who noted that there are no known extant specimens of the type species, *D. ilucoeteoides* Bleeker, 1855, and that none of the numerous literature records for the species agrees with the original description. Although several species have at one time or another been assigned to *Dinematichtys*, Cohen and Nielsen (1978) restricted the genus to the type species. They further defined *Dinematichtys* on the basis of the following six characters: caudal fin free from the dorsal and anal fins, male intromittent organ with two pairs of ossified pseudoclaspers, opercle with a sharp-pointed spine, seven branchiostegal rays, imbricate body scales, and an anterior nostril high above the upper lip. Of these, only the last is diagnostic for the genus; the other

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Figure 1. *Dinematicchthys minyomma*, paratype, USNM 280123, 71 mm SL, male, lateral view.

characters may be shared by the nominal dinematicthyine genera *Ogilbia*, *Brotulina*, and *Monothrix*. It is on the basis of this one diagnostic character that the species here described is provisionally placed in *Dinematicchthys*.

In addition to the type species, knowledge of which is based solely on the original description, the genus presently contains one other species, *D. dasyrhynchus* Cohen and Hutchinsons, 1982. Because a single diagnostic character does not provide convincing evidence of monophyly among these three species, we stress that the placement of *D. minyomma* in *Dinematicchthys* is provisional.

Dinematicchthys minyomma new species

Figures 1–3

DIAGNOSIS. A *Dinematicchthys* that differs from *D. iluocoeteoides* and *D. dasyrhynchus* in having a smaller eye (10.2–

15 vs. 5 and 6.9–9.4 in head), fewer lateral scale rows (79–89 vs. 100 and 140), fewer dorsal fin rays (73–80 vs. 83 and 96–103), and fewer anal fin rays (55–62 vs. 69 and 62–69). It further differs from *D. iluocoeteoides* in having an unsheathed maxillary, and from *D. dasyrhynchus* in having fewer vertebrae (10 + 28–30 vs. 13–14 + 33–34), fewer cephalic pores (19 vs. 22–26), fewer pectoral fin rays (22–24 vs. 25–28), and fewer caudal fin rays (16 vs. 17–18). These differences are summarized in Table 1, and data for the new species are shown in Tables 2 and 3.

STUDY MATERIAL. Holotype. USNM 280122, formerly TABL 67-124, 66.1 mm SL, male, collected in the Caribbean Sea, Honduras, Bay Islands, Guanaja (Bonaca) Island, at 16°26'38"N, 85°53'02"W, from a coral reef at 0–9 m, 21 April 1967, by George Miller.

Paratypes. USNM 280123, 38 specimens, 35.5–74.5 mm SL: 12 males, 47.1–74.5 mm SL, 26 females 35.5–70.7 mm

Table 1. Comparison of the three species of *Dinematicchthys*.^{1,2}

| Character | <i>D. minyomma</i> | <i>D. iluocoeteoides</i> | <i>D. dasyrhynchus</i> |
|----------------------------|--------------------|--------------------------|------------------------|
| Head length/eye diameter | 10.2–15.0 | A little over 5 | 6.9–9.4 |
| Lateral scale rows | 79–89 | About 100 | About 140 |
| Dorsal fin rays | 73–80 | 83 | 96–103 |
| Pectoral fin rays | 22–24 | 22–23 | 25–28 |
| Posterior end of maxillary | Unsheathed | Sheathed | Unsheathed |
| Vertebrae | 10 + 28–30 | — | 13–14 + 33–34 |
| Anal fin rays | 55–62 | 69 | 62–69 |
| Caudal fin rays | 14 + 2 | 14 | 17–18 |
| Lateral pores | 1 | — | 2 |
| Supratemporal pores | 0 | — | 1 or 2 |
| Supraorbital pores | 3 | — | 4 |
| Infraorbital pores | 5 | — | 6, 7 or 8 |

1. Data for *D. iluocoeteoides* and *D. dasyrhynchus* are taken from the original descriptions; data for *D. minyomma* are summarized for all 51 type specimens.

2. Measurements in mm.

Table 2. Data for selected specimens, and summary data for 18 male and 32 female specimens of *Dinematicichthys minyomma*.¹

| | Males, summary | USNM 280122 | USNM 280123 | USNM 280123 | USNM 280123 | Females, summary | USNM 280123 | USNM 280123 | LACM 44201-1 | LACM 44201-1 |
|-----------------|-------------------|----------------|----------------|----------------|----------------|---------------------|----------------|----------------|-----------------|-----------------|
| Vert. | 10 + 29–30 | 10 + 29 | 10 + 30 | 10 + 29 | 10 + 29 | 10 + 28–30 | 10 + 29 | 10 + 29 | 10 + 29 | 10 + 29 |
| D. rays | 74–79 | 75 | 79 | 76 | 76 | 73–80 | 77 | 73 | 75 | 73 |
| A. rays | 56–61 | 58 | 59 | 59 | 57 | 55–62 | 58 | 55 | 57 | 56 |
| P. rays | 22–23 | 23 | 23 | 22 | 23 | 22–24 | 23 | 23 | 23 | 23 |
| L. scale rows | 81–86 | 84 | | 81–85 | 84–86 | 79–89 | 79–82 | | 87–89 | |
| G. rakers total | 2–4 + 12–16 | 3 + 16 | 3 + 14 | 3 + 13 | 2 + 12 | 2–4 + 10–16 | 4 + 14 | 2 + 16 | 2 + 13 | 3 + 14 |
| Dev. G. rakers | 0–3 | 1 | 2 | 1 | 3 | 0–3 | 2 | 0 | 2 | 3 |
| SL | 47.1–74.5 | 66.1 | 61.5 | 72.3 | 54.1 | 35.5–70.7 | 57.7 | 68.8 | 61.0 | 52.1 |
| Depth | 14.4 | 13.6 | 15.7 | 10.8 | | | 12.9 | 15.5 | 13.5 | 11.2 |
| Pre-dorsal | 21.6 | 21.2 | 24.2 | 16.4 | | | 18.7 | 23.6 | 19.8 | 18.0 |
| Pre-anal | 32.8 | 31.3 | 36.3 | 26.4 | | | 28.0 | 34.4 | 28.6 | 26.8 |
| Pect. length | 9 | 8.7 | 9.5 | 7.4 | | | 7.9 | 9.7 | 8.0 | 7.5 |
| Vent. length | 18.5 | 15.2 | 17.1 | 14.0 | | | 14.8 | 17.3 | | 14.2 |
| Head length | 19.3 | 18.0 | 21.6 | 15.0 | | | 16.3 | 20.3 | 17.4 | 15.9 |
| Eye diameter | 1.5 | 1.4 | 1.5 | 1.4 | | | 1.4 | 1.6 | 1.7 | 1.2 |
| Snout length | 4.3 | 4.3 | 5.2 | 3.5 | | | 3.9 | 5.0 | 4.1 | 3.9 |
| U. jaw length | 10.1 | 10.0 | 10.7 | 7.6 | | | 8.3 | 11.0 | 9.0 | 7.5 |
| G. max. width | 3.6 | 3.8 | 3.4 | 2.7 | | | 3.0 | 3.6 | 3.2 | 2.5 |

1. Measurements in mm.

SL; collected with the holotype. LACM 44201-1, 12 specimens, 52.1–70.8 mm SL; 6 males, 53.3–70.8 mm SL, 6 females, 52.1–70.5 mm SL; collected with the holotype. One LACM male specimen, 63.3 mm SL, was cleared and double-stained.

Description. Body compressed, elongate, deepest at or near origin of dorsal fin, depth at vent averaging 4.8 in standard length. Dorsal profile sloping gradually downward to rounded snout. Snout and lower jaw fleshy, with dermal folds and cirri. Upper jaw slightly protruding, maxillary expanded and unsheathed posteriorly. Opercle with stout spine pointing caudad, penetrating the skin slightly anterior to the opercular margin, and just ventral to the upper opercular angle. Eye small, sunken, covered at the surface by a round, translucent spectacle that goes 10.2–15 in head. Posterior nostril, adjacent to eye, with a raised rim longest at the medial and ventral margins. Anterior nostril tubular, 1.5 to 2 eye diameters anterior to posterior nostril, same distance above upper lip.

Fleshy snout with a dermal fold inserted at the symphysis of upper jaw about one eye diameter above upper lip, extending ventrally on each side of symphysis to overhang the premaxillary. The dermal flap formed by this fold extends posteriorly along the premaxillary to a point beneath the posterior margin of the anterior nostril. A second dermal fold extends ventrally from insertion at the lateral margin of the anterior nostril; this fold is somewhat produced anteriorly into an elongate lobe hanging down well below the upper lip and slightly below the horizontal extension of the first dermal fold. The second fold extends posteriorly along the upper jaw, to a point ventral to the eye. The edges of these skin folds may appear fringed due to the presence of dermal cirri.

On the lower jaw, a circular fold lies on the inferior surface of the dentary on either side of the symphysis. Just behind this fold a second semicircular fold extends around the anterior tip of the isthmus. As on the upper jaw, these folds are edged with cirri that also extend along the anterior half of the inferior surface of the dentary.

Table 3. Frequency distributions for fin ray and vertebral counts of *Dinematicichthys minyomma*.

| Dorsal fin rays | | | | | | | | | |
|-------------------|----|----|----|----|------------------|----|----|----|-----------|
| | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | \bar{x} |
| Males | — | 2 | 6 | 5 | 2 | 1 | 2 | — | 76.0 |
| Females | 5 | 5 | 6 | 6 | 2 | 3 | — | 1 | 75.3 |
| Total | 5 | 7 | 12 | 11 | 4 | 4 | 2 | 1 | 75.6 |
| Anal fin rays | | | | | | | | | |
| | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | \bar{x} |
| Males | — | 1 | 4 | 6 | 6 | — | 1 | — | 58.2 |
| Females | 1 | 4 | 7 | 5 | 6 | 4 | — | 1 | 58.0 |
| Total | 1 | 5 | 11 | 11 | 12 | 4 | 1 | 1 | 58.1 |
| Pectoral fin rays | | | | | Caudal vertebrae | | | | |
| | 22 | 23 | 24 | | | | | | |
| Males | 4 | 14 | — | | Males | — | 15 | 1 | |
| Females | 8 | 22 | 1 | | Females | 2 | 22 | 4 | |
| Total | 12 | 36 | 1 | | Total | 2 | 37 | 5 | |

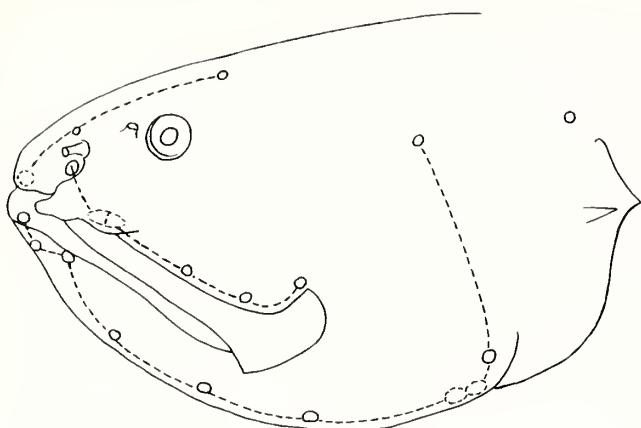


Figure 2. Arrangement of cephalic sensory pores in *Dinematichthys minyomma*, 68.7 mm SL female paratype, USNM 280123. Pores located beneath dermal folds are rendered in broken outlines.

The lateral canal has one pore dorsal to the gill opening (Figure 2). No supratemporal pores. Three supraorbital pores: one large pore (with a diameter about equal to that of the nostril) hidden beneath the first dermal fold that overhangs the upper lip, one small pore medial to the anterior nostril, one posterodorsal to the eye on the frontal region. Five infraorbital pores: one lies lateral to the anterior nostril near the insertion of the second dermal fold on the snout, a second pore (with a diameter about two times that of nostril) lies beneath the flap of skin overhanging the upper lip. The outer edge of this pore is vertically bisected by a septum. Three smaller infraorbital pores are evenly spaced above the posterior half of the upper jaw. Ten preoperculomandibular pores: one large pore in the circular dermal fold on the inferior surface of the dentary, one large pore opening supralaterally within the dermal fold at the tip of the isthmus, one small pore on the anterior outer mandibular margin just beneath the dentary, three small pores spaced along the posterior half of the mandible, two large pores beneath a flap of skin at the angle of the preopercle, one at the preopercular margin just above the angle, one at the juncture with the lateral canal.

Numerous papillae are present on the head, some stout and fleshy, some smaller and less conspicuous; these latter are often obscured by a mucoid covering on some regions of the head. Beginning at the symphysis of the upper jaw: one large papilla at the origin of the first dermal fold on the snout; a second smaller papilla just above the point where this fold meets the upper lip. Beneath the lateral extension of this fold, separated by the third supraorbital pore, are two stalked papillae in a medial position, and three in a lateral position at the posterior end of the fold. Three small papillae surrounding the anterior nostril at the medial, dorsal, and lateral margins. Two small papillae bordering the eye, one on the medial, one on the ventral margin. Two more lie near the medial margin of the posterior nostril, a third medial to these, above the anterior nostril. One small papilla in the infraorbital region, about halfway between the posterior nostril and the upper lip. One small papilla posterodorsal to the eye, three in the interorbital region on each side of the midline.

One on frontal region of the head, just posterior to the first supraorbital pore. One at the dorsal border of the cheek scale patch, in line with the first preopercular pore, five traversing the top of the head from the supraorbital region to the supratemporal region. Three small papillae on opercle: one ventral to the last (tenth) preoperculomandibular pore at the border of the preoperculum, one posterior to the ninth preoperculomandibular pore, one anteroventral to the opercular spine. Two conspicuous papillae near the upper angle of the maxillary at the lower anterior border of the patch of cheek scales: one at the maxillary angle, one along the upper posterior edge of the maxillary. One smaller papilla near the edge of the preoperculum directly posterior to the maxillary, and three small papillae slightly ventral, along the edge of the preoperculum. Seven small papillae distributed irregularly along the mandible. One stout stalked papilla associated with the first preoperculomandibular pore on the dentary.

In addition to the consistent pattern of papillae described above, irregular clusters of numerous smaller papillae may be present on the snout, and near the lower jaw synphysis anterior to the third preoperculomandibular pore.

Lateral line inconspicuous, in two parts. One series of neuromasts originates at the dorsal margin of the head anterodorsal to the lateral pore, and extends caudad to a point above the anal fin origin. The second, midlateral series originates above the anal fin and extends to the caudal peduncle.

All but the posterior quarter of the premaxillary bears an irregular series of elongate conical teeth along the inner margin. These generally decrease posteriorly in size and density. The outer margin and posterior quarter of the premaxillary are covered by granular teeth. The dentary also bears an outer band of granular teeth and an inner band of sharp conical teeth in an irregular series. On both the premaxillary and the dentary, these conical teeth are generally longest at the medial margin and most densely distributed near the symphysis. The vomer bears a triangular patch of conical teeth, longest at the posterior border. Palatines also with conical teeth in an irregular series, longest at the medial margin.

Each gill arch bears a row of flat plates covered with tiny granular teeth on both the outer and inner surfaces; 0–3 developed rakers on the outer face of the ceratobranchial. Three suprabranchial patches of granular teeth, located between the first and fourth arches on each side. One basibranchial patch of granular teeth between the second and third arch on each side.

Dorsal fin originating over the anterior quarter of the pectoral fin, with four cartilaginous predorsals; anal fin originating about equidistant from snout and caudal fin. In both dorsal and anal fins the posterior rays are longest, all are branched, and the last is unsupported by radials. The caudal fin is slightly rounded. The caudal skeleton has two hypural plates, one parhypural, one epural; each hypural bears one short procurent ray, and one unbranched and six branched principal rays. The rounded pectoral fin is about one-half the length of the head. Ventral fins are inserted immediately adjacent to each other, more than one eye diameter behind the symphysis of the cleithra; rays nearly reach the vent, or extend beyond it.

Small, overlapping cycloid scales arranged in regular rows cover the body completely, but are lacking on the head except for a large patch on the cheek.

Ribs articulating with the first five centra; subsequent abdominal vertebrae have ribs articulating with parapophyses. Ribs on the third and fourth centra with anterior and posterior flanges.

The male copulatory apparatus (Figure 3) consists of a penis flanked by two pairs of pseudoclaspers, and by an accessory sclerified structure (the accessory cornified body of Turner, 1946). The apparatus is partially covered anteriorly by a thick fleshy genital flap that originates on the posterior margin of the anus. Embedded in the tissue on the inner (dorsal) side of this flap is another sclerified structure, which apparently provides an anchor for dense tissue connections extending from the pseudoclaspers to the genital flap tissue. This structure is clearly discernable only in cleared specimens, although its contours can be traced in the flap tissue of preserved specimens.

The copulatory apparatus is the distal outgrowth of the urogenital sheath. This sheath originates in the sperm duct near the fusion of the two central canals of the testes, and terminates in the hollow, cylindrical penis. The urinary and sperm ducts pass through the urogenital sheath and through the penis, terminating in a pore at the tip of the penis. The penis is cartilaginous, with a ventral ossified portion near the tip.

Although there appear to be two pseudoclaspers on either side of the penis, dissection of the copulatory apparatus revealed that the two are joined at their base (Figure 3b), so they are here referred to as lobes of a single pseudoclasper. The branched pseudoclasper is anchored in the tissue of the lateral wall of the urogenital sheath. The external lobe of the pseudoclasper appears about twice as large as the internal lobe (Figure 3a). The internal lobe appears similar in shape, but has a spur at its anterior margin; however, dissection reveals that the true shape of the internal pseudoclasper lobe (Figure 3b) is obscured by the dense connective tissue of the genital flap.

The posterior edges of the external lobes of the pseudoclaspers are connected distally by a membrane that passes posteriorly around the base of the penis. Attached to this membrane by a thin ligament is the accessory sclerified structure. This large, rounded structure lies either right or left of the midline, skewing the orientation of the penis by slightly displacing its base (Figure 3a).

Color of holotype in alcohol: an overall pale brown, darker on top of head, lighter on sides of head. Bases of dorsal, anal and pectoral fins darker brown; posterior margins of body scales also darker.

REMARKS. Presence of a single pair of unossified branched pseudoclaspers in this species would seem to invalidate the pseudoclaspers, as used by Cohen and Nielsen (1978), as a defining character for the genus. However, the branched pseudoclaspers possessed by all *Dinematicichthys*, *Ogilbia*, *Monothrix*, and *Brotulina* species are quite distinct from the unbranched pseudoclaspers present in other dinematicichthine species (Sedor, 1985). Clearly, further work is needed to

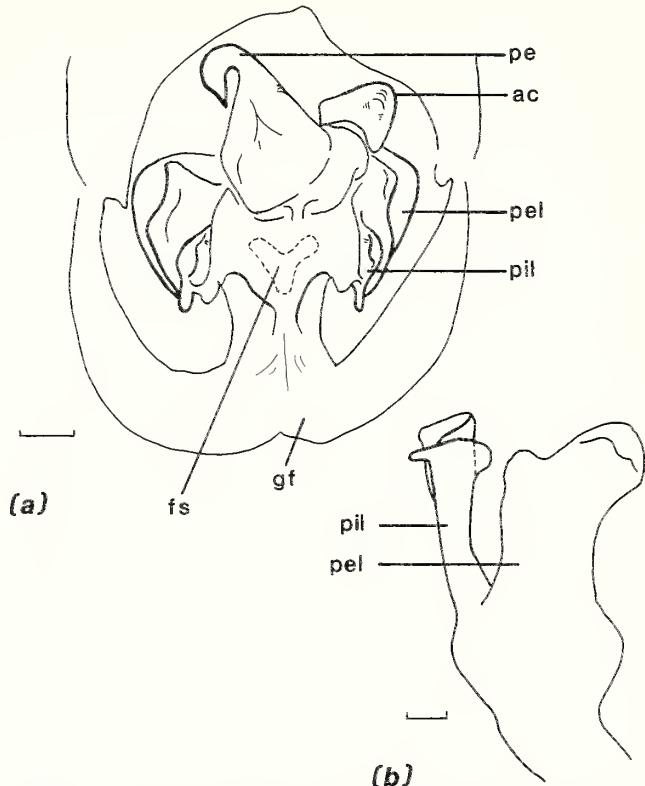


Figure 3. a, *Dinematicichthys minyomma* copulatory apparatus, ventral view, 71 mm SL male paratype, USNM 280123. b, dissected right pseudoclasper, lateral view. Abbreviations: ac, accessory body; fs, flap structure; gf, distal tip of genital flap; pe, penis; pel, pseudoclasper, external lobe; pil, pseudoclasper, internal lobe. Bar indicates 0.5 mm.

characterize properly the pseudoclaspers and assess their taxonomic and phylogenetic significance.

ETYMOLOGY. The species is named *minyomma* (from the Greek minys, small and omma, eye) in reference to its small eye, and is treated as a noun in apposition.

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CONTRIBUTIONS IN SCIENCE

MOLES OF THE *SCAPANUS LATIMANUS* GROUP
(TALPIDAE, INSECTIVORA) FROM THE PLIOCENE AND
PLEISTOCENE OF CALIFORNIA

J. Howard Hutchison



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MOLES OF THE *SCAPANUS LATIMANUS* GROUP (TALPIDAE, INSECTIVORA) FROM THE PLIOCENE AND PLEISTOCENE OF CALIFORNIA

J. Howard Hutchison¹

ABSTRACT. All the California Pliocene and Pleistocene moles of the genus *Scapanus* belong to the subgenus *Scapanus*. Two informal species groups of *S. (Scapanus)* are proposed: the Orarius group with *S. orarius* and *S. townsendii* and the Latimanus group with *S. malatinus* new species and *S. latimanus*. Only fossil members of the Latimanus group are known from California. *Scapanus malatinus* new species from Irvingtonian age deposits (about 1.8 Ma) of San Diego County, California, is the closest morphological ancestor of *S. latimanus*. It exhibits an early stage of enamel excursion below the gum line (hypodonty) in the M₁₋₂. *Scapanus latimanus* is not known earlier than later Irvingtonian and appears to mark the most recent acquisition of advanced hypodonty in the Talpidae.

INTRODUCTION

Moles of the genus *Scapanus* are presently confined to the moister areas of North America from British Columbia to northern Baja California and extend inland nowhere more than 600 kilometers (375 miles) from the ocean (Hall and Kelson, 1959; Palmer, 1937) (Fig. 1). Three living species are commonly recognized: *S. latimanus* (Backman), *S. townsendii* (Backman), and *S. orarius* True. The fossil record expands the range of the genus, principally for members of the subgenus *Xeroscapheus* Hutchison, well into the Great Basin. *Xeroscapheus* represents a group of moles convergent on *Scalopus* Geoffroy St. Hilaire in many respects (Hutchison, 1968:93) and is characterized by relatively shorter jaws, more hypodont teeth, and more powerful forelimbs. Although *Xeroscapheus* became extinct by the end of the Hemphillian (latest Miocene), *S. latimanus* appears, in part, to have taken over the ecologic role of *Xeroscapheus*, particularly in the more southerly part of its range. *Scapanus latimanus* does not presently occupy most of the areas vacated by *Xeroscapheus*, undoubtedly because these areas have now progressed into deserts and semideserts. Since the Clarendonian (late Miocene), progenitors of the modern species, subgenus *Scapanus*, appear to have remained more or less within the present range of the genus.

The only extinct previously named species of *Scapanus*,

S. shultzii Tedford (1961) and *S. proceridens* Hutchison (1968) belong to the subgenus *Xeroscapheus* (Hutchison, 1968). Little was known of the prehistory of the subgenus *Scapanus* except for scattered records of the extant species, *S. latimanus* in the Rancholabrean (late Pleistocene). Pre-Rancholabrean records of *S. (Scapanus)* are rare and fragmentary (Hutchison, 1968). All California records of the subgenus appear to be on the lineage of or closely related to *S. latimanus*, a hardly surprising result considering the present wide distribution of this species. Previously undescribed fossils provide a temporal framework for the acquisition of some diagnostic features of this lineage.

METHODS AND MATERIALS

Terminology of the teeth is from Hutchison (1974). Measurement definitions follow Hutchison (1968) for the bones and Palmer (1937) for the skull. All measurements are in millimeters (mm). Ages are abbreviated as ka (kilo annum) and Ma (Mega annum). Super and subscripted numbers (x for indeterminate tooth number) with the following abbreviations refer to upper and lower teeth respectively: I—incisor, P—premolar, M—molar. Detailed site descriptions are available from the cited literature or may be obtained by qualified investigators from the repository institution.

Institutional acronyms for specimens cited in text are:

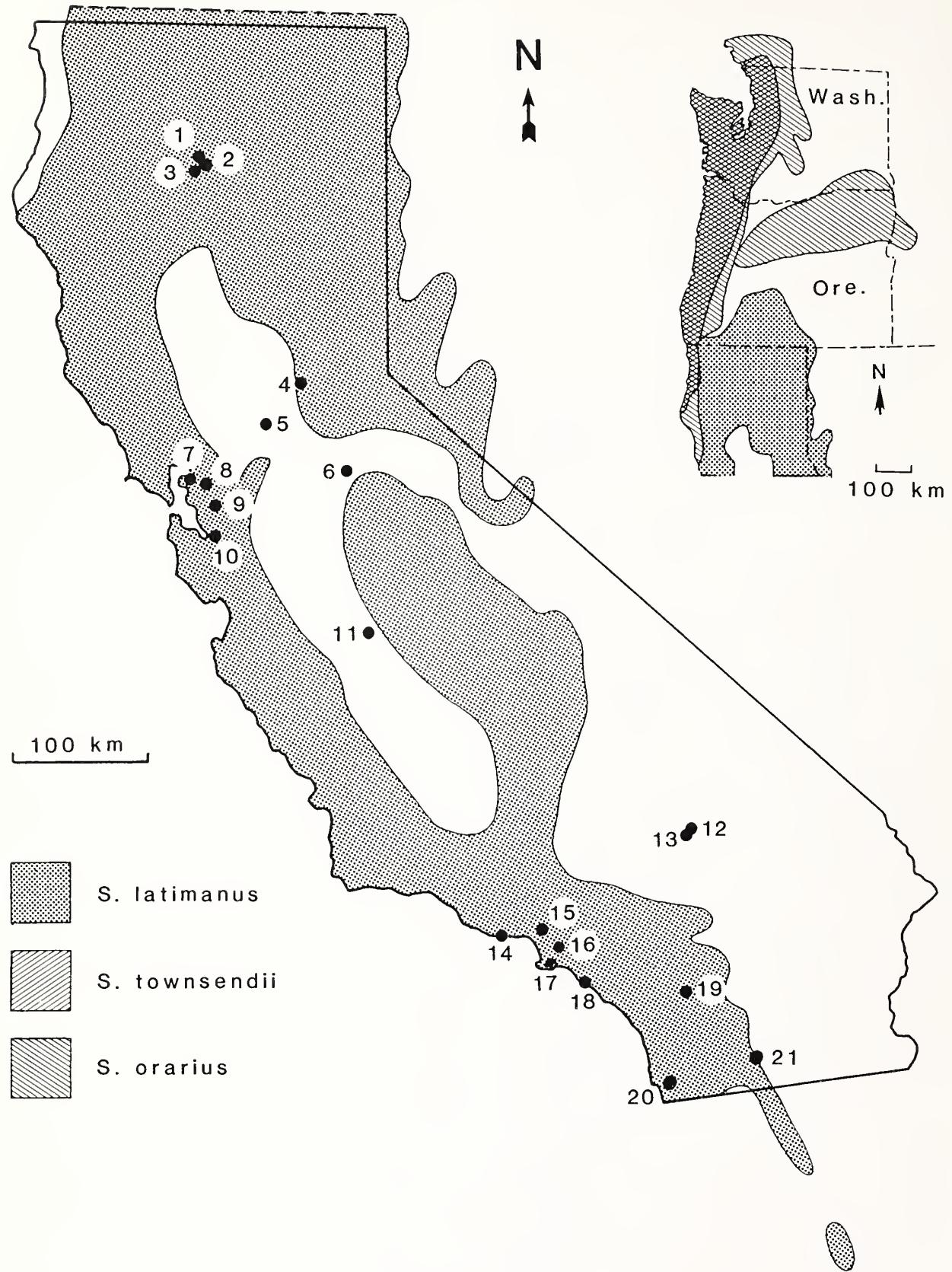
JHH: author's field number.

IVCM: Imperial Valley College Museum, El Centro, California.

LACM: Natural History Museum of Los Angeles County, Section of Vertebrate Paleontology, Los Angeles, California.

MVZ: University of California Museum of Vertebrate Zoology, Berkeley, California.

1. Museum of Paleontology, University of California, Berkeley, California 94720.



SBCM: San Bernardino County Museum, Redlands, California.
 SDNHM: San Diego Natural History Museum, San Diego, California.
 UCMP: University of California Museum of Paleontology, Berkeley, California.
 UCR: University of California, Department of Geological Sciences, Riverside, California.
 UO: University of Oregon Museum of Natural History, Eugene, Oregon.
 USNM: United States National Museum, Washington, D.C.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Insectivora Illiger, 1811

Family Talpidae Vicq d'Azry, 1792

Subfamily Talpinae

Fischer von Waldheim, 1817

Tribe Scalopini Trouessart, 1879

Genus *Scapanus* Pomel, 1848

Subgenus *Scapanus* Pomel, 1848

***Scapanus malatinus* new species**

Figures 2, 3a–c, 4a, 6a

Scapanus, Downs and White, 1968:44, fig. 2 (a faunal list).

DIAGNOSIS. Small size (humerus total length = 12.2–13.3 mm); lower molars with longitudinally compressed trigonids and anterior cingulid and entocingulid spanning the base of the paraconid; M_1 with enamel extending down labial side of root below gum line, at least below the trigonid; M_{2-3} with sharp and well-developed ectocingulids spanning hypoflexids; M_3 does not show enamel excursion down the root; upper molars with metacingulum joining lingual edge of metacone; trough between base of infraorbital bridge and ridge for insertion of masseter muscles narrow and shallow; infraorbital bridge strap-like rather than rod-like; frontal region convexly arched; shaft length of the radius about 60% of humerus length.

HOLOTYPE. LACM 3451, left M_{1-3} , M_2 broken into two parts and heavily damaged. The teeth were found as isolated fragments in a small sieved sample from a 2–3 square foot area and originally were catalogued together. Because some

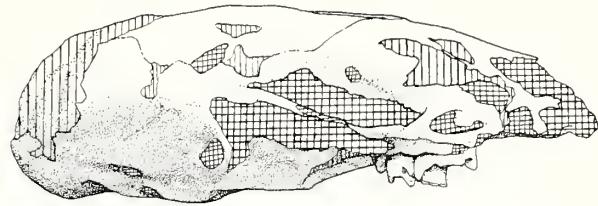


Figure 1. Distribution map of the Latimanus group species of *Scapanus* (*Scapanus*) in California (modified from Palmer, 1937, and Hall and Kelson, 1959). Fossil sites are: 1, Samwell Cave (UCMP 1008); 2, Galen's Pit (UCMP V75068); 3, Potter Creek Cave (UCMP 1055); 4, Hawver Cave (UCMP 1069); 5, Teichert (UCMP V69129); 6, Mercer's Cave (UCMP V67108); 7, Rodeo area (UCMP V6312, V71001–V71003); 8, Pacheco 2 (UCMP V78027); 9, Maxum (UCMP V6869); 10, Irvington (UCMP V3604) and Prune Avenue (UCMP V5301); 11, Tranquility (UCMP V4401); 12, Calico Lakes (SBCM 1.76.35); 13, Solid Waste site (SBCM 1.76.33); 14, Zuma Creek (LACM 1754); 15, Rancho La Brea (LACM 6909 and Pit 91); 16, Emery Borrow Pit (LACM 7053); 17, San Pedro (UCMP 2047); 18, Newport Mesa (LACM 3877); 19, Redec A (USGS M1451); 20, San Diego area (SDNHM 3181-E, 3131-B); 21, Anza-Borrego Desert (LACM and IVCM sites). Small map of the distribution of the extant species of *Scapanus* north of California from Hall and Kelson, 1959.

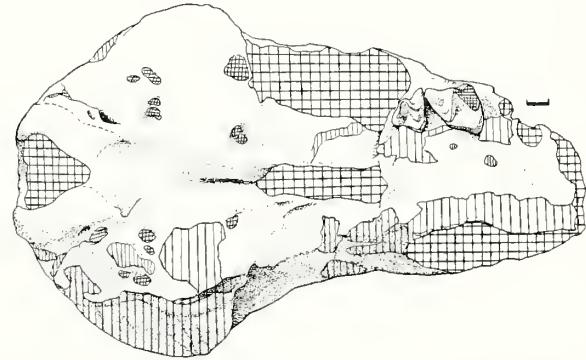


Figure 2. *Scapanus malatinus*, IVCM 15/61, partial skull with right M^{2-3} . Hatched areas represent the major areas where the bone was spalled off exposing a natural endocast. Cross-hatched areas represent matrix or broken surfaces. Scale line equals 1 mm.

of the fragments fit together and all the teeth are in the same stage of wear and of the same side, there is little doubt that they are from the same individual. Collected by Harley Garbani, 18 January 1954.

TYPE LOCALITY. LACM locality 1114 (Rodent Hill). Latitude 32°25'21"N; longitude 116°12'7"W. Vallecito badlands of the Anza-Borrego Desert, San Diego County, California. Palm Springs Formation, Huesos "Member," T. Downs "zone" 57.6. From about a foot thick whitish-gray-greenish, semi-consolidated, micaceous, unstratified silt or mudstone (T. Downs' notes of 13 December 1954).

AGE. Irvingtonian Land Mammal Age (Downs and White, 1968), Irvingtonian I of Repenning (1980, 1985), Matuyama Epoch of the paleomagnetic scale (Opdyke et al., 1977), within the Olduvai event (Downs, pers. comm. 1983), about 1.7–1.9 Ma (Repenning, 1985).

ETYMOLOGY. *Malatinus* is an anagram of *latimanus*.

HYPODIGM. LACM locality 1114 (=IVCM loc. 15); Type; IVCM 15/61, associated individual with skull lacking

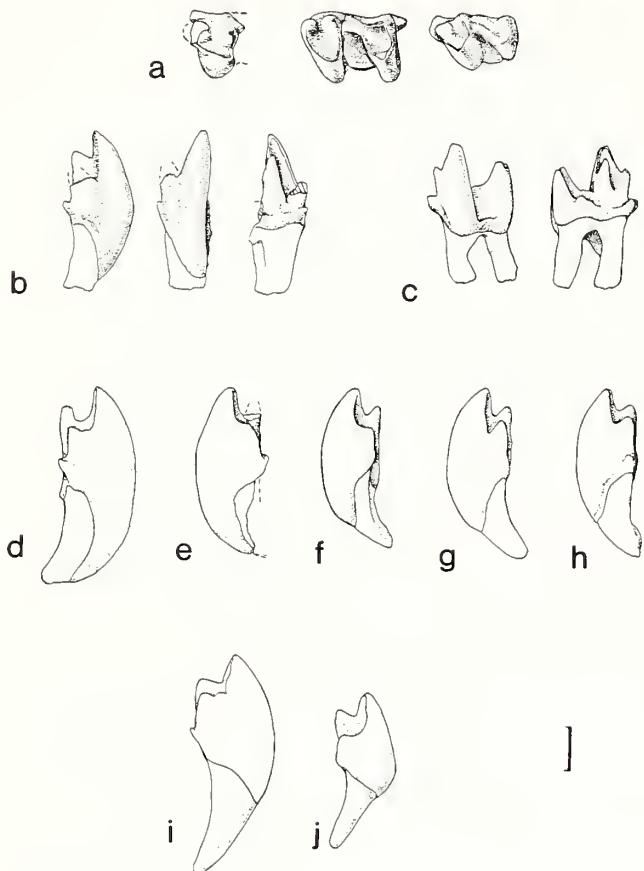


Figure 3. a–c, Teeth of *Scapanus malatinus*, LACM 3451 (Holotype); a, occlusal views of left M_1 (trigonid) to M_3 ; b, M_1 trigonid, anterior, labial, and lingual views; c, M_3 , labial and lingual views. d–j, M_1 trigonids of *Scapanus* (*Scapanus*), anterior views; d, *S. latimanus* cf. *caurinus*, UCMP 131165; e, *S. latimanus*, UCMP 81729, Irvington site; f, *S. l. occultus*, MVZ 4036; g, *S. l. anthonyi*, MVZ 6216; h, *S. l. cf. anthonyi*, SDNHM 26232, Glen Abbey site; i, *S. townsendii*, JHH "G"; j, *S. orarius*, JHH "A." Scale line equals 1 mm.

anterior and left side of rostrum but with right M^{2-3} , right humerus, anterior part of manubrium, proximal right femur, proximal right radius, fragment of right dentary, scapular blade fragment, a thoracic and caudal vertebra, proximal rib fragment, medial and ungual phalanx of manus; LACM 122848, M^x fragment; LACM 122849, M_x talonid; LACM 3450, 9804, 122850–122851, humeri fragments; LACM 122852, ulna fragment; LACM 122853–122855, radii; LACM 122856, lunar; LACM 122857, magnum; LACM 122858–122859, metacarpals I; LACM 122860, metacarpal II; LACM 122862–122863, metacarpals III; LACM 122863–122864, metacarpals IV; LACM 122865, metacarpal V; LACM 122866–122867, 122880, manus sesamoids; LACM 122868–122872, manus proximal phalanges; LACM 122873–122879, manus medial phalanges; LACM 122881–122887, manus ungual phalanges; LACM 122888, femur; LACM 122889, femur head; LACM 122890, proximal tibia; LACM 122891, astragalus; LACM 122892, cuboid; LACM 122893, navic-

Table 1. Stratigraphic sequence of selected *Scapanus malatinus* localities, from the Anza-Borrego Desert, San Diego County. Localities between the dashed lines indicate the level of the Olduvai event.

| Land Mammal Age | T. Downs Zone | LACM locality |
|--------------------|---------------|---------------|
| | 59.2 | 1191 |
| Irvingtonian | 58.5 | 1142 |
| | 57.7 | 1461 |
| | 57.6 | 1114 (type) |
| | 55.5 | 1615 |
| Blancan | | |
| | 50.4 | 1428 |

ular; LACM 122896, metatarsal II; LACM 122894, metatarsal III; LACM 122895, metatarsal IV; LACM 122900–122905, pes phalanges; LACM 122897–122899, pes ungual phalanges.

REFERRED MATERIAL. LACM locality 1191: LACM 3596, distal humerus. LACM locality 1245: LACM 4424, distal humerus. LACM locality 1428: LACM 122910, heavily worn right M_1 . LACM locality 1442: LACM 9806, distal humerus. LACM locality 1461: LACM 122906, magnum; LACM 122907, metacarpal V; LACM 122908, manus medial phalanx; LACM 122909, manus ungual phalanx. LACM locality 1615: LACM 4450, distal humerus; LACM 122911, carpal; LACM 122912, manus ungual phalanx. LACM locality 1768: LACM 4451, distal humerus. IVCM locality 124: IVCM 1060, 1061, incomplete humeri. IVCM locality 333: IVCM 1362, humerus fragment. All the referred specimens are from the Vallecito badlands and same formation and "member" as the type. They are all in the Matuyama Epoch but vary in stratigraphic position (see Table 1).

DESCRIPTION. The skull (Fig. 2), although chipped, preserves all the cranium and most of the posterior part of the rostrum. Because the skull is only slightly distorted, some of the standard skull measurements used on extant species may be taken (Table 2). The frontal region is noticeably convex dorsally as in some specimens of *S. latimanus* (see Jackson, 1915, pl. 5, fig. 4). Aside from the dentition, size, and relative rostral proportions, the skulls of extant species of *Scapanus* closely resemble one another. The preserved parts of the fossil skull share those features common to the three extant species. Unfortunately the tip of the rostrum is lacking in IVCM 15/61 so its relative length or number and size of the antemolar teeth cannot be determined. The arching of the frontal region appears to be related to shortening of the snout in recent species so some shortening of the snout is inferred in *S. malatinus*. The bridge of bone forming the lateral wall of the infraorbital foramen is relatively narrow and strap-like as in *S. orarius* and unlike the rod-like structure in *S. latimanus*. Lateral to the base of the infraorbital bridge is a longitudinal and slightly dorsally deflected ridge of bone for insertion of the masseter muscles. A shallow and relatively

Table 2. Measurements of the skull of *Scapanus malatinus*, IVC 15/61, compared to selected *S. latimanus* samples.

| Measurement | IVC 15/16 | <i>anthonyi</i> | <i>occultus</i> | <i>all latimanus</i> |
|----------------------|-----------|-----------------|-----------------|----------------------|
| Mastoidal breadth | 15.9 mm | 15.3–16.0 | 15.3–16.3 | 15.3–18.6 |
| Interorbital breadth | 7.3 | 6.9–7.4 | 6.9–7.7 | 6.9–8.6 |
| Maxillary breadth | 9.1* | 8.9–9.4 | 8.9–9.8 | 8.9–10.8 |
| Depth of skull | 8.5 | 8.3–8.9 | 9.0–9.8 | 8.3–10.8 |
| Length of orbit | 7.8 | 8.2–8.7 | 7.6–8.8 | 7.6–10.0 |

* Only the right side preserved and measured to midline then doubled to give standard maxillary breadth.

narrow trough lies between this ridge and the base of the infraorbital bridge and resembles that in *S. latimanus*. In *S. orarius* and *S. townsendii* this trough is wider and the ridge is better developed dorsally.

The upper molars strongly resemble those of *S. townsendii* and *S. orarius*, although the pre-ectoflexus of the M^3 forms a more open angle. The metacingulum on all the upper molars joins the lingual-most part of the metacone whereas in *S. latimanus* it usually joins the metacone anterior and labial to this point.

Of the five lower molar specimens (Figs. 3, 4), only the M_3 is complete. The trigonid of the left M_1 of the type lacks the tip of the paraconid. There is a small but distinct lingual parastylid at the base of the anterior part of the paraconid from which a short entocingulid extends posteriorly to the metaconid. This cingulid is absent in extant species, and, excepting *S. latimanus*, the parastylid is smaller or absent in extant species. The base of the trigonid valley is about the same level as in the M_2 . A small hairline-like precingulid, absent in extant species, spans the base of the paraconid but falls short of joining the parastylid. The most striking feature of the tooth is the extent to which the enamel extends down the labial side of the root (Fig. 3b), a condition approaching or equaling that of *S. latimanus anthonyi*. The arch of the labial margin of the protoconid is uniform, unlike the asymmetrical curvature that occurs there in *S. orarius*.

The M_2 (LACM 3451) lacks the parastylid due to breakage but shows that the trigonid is compressed longitudinally to an equal or slightly greater extent than in observed specimens of *S. latimanus* which in turn has the most compressed trigonids of the extant species (Fig. 4). The floor of the trigonid basin is at the same level as the crest of the crista obliqua at its juncture to the metaconid. Although the parastylid along with the root and basal enamel margin is broken away, there is a trace of a precingulid extending labially at least two-thirds the distance across the base of the paracristid. The trigonid of the M_2 (LACM 3451 and ?LACM 122849) shows the same strong development of the entocingulid and enamel margins as in the M_3 . The entoconid and crista obliqua are sharply defined and continuous with the entoconid and hypoconid respectively. The entoeristid is lower than the crista obliqua. As in the extant species there is a distinct entostyloid and no ento- or postcingulid. The enamel margins show no tendency to extend onto the roots with the possible exception of the margin (not complete) below the protoconid.

The M_3 , while resembling that in the extant species in the disposition and size of the major cusps, differs from them in having 1) a sharp and well-developed ectocingulid spanning the hypoflexid (variable in *S. latimanus* but when present not strongly united to the protocone), 2) the parastylid con-

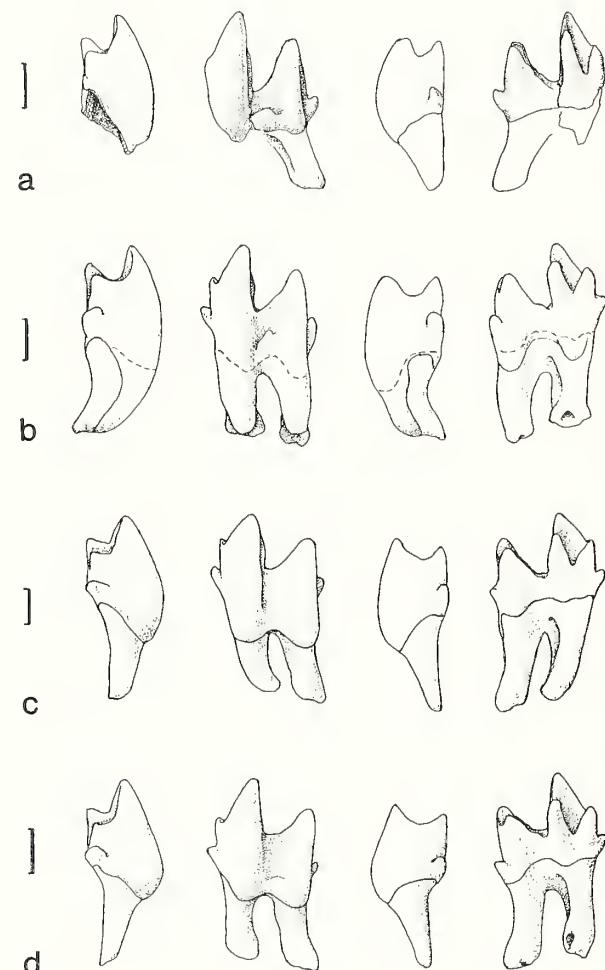


Figure 4. Comparison of the left M_2 of four species of *Scapanus* (*Scapanus*), anterior, labial, posterior, and lingual views; a, *S. malatinus*, LACM 3451 (holotype); b, *S. latimanus* cf. *caurinus*, UCMP 131165, dashed line indicates limit of cementum; c, *S. townsendii*, JHH "G"; d, *S. orarius*, JHH "A." Scale lines equal 1 mm.

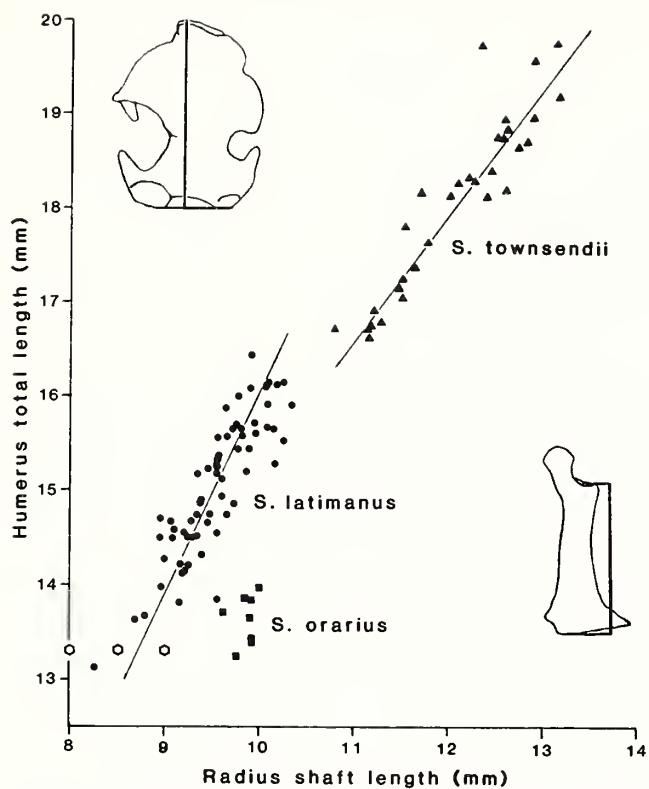


Figure 5. Plots of the radius to humerus proportions and regression lines in three Recent species of *Scapanus*. The plots (open symbols) of *S. malatinus* are based on the one isolated measurable humerus with each of the three isolated radii from LACM locality 1114. *Scapanus latimanus* plots based upon specimens in the UCMP and MVZ including all the subspecies mentioned by Palmer (1939) excepting *S. insularis*, *S. sericatus*, *S. monoensis*, and *S. anthonyi*.

tinuous with a precingulid which extends along the lingual two-thirds of the base of the paracristid, 3) entocingulid well defined along the entire lingual base of the paraconid, and 4) an entocristid which is distinctly lower than the crista obliqua and is truncated by a notch between it and the entoconid. The enamel margins at the base of the M_3 crown are only moderately sinuous as in *S. townsendii* and *S. orarius* and do not extend down the labial sides of the roots as in *S. latimanus*. The trigonid is more compressed longitudinally than in *S. orarius* and resembles that of *S. latimanus*.

The radius resembles *S. latimanus* and *S. townsendii* in proportions and falls within the size range of *S. latimanus*. The total length of the only complete humerus (IVCM 15/16) is plotted in Figure 5 with each of the three radii from the same site; the resulting proportions all fall within or adjacent to the plots of small *S. latimanus* and away from those of *S. orarius*. The smallest measurable humerus (IVCM 1061) is 12.2 mm in length, smaller than any living specimen measured.

One ulna (LACM 122853) lacking the proximal and distal ends resembles that of *S. latimanus* and *S. townsendii* in its relatively short robust shaft and short fusiform brachialis

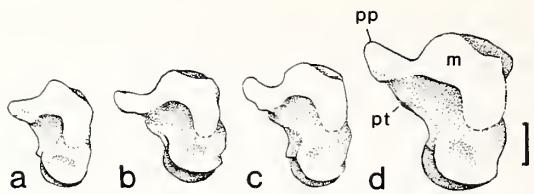


Figure 6. Right metacarpal II of *Scapanus* (*Scapanus*), lateral view; a, *S. malatinus*, LACM 122860; b, *S. latimanus*, UCMP 131166; c, *S. orarius*, JHH "A"; d, *S. townsendii*, JHH "G." m = magnum articular facet, pp = proximal process, pt = palmar tuberosity. Scale line equals 1 mm.

scar. It differs from the observed extant species in its relatively longer radial facet and more open semilunar notch.

Metacarpal I (LACM 122858) resembles those of the extant species but is relatively short as in *S. orarius* and *S. latimanus*. Metacarpals II–V resemble those of *S. townsendii* and *S. latimanus* in their relative shortening. Metacarpal II resembles that of *S. latimanus* in the less protuberance of the palmar tuberosity (Fig. 7) and lack of a deep trough-like depression which separates the palmar tuberosity from the trapezoid facet. The proximal prominence also resembles that of *S. latimanus* in extending away from the metacarpal axis at nearly a right angle, not being curved as in *S. townsendii* and *S. orarius* (Fig. 6). There is a medial low tuberosity on the medial part of the palmar side of metacarpal III just distal to the magnum facet. This tuberosity bears a roughly circular palmar facing facet as in *S. latimanus*, unlike the rounded surface in the other species.

The femur is relatively short but not noticeably different in morphology from the modern species. The humerus, tibia, anterior part of the manubrium, palmar sesamoids, and median and ungual phalanges resemble those of the extant species.

REMARKS. Whereas all of the specimens come from the Vallecito Creek "Local Fauna" of Downs and White (1968), two of the localities (LACM 1245, LACM 1768) are of uncertain stratigraphic provenience. The other sites (Table 1) are arrayed on either side of the T. Downs "zone" 56, which probably coincides with the Olduvai magnetic polarity event (Opdyke et al., 1977; T. Downs in letter, 1977). The Olduvai event is dated elsewhere at about 1.72 to 1.88 Ma (N. Johnson, in prep.).

Scapanus latimanus (Backman, 1842)

Scalops latimanus Backman, 1842: Boston Journal of Natural History, 4:34.

See Hall and Kelson, 1959:69–71 for additional synonymies.

The extant species, *S. latimanus*, is moderately common in Rancholabrean microvertebrate sites but several new records can be added to those previously published. The most interesting record of the species, however, is from the type locality of the Irvingtonian and the oldest record of the species thus far.

In most cases I do not attempt to describe in detail all the

new material referable to this species but list it briefly. The records are ordered by county and institutional locality number. The asterisk preceding some localities indicates the first published record of *S. latimanus* from these localities. All the localities are Rancholabrean in age except UCMP locality V3604.

ALAMEDA COUNTY. *UCMP locality V3604 (Irvington site 2). Specimens: UCMP 81729, trigonid of right M_1 ; UCMP 81730, left humerus lacking the head and tips of minor processes.

Remarks: The lower molar fragment (Fig. 3e) exhibits extensive enamel on the labial side of the root, loss of the precingulid, and high paracristid. These features are diagnostic for *S. latimanus* and distinguish it from *S. malatinus*.

This site is within the present geographic range of *S. l. latimanus*, a subspecies which the fossil closely resembles. The locality is the type of the Irvingtonian Land Mammal Age (Stirton, 1939; Savage, 1951; Casteel and Hutchison, 1973; Kurtén and Anderson, 1980) from the Irvington Gravels. This is the earliest record of *Scapanus* that can be assigned with confidence to *S. latimanus*. Lindsay et al. (1975) placed the type locality in the upper portion of the Matayama magnetic interval, which has a time range of about 0.7 to 1.5 Ma. Kurtén and Anderson (1980) place the Irvingtonian locality in the middle Irvingtonian.

*UCMP locality V5301 (Prune Avenue). Specimens: UCMP 43247, 119270–119278, including a dentary with P_{1-2} , dentary fragments (4), M^1 , lunar, and proximal, medial and ungual phalanges of the manus.

Remarks: The site lies within the range of *S. l. latimanus*. Fish from this locality were described by Casteel and Hutchison (1973).

CALAVERAS COUNTY. *UCMP locality V67108 (Mercer's Cave). Specimen: UCMP 119249, dentary fragment.

Remarks: The site falls between the ranges of *S. l. sericatus* Jackson and *S. l. minusculus* Bangs. Sinclair (1905) described a sloth *Megalonyx sierrensis* (=*M. jeffersoni* Leidy) from this site. Other mammals from the locality in the UCMP collections include the extinct *Euceratherium collinum* and extant *Neotoma*, *Myotis*, *Lepus*, *Sylvilagus*, *Marmota*, *Spermophilus*, and *Peromyscus*.

CONTRA COSTA COUNTY. UCMP locality V6312 (Garretson). Specimens: UCMP 92478–92481, 94309–94311, including a dentary fragment, M_1 , M^3 , radius and ungual phalanges of manus.

Remarks: These specimens and those of the following three localities form the basis of the records of *S. latimanus* listed by Wolff (1973, 1975) from the Montezuma Formation of the Rodeo area. All the sites lie within the present range of *S. l. latimanus*.

UCMP locality V71001 (Central Channel). Specimens: UCMP 92483–92487, 92489, 119250–119252, including a dentary fragment, M^1 , M^2 , incomplete humerus, metacarpal IV, calcaneum, and ungual phalanges.

UCMP locality V71002 (Lawlers Boundary). Specimens: UCMP 93951–93952, proximal humerus and phalanx 2 of manus.

UCMP locality V71003 (Northern Cove). Specimens:

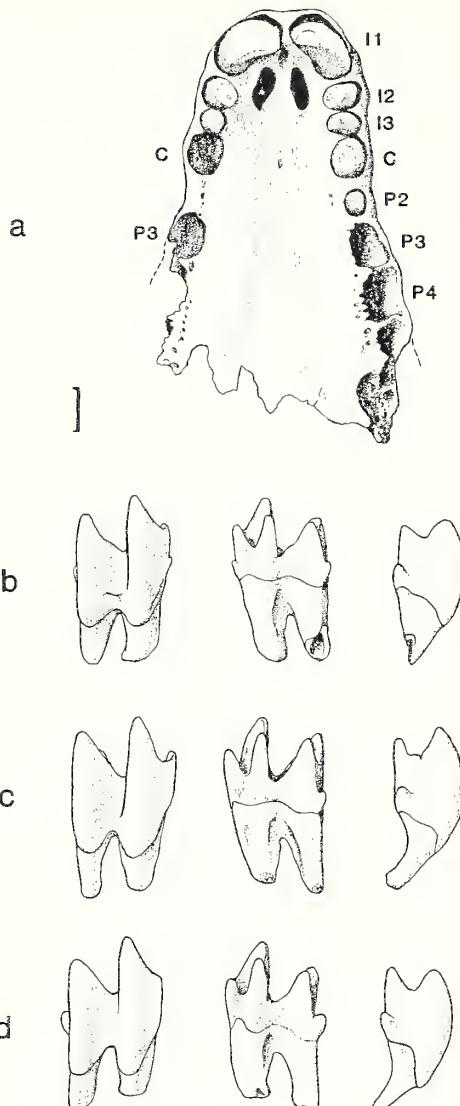


Figure 7. a, *Scapanus latimanus* cf. *anthonyi*, SDNHM 26231, ventral view of rostrum; b–d, labial, lingual, and posterior views of M^1 ; b, *S. l.* cf. *anthonyi*, SDNHM 26232; c, *S. l. anthonyi*, MVZ 6216; d, *S. l. occultus*, MVZ 4036. Scale line equals 1 mm.

UCMP 92476, 92477, 93983, M^1 , dentary fragment with M_{2-3} , and ulna fragment, respectively.

*UCMP locality V78027 (Pacheco 2). Specimens: UCMP 119287, 125567, including clavicle, dentary fragments, upper and lower molars, humerus, distal femur, medial phalanx of manus.

Remarks: This site is a concentrated pocket of mostly small vertebrates. No extinct vertebrates have yet been identified (with the possible exception of a bird—D. Steadman, pers. comm.) from the sample which is not yet completely sorted. The pocket occurs in a series of cross-bedded alluvial deposits that contain *Megalonyx*, *Mammut*, *Mammuthus*, and *Equus*. The presumption that the microvertebrate site is also Rancholabrean is tempered by the possibility that the deposit is

a later cut and fill episode than that represented by the extinct larger vertebrates, although the preservation is the same as for the extinct forms. The site is within the present geographic range of *S. l. latimanus*.

EL DORADO COUNTY. UCMP locality 1069 (Hawver Cave). Specimens: UCMP 21143, 119242–119248, including humerus, femur, and pelvis.

Remarks: Locality listed as Wisconsin in Kurtén and Anderson (1980) and Harris (1985) and lies between the present geographic ranges of *S. l. dilatus* True and *S. l. sericatus*. Stock (1918, 1925) thought that the original specimens (UCMP 21143, a humerus and edentulous dentary fragment, since lost) might represent a new species. Additional material and the variation in the living species do not support the significance of the characters of the humerus that Stock (1918) used to indicate distinction from *S. latimanus*.

FRESNO COUNTY. UCMP locality V4401 (Tranquility). Specimen: UCMP 37698, incomplete humerus.

Remarks: Hewes (1946) listed this occurrence as *Scapanus* sp. and gave an accurate and detailed locality description. Brattstrom (1959) replicated the UCMP files as to location of the site but these appear to be somewhat misplaced by modern map standards. It is not known if the *Scapanus* is the same age as the Pleistocene fauna listed by Hewes (1946) because human artifacts and burials also are found in this general locality and the surface collections represent a mixture of the two assemblages. The human remains were radiocarbon dated at about 2550 years (Berger et al., 1971). The site lies west of the geographic range of *S. l. campi* Grinnell and Storer.

LOS ANGELES COUNTY. *LACM locality 1754 (Zuma Creek). Specimen: LACM 124286, dentary fragment with alveoli of P³–M³.

Remarks: The locality lies within the present geographic range of *S. l. occultus* Grinnell and Swarth. Additional fauna are recorded in Kurtén and Anderson (1980).

LACM locality 6909 (Rancho La Brea Pit 91). LACM R-21363, right humerus, LACM R-52177, heavily worn M₃.

Remarks: The humerus was figured and described by Akersten et al. (1979:fig. 1c). Chemical or radiometric dates from this pit range from 25,100 to greater than 33,000 years before present (Marcus and Berger, 1984). Considering the vast quantity of small vertebrates from this and other pits in the Rancho La Brea deposits, *S. latimanus* was exceedingly rare in this area. Woodard and Marcus (1973) placed the Rancho La Brea deposits in the upper part of Member B of the Palos Verdes Sand. Rancho La Brea lies within the present geographic range of *S. l. occultus*.

***LACM locality Pit A (Rancho La Brea).** LACM 20420, distal femur; LACM 20419, synsacrum.

Remarks: Howard (1962) postulated on the basis of the bird remains that Pit A was “probably active nearer the end of the Pleistocene than the other eight pits” studied from Rancho La Brea.

UCMP locality 2047 (San Pedro). Specimens: UCMP (if initially properly identified) uncatalogued and since lost.

Remarks: The location and stratigraphy of this locality are given in Miller (1971), although the locality number is er-

roneously listed as V-2047. The locality is in a marine terrace of the Palos Verdes Sand. The Palos Verdes Sand has been radiometrically dated (Fanale and Schaeffer, 1965:314) and ranges in age from 100 to 130 ka. Wehmiller et al. (1977:fig. 18) estimated a more restricted age range of about 122 to 132 ka for the Palos Verdes Sand. A general summary of the fauna from this general area of the Palos Verdes Sand is given in Langenwalter (1975). The site lies within the present geographic range of *S. l. occultus*.

ORANGE COUNTY. LACM locality 3877 (old number 1067) (Newport Mesa). Specimen: LACM 20839, distal humerus, radius, palmar sesamoid and phalanges of manus.

Remarks: The locality and specimens are described by Miller (1971), Hudson and Brattstrom (1977), and Kurtén and Anderson (1980). The site lies within the present geographic range of *S. l. occultus* and is in the Palos Verdes Sand and the same age as given for UCMP locality 2047.

***LACM locality 7053 (Emery Borrow Pit I).** Specimen: LACM 27099, humerus.

Remarks: The locality is in the La Habra Formation, see Kurtén and Anderson (1980). Site lies within the present geographic range of *S. l. occultus*.

SACRAMENTO COUNTY. UCMP locality V69129 (Teichert Gravel Pit East 1). Specimens: UCMP 119253–119256, M² fragment, radius, ulna fragment, and proximal phalanx of manus respectively.

Remarks: Hutchison and Williams reported this material in a faunal list published by Hansen and Begg (1970). The site is within the Riverbank Formation (San Joaquin loam) and has been dated by uranium and actinium series method at 103 ± 6 ka or greater. The locality lies between the present geographic range of *S. l. latimanus* and *S. l. minusculus*.

SAN DIEGO COUNTY. *SDNHM locality 3131-B (Glen Abbey). Specimens: SDNHM 26231–26238, anterior part of rostrum, M₁ (2), humeri (2), ulnae (3), femur, and clavicle.

Description: The anterior part of the rostrum (Fig. 7A) is well preserved and retains eight of the anterior teeth. The I^{1–3} are preserved on both sides as well as the C and P² on the left side. Both sides preserve complete or partial alveoli of the P³ to M¹. The P² alveolus is absent on the right side but a diastema equivalent to the distance between left C–P³ remains. The P¹'s are absent and there are no spaces marking their loss. The left P² is the smallest antemolar and does not fill the space between P³ and C.

Of the two M₁'s from the site, one (SDNHM 26232, Fig. 3h, 7b) is little worn and well preserved, the other is heavily worn and abraded but agrees with the former in general features. The M₁ closely resembles that of *S. l. anthonyi* Allen in degree of enamel excursion down the roots and general conformation and size. If differs from *S. l. anthonyi* and resembles *S. malatinus* in presence of a narrow and incomplete precingulid and distinct parastylid. A remnant of the ectocingulid occludes the base of the hypoflexid unlike *S. l. anthonyi*, and possibly resembling that of *S. malatinus* but this area is not preserved in known specimens of *S. malatinus*.

The humerus is small, measuring 12.8 mm in total length.

Remarks: The rostrum resembles *S. l. anthonyi* in size,

loss of the P^1 on both sides and the loss of the right P^2 as well. *Scapanus l. occultus* may resemble *S. l. anthonyi* in size and in the loss of one or both P^1 (Palmer, 1937:312) but no cases of a P^2 being lost as well have been reported. This presumably derived pattern of tooth loss would thus normally justify assignment of the San Diego specimen to *S. l. anthonyi*. The area of San Diego is presently occupied by *S. l. occultus* with *S. l. anthonyi* occurring to the south in the mountains in Baja California (Palmer, 1937; Hall and Kelso, 1959). Presence of *S. l. anthonyi* in San Diego would thus constitute a range extension of the species during the late Pleistocene. This picture is complicated, however, by the rather primitive morphology of the M_1 of the San Diego fossil, the only lower tooth thus far known of the taxon. The degree of enamel extension down the roots more closely resembles that of *S. malatinus* than *S. l. anthonyi* (Fig. 3). The presence of a small parastylid, narrow precingulid, and distinct transverse ectocingulid cuspid resemble the primitive conditions as those in *S. malatinus* and were not observed in *S. l. anthonyi* (Fig. 9). The small ectocingulid cuspid may, however, occur on the M_1 of other *S. latimanus*.

Chandler (1982) described a passenger pigeon, *Ectopistes migratorius*, from this locality but the rest of the fauna is undescribed. The locality lies in unnamed river terrace deposits (Chandler, 1982). The age of the site is not precisely determined. The only temporally significant species presently known from the site is an *Equus occidentalis* tooth identified by Chandler (1982) but the basis of the identification was not given. Whereas *Equus occidentalis* is best known from the Rancholabrean (especially Rancho La Brea), it may be present in earlier deposits (Kurtén and Anderson, 1980). As the morphology of the M_1 of the San Diego mole appears to be intermediate between *S. malatinus* and *S. l. anthonyi*, the Rancholabrean age of the site should be considered as tentative. The San Diego specimens are here tentatively referred to *S. l. cf. anthonyi* on the basis of dental formula, but further comparison with Recent material from San Diego (not seen) is desirable. Moreover, more and better material of *S. malatinus* and the fossil San Diego form may indicate another assignment.

SAN BERNARDINO COUNTY. Reynolds and Reynolds (1984) and Reynolds (1984) published a record of *S. latimanus* in a list with the other vertebrates and invertebrates from SBCM locality 1.76.34 (Luz Foundation). The tooth fragment upon which this was based is indeterminate as to genus and is not here regarded as a valid record.

SBCM locality 1.76.33 (Solid Waste site). Specimen: SBCM A 1776-173, clavicle.

Remarks: This specimen was reported in a list with the other vertebrates and invertebrates by Reynolds and Reynolds (1985) who provided a radiocarbon date for the site of $12,210 \pm 430$ years. The site lies northeast of the nearest approach of the present geographic range of *S. l. occultus*.

SBCM locality 1.76.35 (Calico Lakes Phase I). Specimen: SBCM A 1855-1, clavicle.

Remarks: Published in a list with the other vertebrates and invertebrates by Reynolds and Reynolds (1985). This material is associated with a radiocarbon date of 9050 ± 350

years. The site lies northeast of the nearest approach of the present geographic range of *S. l. occultus*.

SHASTA COUNTY. UCMP locality 1008 (Samwell Cave 1). Specimens: UCMP 9623, 35685, 119257–119261, anterior part of skull with right and left M^2 , dentary, rostral fragment with M^1 , incomplete femur, pelvi.

Remarks: Furlong (1906), Stock (1918), and Hibbard (1958) recorded these specimens. Graham (1959) and Treganza (1964) provided detailed maps of the cave and Treganza documents the lack of positive evidence for human and Pleistocene faunal associations. Harris (1985) presumed the fossil material to be late Wisconsinan in age. Graham (1967) suggested that the fossil moles from Samwell Cave were distinct enough to merit a new fossil subspecies, but formal description has not yet appeared. The cave lies within the present geographic range of *S. l. dialatus*.

UCMP locality 1055 (Potter Creek Cave). Specimens: UCMP 5630, 33164, dentaries with M^{1-3} ; UCMP 7648, 7046, pelvi; UCMP 7532, ulna; UCMP 5343, 6395, 6538, 6539, 6819, 6821, 7464, 7465, 7506, 7576–7578, 7668, 7853, 8249, 33167, humeri.

Remarks: The locality was described and the fauna was listed by Sinclair (1904) and Miller (1912). Hibbard (1958), Brattstrom (1954, 1958), and Hutchison (1967) added additional taxa to the list. Sinclair (1904) and Harris (1985) regarded the site as late Wisconsinan or older in age. Sinclair listed the Potter Creek Cave mole as *Scalops cf. townsendii* in 1903 but corrected this to *S. californicus*(?) Ayres in 1904 (now a junior synonym of *S. latimanus*). Stock (1918) presented a revised list from this cave and listed the mole as *S. latimanus* for the first time. The cave lies within the present geographic range of *S. l. dialatus*.

***UCMP locality V75068 (Galen's Pit).** Specimens: UCMP 119262–119269, including pelvis fragment, ulnae fragments, scaphoid, trapezium, metacarpals II and III, and calcaneum fragment.

Remarks: This site has not been previously published. It is a cave in the Hosselkus Limestone collected by Jens Munthe. Specimens came from a flowstone breccia including such extinct taxa as *Equus*, *Mammuthus*, *Euceratherium*, and extant genera *Gymnogyps* (cf. *G. californicus*), *Odocoileus*, *Aplodontia*, *Thomomys*, *Neotoma*, and *Peromyscus*. The cave lies within the present geographic range of *S. l. dialatus*.

Scapanus new species?

Figures 8a–d

MATERIAL. UCMP 126753, left M^2 fragment (Fig. 8c); UCMP 126754, damaged right M_1 (Fig. 8a); UCMP 126755, damaged left M_2 (Fig. 8b); UCMP 126756–126778, scapula fragment, humerus, lunar, metacarpals I–V, proximal, medial, and ungual phalanges of the manus, astragalus, metatarsals, and pedal phalanx.

UCMP locality V6869 (Maxum), Contra Costa County, California. Tassajara Formation.

AGE. Pliocene, earliest Blancan, Blancan I of Repenning

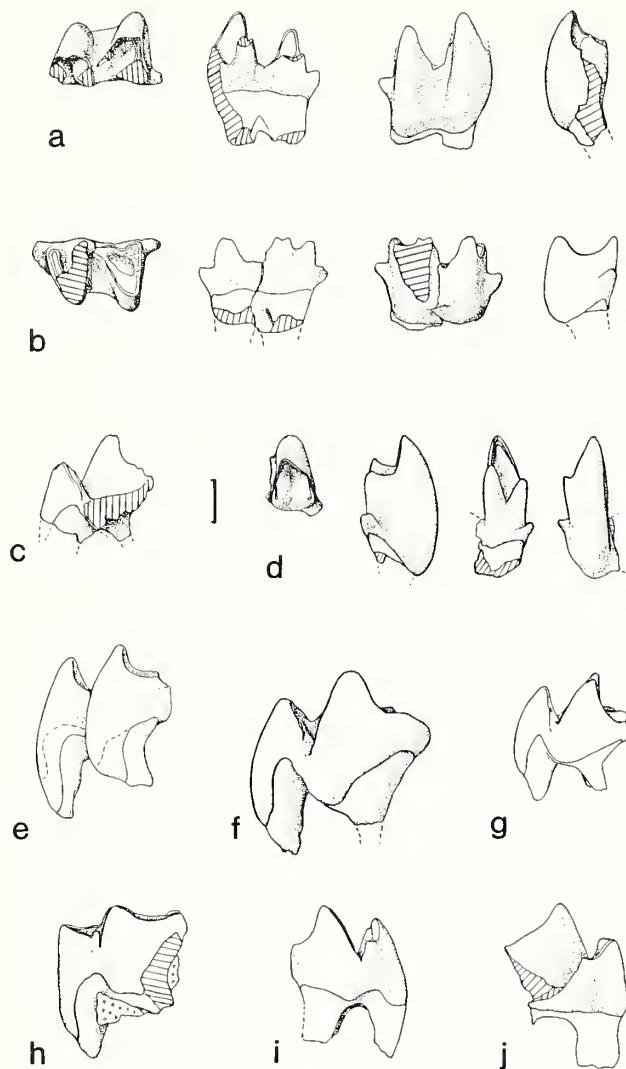


Figure 8. a–c, *Scapanus (Scapanus)* new species? from the Maxum locality; a, UCMP 126754, right M_1 , occlusal, lingual, labial, and anterior views; b, UCMP 126755, left M_2 , occlusal, lingual, labial, and posterior views; c, UCMP 126753, left M^2 , posterior view; d, *Scapanus (Scapanus)* new species?, USNM 264301, trigonid of left M_2 , occlusal, anterior, lingual, and labial views. e–j, comparison of posterior views of M^2 ; e, *S. (S.) latimanus* cf. *caurinus*, UCMP 131165, dashed line indicates limit of cementum; f, *S. (Scapanus) townsendii*, JHH “C”; g, *S. (Scapanus) orarius*, JHH “A”; h, *S. (Xeroscapheus) proceridens*, UCMP 124433, worn; i, *Scapanus (X.) shultzii*, UCMP 124434; j, *Scapanoscapter simplicidens*, UO 24290. Scale line equals 1 mm.

(1980), 4.3–4.8 Ma, Gilbert reversed magnetic polarity epoch, upper chron 2 of May and Repenning (1982).

REFERRED MATERIAL. USNM 264301, trigonid of $?M_2$ (Fig. 8d) USGS locality M1451 (Radec A), Riverside County, California. Temecula Arkose Formation, ascribed to the late Blancan, 2.2–2.7 Ma by Golz et al. (1977), but considered to be early Blancan by Repenning (pers. comm.) and close to the Maxum locality in age.

DESCRIPTION. The M^2 fragment (UCMP 126753) resembles that tooth of *S. orarius* and *S. townsendii* and differs from *S. shultzii* (Fig. 8i) in greater size of the lingual root with respect to the labial roots, strong ventrally directed notch in the enamel margin on the posterior side of the protocone and lack of well-defined conules. The M_1 , although damaged, appears to be rather high crowned compared to *S. orarius* and *S. townsendii* and has a more compressed trigonid. There is no enamel excursion down the roots as in *S. malatinus*, *S. latimanus*, and *S. proceridens*. The region of the parastylid is broken away and there is no indication of a precingulid on the remaining part of the tooth. The M_2 (UCMP 126755) also exhibits a high-crowned condition with compressed trigonid but retains a well-developed precingulid as in *S. shultzii* and unlike the extant species. The $?M_2$ trigonid of the Radec specimen lacks a defined precingulid.

Metacarpal II (UCMP 126760) resembles that of *S. malatinus* and *S. latimanus* in the separation of the proximal tuberosity (the proximal prominence is broken away).

REMARKS. Whereas the above material is not referable to a known species, the material is too fragmentary to form the basis of a new taxon at present.

Scapanus species indet.

MATERIAL. SDNHM locality 3181-E (J Street II), San Diego County. “Upper” member San Diego Formation, Blancan (Deméré, 1983; Domning and Deméré, 1984). Specimen: SDNHM 26230, humerus lacking part of proximal end.

REMARKS. The humerus is in the size range of *S. malatinus*, *S. orarius*, and small *S. latimanus* but is not specifically diagnostic. The age of the site would suggest relationship to the questionable new species *Scapanus* described above.

The locality is a marine shell bed containing a variety of sharks, a ray and such terrestrial vertebrates as rodent, snake, lagomorph, felid, *Equis*, and an artiodactyl. The locality lies very high in the San Diego Formation (“upper” member of Deméré, 1983) and was deposited in a very shallow nearshore marine environment (Deméré, pers. comm., 1985).

DISCUSSION

Whereas a respectable suite of genetic (Yates and Greenbaum, 1982), gross proportional, and soft tissue character states (Jackson, 1915; Palmer, 1937; Hall and Kelson, 1959) distinguish the extant species of *Scapanus* from each other, these are not preserved in typical fossil remains. Fortunately, a number of dental and osteological features may also be used (Table 3). *Scapanus latimanus* is more distinct from *S. orarius* and *S. townsendii* in skull and dental features than either of the latter species are from each other. *Scapanus townsendii* and *S. orarius* are in part sympatric (Fig. 1) and probably partition the resource in their range on the basis of size (McNab, 1971). *Scapanus townsendii* is distinctly larger (195–237 mm body length) than *S. orarius* (162–175 mm). *Scapanus latimanus* occupies a larger range than either of the other species and shows a greater range (Hall and Kelson,

Table 3. Selected character state matrix for species of *Scapanus*, using *Scapanoscapter* as the immediate primitive outgroup. Primitive, derived and variable states indicated by 0, 1, and V respectively.

| Derived character state | <i>Scapanus</i> | | | | | | | |
|--|-----------------------------------|-----------------|--------------------------------|----------------|-------------------------------|---------|------------------|------------------|
| | <i>Scapano-</i> <i>scapter</i> | <i>shultzii</i> | <i>proceri-</i> <i>dens</i> | <i>orarius</i> | <i>town-</i> <i>sendii</i> | (Maxum) | <i>malatinus</i> | <i>latimanus</i> |
| 1. Sinuous enamel M_{1-2} margin | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2. P_{1-2} single-rooted | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3. P_4 with fused roots | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 4. P_4 single-rooted | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| 5. M_{1-2} conules reduced | 0 | 0 | 0? | 1 | 1 | 1 | 1 | 1 |
| 6. Crown hypsodonty | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| 7. Cingulids lost | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1? |
| 8. Trigonids open | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| 9. M_1 labial enamel excursion | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 10. M_{1-3} with labial excursion | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11. Radius elongate | ? | 0 | 0 | 1 | 0 | ? | 0 | 0 |
| 12. Reduction in premolar no. | 0 | 1 | 1 | 0 | 0 | ? | ? | V |
| 13. Hypertrophy of I_2 | 0 | 1 | 1 | 0 | 0 | ? | ? | 1 |
| 14. Cementum development | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 15. Infraspinatus fossa of scapula not extending to acromion process | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| 16. Deltoid process of tibia spine-like | ? | 0 | 0 | 1 | 1 | ? | 1 | 1 |
| 17. Small vascular notch on clavicle | ? | 0 | 0 | 1 | 1 | ? | ? | 1 |

1959) in body size (132–192 mm). In general *S. latimanus* shows a decrease in size and tooth formula from north to south (Palmer, 1937; Ziegler, 1971) and this is generally coincident with increasing aridity to the south. Whereas it is clear that hypsodonty in moles is a derived character (Hutchison, 1968), the polarity of the limb proportions is unclear. The very large size attained in *S. townsendii* is probably derived but simple size characters are notoriously unreliable indices of relationship. The size trend of *S. latimanus* to *S. townsendii* can be viewed as an example of Bergmann's rule (Palmer, 1937). The radii of both show some negative allometry with regard to the humerus (Fig. 5), that may reflect a simple size/power relationship. *Scapanus malatinus*, *S. latimanus*, and *S. townsendii* appear to lie along approximately the same trend line. The sample of *S. orarius* is small but the humerus/radius plots are clearly transposed to the right of the other's curve. Whereas *S. latimanus* exhibits clear specializations such as hypsodonty and tooth crowding or reduction with regard to the other two species, the relationship of the latter to each other is far from clear.

The hypothesized cladistic relationships of the five species are presented in Figure 9 with the numbered nodes indicating the derived character states at each level (Table 3). A postulated phylogeny of the five species based on the cladistic analysis, stratigraphic sequence, and geography is also presented in Figure 9.

The species *S. latimanus* can be traced back in time to the later Irvingtonian. *Scapanus malatinus* from the early Irvingtonian provides a morphological link between *S. lati-*

manus on one hand and *S. townsendii* and *S. orarius* on the other. The high-crowned lower molars with evidence of enamel excursion down the roots, at least in M_{1-2} , arching of the skull and probable shortening of the snout are derived character states shared with *S. latimanus*, but not with the other two. The radius in *S. malatinus* is also relatively short (Fig. 5) as in *S. latimanus* and *S. townsendii*. *Scapanus malatinus* has very well developed ectocingulids, remnants of precingulids, and compressed trigonids—all character states that can be considered as primitive (using *S. shultzii* and *Scapanoscapter* as outgroups). The loss of these character states in the case of the cingulids or modification in the case of the spreading of the trigonid cusps in both *S. orarius* and *S. townsendii* suggest that these species share a common ancestor not shared by *S. malatinus* and *S. latimanus*. This arrangement is also favored by the distribution of the species. Shortening of the radius is a widespread phenomenon in diverse lineages of talpids but, based on comparison to *Xeroscaphus* and its distribution in modern *Scapanus*, it is here tentatively considered as primitive for *Scapanus*. On the basis of the above features and supported by their geographic array, the species of the *S. (Scapanus)* are here divided into two informal groups, the Orarius group consisting of *S. orarius* and *S. townsendii* and the Latimanus group consisting of *S. malatinus* and *S. latimanus* plus all other known fossils of the subgenus in California.

The Blancan specimens from the Maxum locality that represent an unnamed species are high crowned with compressed trigonids but lack enamel excursion down the roots. The

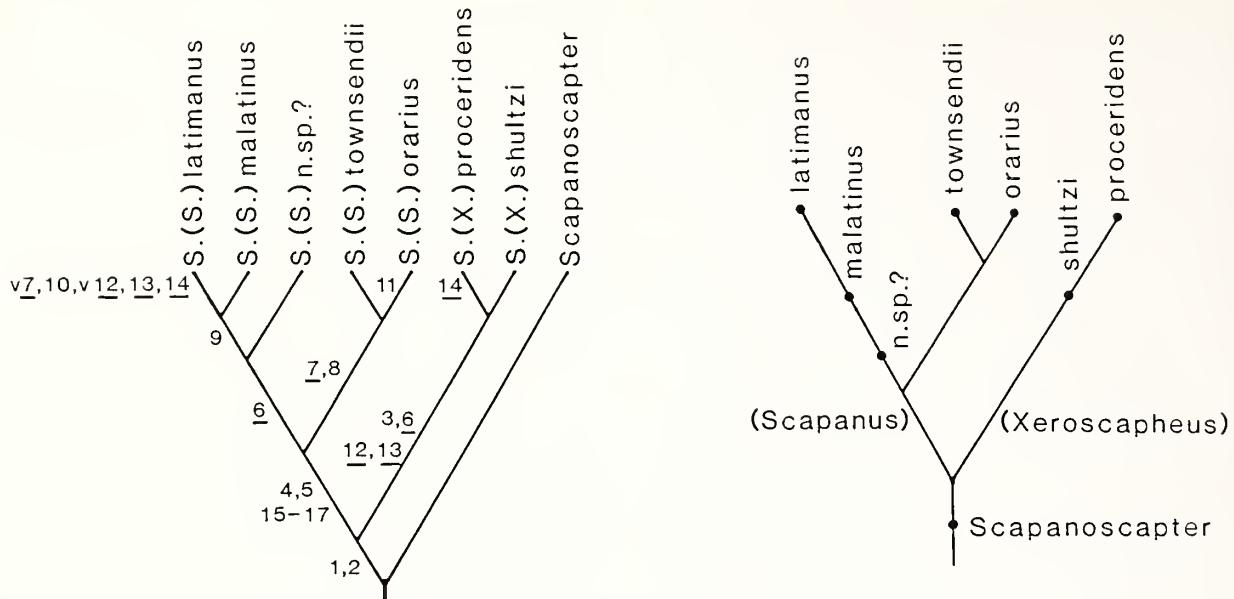


Figure 9. Cladogram of the species of *Scapanus* using *Scapanoscapter* as an outgroup and the favored phylogeny for the same species. Numbers indicate derived characters in Table 3. Characters derived twice are underlined, "v" indicates variable.

cingulids vary from poorly to well defined. In general, the teeth closely resemble *S. malatinus* and the location of the Maxum site in central California also favors a relationship with the Latimanus group.

The subspecies of *S. latimanus* (Palmer, 1937; Hall and Kelson, 1959) exhibit a wide range of tooth morphology with the smaller southern species generally less hypodont than the northern forms. The presence in the Irvingtonian of northern California of a very derived type of tooth morphology such as that in *S. l. latimanus* and a more primitive state in *S. malatinus* (and *S. l. cf. anthonyi*) from the south may indicate a long-standing north-south cline in hypodonty in which *S. l. anthonyi* and *S. l. occultus* are the most conservative extant members. The reduction in tooth number may be an even older chronological phenomenon and may persist through ancestor descendant morphospecies erected on tooth morphology. The presence of a highly reduced tooth count in late Pleistocene species (*S. l. cf. anthonyi*) from San Diego coupled with a relatively primitive tooth morphology may presage a reduced tooth count in *S. malatinus* which will become recognizable only when the species is better known.

The development and degree of hypodonty in *Scapanus* may be partly size dependent. The large northern subspecies have the most extreme development of enamel excursion down the lower molar roots and the smaller subspecies, *S. l. anthonyi*, the least. The very large *S. townsendii* is also higher crowned than the small and partly sympatric *S. orarius*. This general pattern in *S. latimanus* may have extended back in time as far as the Irvingtonian. Some Pleistocene *S. latimanus* occur in a few areas not presently within the range of the living species, indicating a greater range

during at least the Wisconsin glacial interval. *Scapanus l. anthonyi* is a likely relict of this greater Pleistocene range.

The cladistic relationships of populations are not necessarily determinable or meaningful where there is a sufficient genetic flow between them to allow character states derived in one area to diffuse into another. Populations may be divided into several practically recognizable taxa (subspecies, demes, etc.) but if character state (genetic) interchange continues, a cladistic analysis may provide a set of pseudotaxa determined principally by the choice of characters used and subject to the vagaries of historical and ecological changes. The incidence of the character state could indicate the timing of relationships (cladistic division) or only differential acceptance of the state throughout the varied range of the species group. A much denser and well-dated fossil record may resolve these opposing hypotheses. Whereas *S. malatinus* is just outside of the range of variation of extant species, a better fossil record may show that it is only a segment of a heterochronically evolving set of character states within the biological concept of *S. latimanus*. Meanwhile practicality is served by treating *S. malatinus* as a paleospecies and not blurring the morphological definition of an extant species.

The earliest evidence of "true" molar hypodonty (enamel below the gum line, cementum) in *S. (Scapanus)* appears between 1.2 and 1.7 Ma. This constitutes the latest apparent acquisition of hypodonty in the Talpidae. "True" molar hypodonty occurs in two other lineages of talpids: *Scapanus* (*Xeroscapheus*) and *Scalopus* (and also in the proscalopids, *Mesoscalops* Reed). Two other lineages (*Dominioidea* Green, *Scaptocirrus* Milne-Edwards) also show extreme crown hypodonty but do not develop enamel excursion or cementum in the lower molars. The development of high-crowned or

hypodont molars is associated in each case with hypertrophy of the I_2 , reduction in the length of the antemolar region with crowding and frequently loss of some antemolars (Hutchison, 1968; Ziegler, 1971). All the high-crowned moles are also highly derived burrowers but not all highly derived burrowers show a tendency toward hypodonty (e.g., *S. orarius*, *S. townsendii*, *Talpa europea* Linnaeus, *Parascalops breweri* (Bachman), *Proscapanus sansaniensis* (Lartet)). If abrasive characteristics of the diet were held constant then acquisition of hypodonty would allow a longer tooth life (i.e., potential animal longevity). There is no indication among any of the living members of this group of a longevity advantage over the non-hypodont burrowing moles. If all the moles live to about the same actuarial age, the hypodonty is of little functional advantage except where the environment is dentally more abrasive. Such adaptations would permit these moles to expand into more xeric and mountainous areas where coarse-grained soils predominate. Hypodonty in these otherwise marginal edaphic environments would compensate for increased tooth wear and allow the moles to live normal life spans. Crown hypodonty in *Domininoides* develops in the Great Plains during the Clarendonian, a time of developing aridity in the Great Plains of North America (Gregory, 1971; Elias, 1942; Hutchison, 1982). The Great Basin subgenus *Xeroscapheus* apparently originates also during the Clarendonian (Hutchison, 1968) and also during a time of increased aridity (Shotwell, 1964; Axelrod, 1980) and continued volcanism. *Scalopus aquaticus* (Linnaeus) presently occupies the largest geographic range of any living North American mole including many humid and humus-rich soils (Hall and Kelson, 1959). *Scalopus* successfully utilizes coarse-grained edaphic environments such as the deep loose sands in central Florida and upper beach sands (both of which may be considered as ecologically xeric) and the humus-poor soils of the Great Plains. The earliest fossil *Scalopus* (Hemphillian) are from areas of Kansas (Hutchison, 1968:7) and Texas (Dalquest, 1983) that show sedimentary indications of distinct seasonal aridity such as development of caliches or prevalence of volcanic ash. The extant *S. latimanus* in general occupies the least humid areas of the range of the genus, although much of the Pacific slope is edaphically abrasive (high in silica and other hard minerals). *Scaptochirus* occupies mountainous areas in the northern province of China (Schwartz, 1948) where soil profiles are probably shallow or young and therefore coarse.

The hypertrophy of the I_2 and shortening of the rostrum, which is concurrent with the development of high-crowned or hypodont teeth, is not as readily explained by coarsening soils because these teeth are used more in grasping than crushing. Development of powerful piercing teeth along with short snouts is likely to reflect changes in the nature of the food resource itself. In semiarid and coarse-grained environments as noted by Palmer (1937:283) the edaphic fauna is likely to consist of fewer soft-bodied animals (worms, slugs, and thin-shelled insect larvae) and more hard-shelled forms (hard-shelled larvae, shelled snails, and burrowing adult insects) adapted to resist soil abrasion and periodic desiccation. Because the hardness of chitin and shell is much less than

enamel, this does not readily account for development of hypodonty but would indicate a need for a more powerful bite at the tip of the rostrum in order to hold and pierce the prey. This is accomplished by concentrating the bite to a single point (clustered I^1+I_2) for prey penetration and by shortening of the rostrum to increase the mechanical advantage of the incisors at the tip of the dentary. It would be interesting to know if there is an increase in the effective size of the prey in these areas. If this were so, bite strength at the tip of the snout would be useful in subduing larger prey. An increase in gape angle might also be expected in short-snouted moles, if only to maintain the vertical span of the gape.

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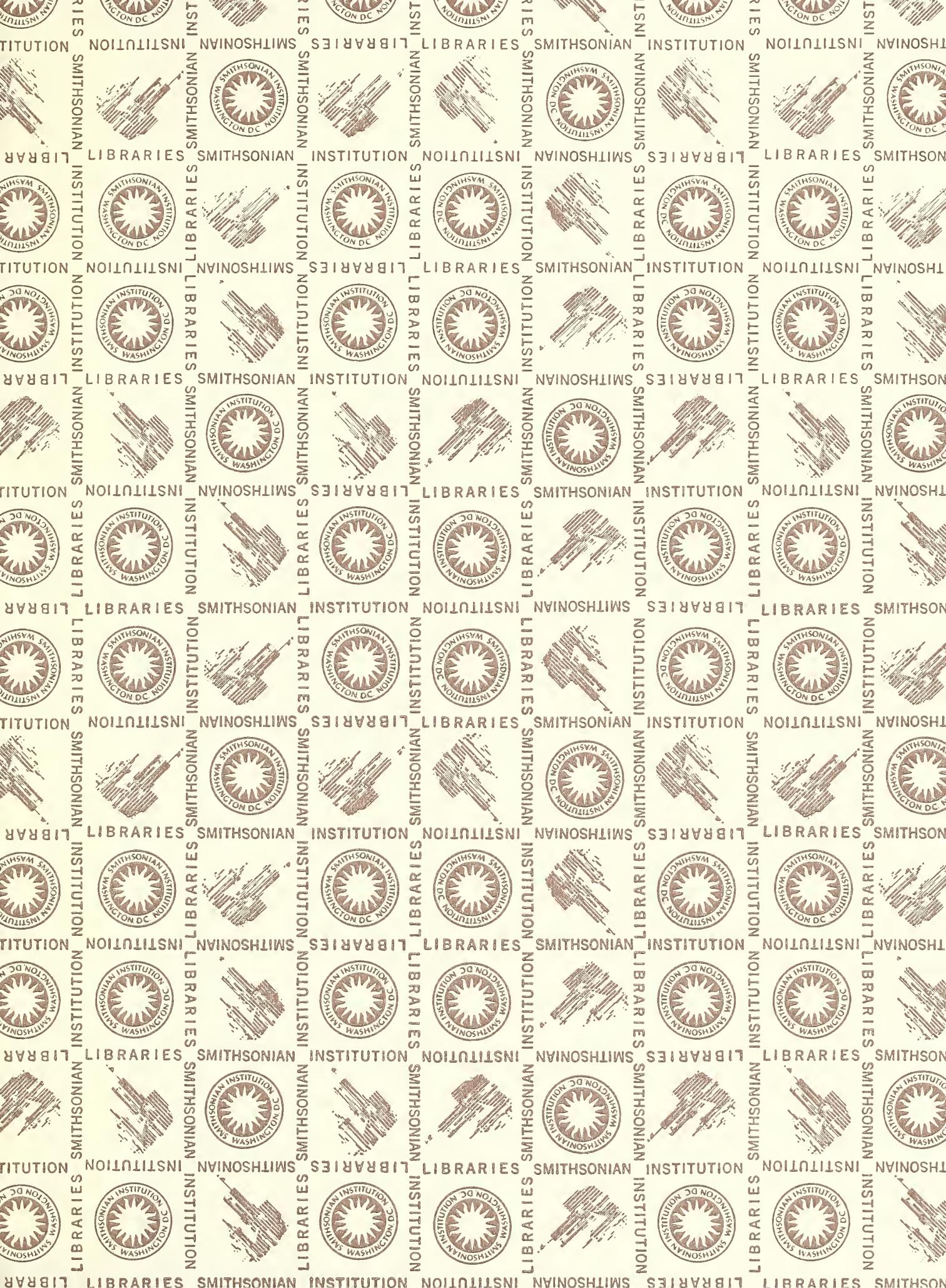
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